Behavioural Interactions Selecting for Symmetry and Asymmetry in Sexual Reproductive Systems of Eusocial Species

Lars Witting

Greenland Institute of Natural Resources, P.O. Box 570, DK-3900 Nuuk, Greenland

Abstract Understanding the life-history complex of eusociality has remained an enduring problem in evolutionary ecology, partially because natural selection models have considered traits in relative isolation. I aim for a more inclusive model that uses ecological interactions to predict the evolutionary existence of sexual reproduction, sexual reproduction asymmetry, and sex ratios in eusocial species. Using a two-level selection process, with within-population selection on the sex ratio of the sexual caste and between-population selection on the worker sex ratio and the degree of sexual reproduction asymmetry, it is found that a male-haploid genome and a worker caste of pure females is the evolutionary optimum of most initial conditions when, like in eusocial hymenoptera, there is no pair bond between the sexual male and female. That a diploid genome and a worker caste with both males and females is the evolutionary optimum of most initial conditions when, like in eusocial termites, there is a pair bond. That sex-linked genomes may evolve in diploid eusocials, and that the model will not generally maintain sexual reproduction by itself. These results hold for ploidy-levels that behave as quantitative or discrete traits, over a relatively wide range of the relative investment in a sexual male versus sexual female, and for partial sexual systems where the genomic portion with diploid inheritance is either fixed or random.

1. Introduction

The evolution of life-history complexes is only rarely considered as a whole in evolutionary ecology. Natural selection models tend instead to focus on a few traits while the larger life-history complex is given by assumption. This is, e.g., the case

E-mail address: larsw@natur.gl

for the complex of eusociality, where the average sex ratio of the sexual caste has been predicted from an assumed worker sex ratio and an assumed genomic ploidy level (Trivers and Hare, 1976). But in order to obtain a deeper understanding of the sex ratio and ploidy-level complex in eusocial species, we need to aim for natural selection models that explain all the traits from a few unifying principles.

This paper pursuit the latter approach by investigating whether in eusocial species there is a simple and general ecological difference that may explain why some taxa, like many termites, have male and female workers, relatively even sex ratios in the sexual caste and a symmetrical sexual system (diploid genome), while other taxa, like many hymenoptera, have female workers only, female biased sex ratios in the sexual caste and an asymmetrical sexual system (male-haploid genome).

Asymmetrical sexual systems are highly correlated with eusocial reproduction. Of the five insect orders with eusocial species listed by Crozier and Pamilo (1996), the four are contained in the set of five insect orders that Bull (1983) lists as those that contain species with male-haploid genomes. The remaining order with eusocial species is termites, and although many termites have symmetrical sexual reproduction, many others have asymmetrical systems where up to 50% of the diploid genome has sex-linked inheritance (Syren and Luykx, 1977; Rowell, 1987; Crozier and Pamilo, 1996; Thorne, 1997). Sex-linked inheritance is also disproportionally represented in eusocial species, mainly in termites, where it apparently has evolved on several occasions after the evolution of the sterile worker caste (Crozier and Luykx, 1985; Rowell, 1987).

Asymmetrical sexual reproduction may therefore likely be selectively beneficial in eusocial species under some ecological conditions, while in other eusocial ecological systems it may be the more common symmetrical sexual reproduction that is selectively beneficial. One ecological component that has a dichotomous occurrence in eusocial species is the interaction between the sexual male and female, where two different types of interactive behaviour tends to co-vary with the presence versus absence of asymmetrical sexual reproduction. The asymmetrically reproducing eusocial hymenoptera have nuptial flight where virgin females fly out to mate in the air leaving their males to die. In ants the mated female generally establish the eusocial colony by herself, while in bees the female usually returns to the colony where she was born, leaving later with a swarm of workers to settle a new colony. This lack of pair formation between the sexual male and female is in contrast to the symmetrically reproducing eusocial termites, where males and virgin females fly out to form pairs. When a termite female has accepted a male they form a new colony and settles into a monogamous relationship, with cooperative rearing of the first eggs and a king that remains with the queen.

A first examination of the ecological hypothesis for sexual systems in eusocials showed that the occurrence of symmetry versus asymmetry in the ploidy level, worker sex ratios and sexual sex ratios in eusocial species can indeed be explained by a dichotomous selection pressure that arises from the two different kinds of interactions between the sexual male and female (Witting, 1997). Traditional sex ratio selection, as introduced for eusocial species by Trivers and Hare (1976), was extended to cover the full range of worker sex ratios and ploidy levels on a continuum from a male-haploid genome over the diploid genome to a female-haploid

genome. While this extension predicts the average sex ratio of the sexual caste from the average worker sex ratio and ploidy level in the population, it will not by itself induce selection on the worker sex ratio and the genomic ploidy level. But, as the relationship between the population dynamic growth rate and the sexual sex ratio depends on the interactions between the sexually reproducing individuals, between-population selection on the worker sex ratio and ploidy level can arise if the eusocial species is sub-structured into more or less isolated populations.

In the hymenoptera-like case, the absence of interactions between the sexual male and female beyond insemination implies an energetically based fitness cost to the male, where the population dynamic growth rate declines if more energy is invested into sexual males at the cost of females. This cost induces between-population selection for a female bias in the sex ratio of the sexual caste, almost as it is the case in traditional sex ratio models for local mating (Hamilton, 1967). And when, as expected by traditional within-population sex ratio selection, between-population variability in the sexual sex ratio can arise from underlying heritable variation in the worker sex ratio and ploidy level, it follows that the between-population selection for a female biased sexual sex ratio imposes between-population selection for a male-haploid genome and a worker caste with females only. This contrasts to the termite-like case, where the pair bond between the sexual male and female may imply the absence of an energetic fitness cost to the sexual male. A pair bond with no fitness cost on the male induces between-population selection for an even sexual sex ratio, and this tends to select for a symmetrical sexual system with a diploid genome and a worker caste with males and females.

In this paper, I relax some of the assumptions in Witting (1997) to examine in more detail the ecological constraints that may select for the life-history complex of symmetry and asymmetry in the sex ratios and sexual reproduction systems of eusocial species. Witting implicitly assumed sexual reproduction for the complete genome, in the sense that all gametes are haploid and that the complete genome is diploid in at least one of the two sexes. This assumption is relaxed by a modelling of the full continuum of the two-dimensional ploidy-level space where haploid, diploid, and/or partial diploid genomes are allowed simultaneously in both of the two sexes. This allows not only for complete sexual reproduction but also for asexual and partial sexual reproduction, with partial sexual reproduction occurring when some fractions of the genome are haploid in both sexes and other fractions are diploid in one or both of the two sexes. By this extension, I want to examine if the two-level selection process can explain not only the differentiation in ploidy-level asymmetry but also the presence of sexual reproduction. If the model fails to explain sexual reproduction, it will support the original hypothesis (Witting, 1997, 2002, 2003), where the proposed sex ratio model may explain the degree of sexual reproduction asymmetry while sexual reproduction per se is explained by an alternative mechanism; in the Witting (Witting, 2002, 2003) case by selection by density-dependent interactive competition.

The part of the genome with diploid inheritance in the sex with a partial diploid genome was originally assumed to vary randomly among the individuals of a variant. This implies that mutation variants specify only what percentage of the genome that has diploid instead of haploid inheritance. A different case is where

the portion of the genome that has diploid inheritance is fixed among the individuals of a given variant. Both cases are considered in this paper.

The model variants above treat the ploidy-level as a quantitative trait with continuous variation between the different ploidy-levels. As an alternative model, I also examine the case where the ploidy-level is a discrete trait with one-step mutations between the diploid genome, the male-haploid genome, and the female-haploid genome.

The original model assumed also that the energetic investment in a sexually reproducing male and female offspring is the same. This may influence the results because the classical sex ratio theory is an investment theory, where the sexual sex ratio refers to the amount of resource allocated into the two sexes, instead of the numerical sex ratio. In this paper, I use the investment sex ratio based on the energetic qualities of male and female offspring.

Another assumption in the original analysis was autosomal inheritance for the complete genome. This is known to be violated in many termites, where up to 50% of the genome may have sex-linked inheritance (Syren and Luykx, 1977; Rowell, 1987; Crozier and Pamilo, 1996; Thorne, 1997). As an appendix, I extend the model to show that between-population selection may also select for sex-linked genomes in diploid eusocials. Most of the symbols in the model are defined in Table 1.

2. Within-population selection

Natural selection may be defined by interactors and replicators (Hull, 1980, 1981; Sober and Wilson, 1998; see also Dawkins, 1976, 1982), with the replicating unit of selection through sexual reproduction within a closed population of a eusocial species being the genes that the sexual males and females pass on to future generations through sexual reproduction. The interactors that modify the rates of gene replication may operate at various levels, with one important interactor being the eusocial colony. The colony is an important interactor because the expected number of genes that is passed on by the sexual individuals will depend on the overall behaviour of the colony.

Table 1   Important symbols

λ	Population growth rate at colony level
n_θ	Number of sexual female offspring per colony
n_ϕ	Number of sexual male offspring per colony
n_θ/n_ϕ	Numerical sex ratio
ϵ_θ	Energetic investments per female
ϵ_ϕ	Energetic investments per male
ϵ	Colony investment in sexual offspring, $\epsilon = n_\theta \epsilon_\theta + n_\phi \epsilon_\phi$
θ	Relative investment in sexual female offspring, $n_\theta \epsilon_\theta/\epsilon$
ϕ	Relative investment in sexual male offspring, $n_\theta \epsilon_\theta/\epsilon \wedge \phi = 1 - \theta$
θ/ϕ	Investment sex ratio
θ_w	Fraction of offspring workers that are females
ϕ_w	Fraction of offspring workers that are males, $\phi_w = 1 - \theta_w$
$p_{i,j}$	Genetic relatedness coefficient between i and j
m	Ploidy level of male; diploid: $m = 1$, haploid: $m = 0$
h	Ploidy level of female; diploid: $h = 1$, haploid: $h = 0$

For sex ratio selection within a closed population let the fitness component, or reproductive value, of gene replication be described by the expected number of genes that males and females pass on to future generations through sexual reproduction. This concept was first described by Fisher (1930), and elaborated for kinselection in eusocial species by Trivers and Hare (1976) in order to account for the interactions of the workers in the eusocial colony. As assumed here, they assumed that colonies have a single queen that is randomly mated with a single male, that there is no worker reproduction, and that it are the workers that control the sex ratio of the sexual caste.

Worker control may work when workers allocate resources to offspring and workers are capable of determining the sex of the offspring. At least for hymenoptera, it has been argued, e.g., by Oster et al. (1977), MacNair (1978) and Bulmer and Taylor (1981), that the queen must also have some control over the sex ratio by deciding the number of fertilised and unfertilised eggs that are laid. Empirical evidence on the relative power of worker versus queen control is generally lacking, although good cases of worker control has been documented for some species (e.g., Boomsma, 1991; Mueller, 1991; Sundström, 1994; reviewed Crozier and Pamilo, 1996).

The expected number of genes passed on can be described by the reproductive values of mated males and females, and for kin-selection and worker control we also need to consider the inclusive fitness perspective of the worker caste taking into consideration the relatedness among sisters and brothers. Taylor (1988) studied potential problems of using inclusive fitness, reproductive values and relatedness for sex ratio evolution with asymmetrical sexual reproduction, concluding that the method is appropriate when mating is random and selection is weak.

To incorporate the inclusive fitness of a worker, consider an extension of the Shaw–Mohler equation (Shaw and Mohler, 1953) that resembles the formulation of Taylor (1988), Pamilo (1991), and Crozier and Pamilo (1996). Let n_θ be the number of sexually reproducing female offspring produced by the colony, and let n_ϕ be the corresponding number of male offspring. Let $n_\theta \epsilon_\theta$ and $n_\phi \epsilon_\phi$ be the energetic investment in these sexual female and male offspring, with ϵ_θ and ϵ_ϕ being the energetic investments per female and male. The total energy ϵ allocated into sexually reproducing offspring is then $\epsilon = n_\theta \epsilon_\theta + n_\phi \epsilon_\phi$, and the total relative investment is $1 = n_\theta \epsilon_\theta / \epsilon + n_\phi \epsilon_\phi / \epsilon = \theta + \phi$, with θ and $\phi = 1 - \theta$ being the relative investment in sexual female and male offspring. Hence, the investment sex ratio is θ / ϕ, and the numerical sex ratio

$$\frac{n_\theta}{n_\phi} = \frac{\theta \epsilon_\phi}{\phi \epsilon_\theta}. \tag{1}$$

Let the inclusive fitness of a worker be reflected by the number of female offspring that survive and reproduce plus the number of females inseminated by surviving male offspring. Let $\dot{n}_\theta = p_\theta \epsilon / \epsilon_\theta$ be the number of female offspring that survive given that all the energy ϵ is invested into females, and let $\dot{n}_\phi = p_\phi \epsilon / \epsilon_\phi$ be the corresponding number of male offspring, with p_θ and p_ϕ being the probabilities that a female or male offspring survive to the reproductive age. Assuming that surviving females can always be inseminated and reproduce successfully,

for the ith phenotypic variant in the population, the number of female offspring that reproduce is $\theta_i \dot{n}_\theta$ and the number of females inseminated by male offspring is $(\theta \dot{n}_\theta / \phi \dot{n}_\phi) \phi_i \dot{n}_\phi$, with subscript i denoting the ith variant and no subscript denoting the population average. The inclusive fitness of a worker of the ith phenotypic variant is then

$$\lambda_i = \dot{n}_\theta [\vartheta_d \theta_i + \vartheta_s (\theta/\phi) \phi_i], \tag{2}$$

where ϑ_d is the product between the reproductive value of a mated sexual daughter (subscript d) and her relatedness to an average worker, and ϑ_s is the corresponding product for a mated sexual son (subscript s). From Eq. (2), the selection gradient on the average investment in sexual females is

$$\left. \frac{\partial \lambda_i}{\partial \theta_i} \right|_{\theta_i = \theta} = \dot{n}_\theta [\vartheta_d - \vartheta_s (\theta/\phi)], \tag{3}$$

with $|_{\theta_i = \theta}$ indicating that the partial derivative is to be taken at the limit $\theta_i = \theta$. Thus, the equilibrium is

$$\theta^{*w} = \vartheta_d / (\vartheta_d + \vartheta_s). \tag{4}$$

By substituting $(\theta/\phi)^{*w} = \vartheta_d / \vartheta_s$ for θ/ϕ in Eq. (2), we find that $\lambda_i = \dot{n}_\theta \theta^{*w}$ implying that the equilibrium variant (θ^{*w}) is just as fit as any other variant ($\theta^{*w} + \rho$ with $\rho \neq 0$) in the equilibrium population, i.e., $f(\theta^{*w}, \theta^{*w}) = f(\theta^{*w} + \rho, \theta^{*w})$. By calculating $f(\theta^{*w}, \theta^{*w} + \rho)$ and $f(\theta^{*w} + \rho, \theta^{*w} + \rho)$, we also find that

$$\begin{aligned} &f(\theta^{*w} + \rho, \theta^{*w} + \rho) \\ &= f(\theta^{*w}, \theta^{*w} + \rho) + \vartheta_d \rho (1 - \theta^{*w} - \rho)/(\theta^{*w} + \rho) - \rho \vartheta_s, \end{aligned} \tag{5}$$

and as $\vartheta_d \rho (1 - \theta^{*w} - \rho)/(\theta^{*w} + \rho) - \rho \vartheta_s < 0$ for all $\rho \neq 0$ it follows that the equilibrium variant θ^{*w} is more fit in any other population $\theta^{*w} + \rho$ than those population variants. Thus, the equilibrium is an Evolutionary Stable Strategy (ESS) (Maynard Smith and Price, 1973; Maynard Smith, 1982). And as

$$\left. \frac{\partial}{\partial \theta} \left(\left. \frac{\partial \lambda_i}{\partial \theta_i} \right|_{\theta_i = \theta} \right) \right|_{\theta = \theta^{*w}} = \frac{-\dot{n}_\theta \vartheta_s}{(1 - \theta)^2}, \tag{6}$$

is negative it follows that the equilibrium is also a Continuously Stable Strategy (CSS) (Eshel and Motro, 1981; Eshel, 1983), denoted θ^{css}.

For Eqs. (2)–(6), it is assumed that females can be inseminated independently of the investment sex ratio, which is expected for hymenoptera-like cases where the males contribute to reproduction only through the insemination of females. If the investment sex ratio is strongly female biased and a male may inseminate only a single female we can expect selection for a smaller investment per male so that the male fraction increases to provide sufficient males to inseminate the females.

A different case is termite-like situations, where successful reproduction depends upon the formation of a pair between the sexual male and the sexual female. The replication rate of the genes will then depend on the opportunities to form male–female pairs. When the numerical sex ratio is female biased $[\theta \dot{n}_\theta/(\theta \dot{n}_\theta + \phi \dot{n}_\phi) > 1/2]$, there will be a mate for all $\phi_i \dot{n}_\phi$ males, while the chance that a female obtains a mate is only $\phi \dot{n}_\phi/\theta \dot{n}_\theta$. Likewise, when the numerical sex ratio is male biased, there will be a mate for all $\theta_i \dot{n}_\theta$ females, while the chance that a male obtains a mate is only $\theta \dot{n}_\theta/\phi \dot{n}_\phi$. Thus, the expected fitness expression is

$$\lambda_i = \dot{n}_\theta[\vartheta_d \theta_i + \vartheta_s(\theta/\phi)\phi_i] \quad \text{for} \quad \theta \leq \dot{n}_\phi/(\dot{n}_\theta + \dot{n}_\phi)$$
$$\lambda_i = \dot{n}_\phi[\vartheta_d(\phi/\theta)\theta_i + \vartheta_s \phi_i] \quad \text{for} \quad \theta \geq \dot{n}_\phi/(\dot{n}_\theta + \dot{n}_\phi),$$
(7)

with the top equation being identical to Eq. (2). For Eq. (7), the female investment at the classical equilibrium is $\theta^{*w} = \vartheta_d/(\vartheta_d + \vartheta_s)$, as predicted also by Eq. (2). By following the stability analysis for Eq. (2), it is easily seen that the equilibrium of Eq. (7) is an ESS because $f(\theta^{*w}, \theta^{*w}) = f(\theta^{*w} + \rho, \theta^{*w})$ and $f(\theta^{*w}, \theta^{*w} + \rho) > f(\theta^{*w} + \rho, \theta^{*w} + \rho)$ for $\rho \neq 0$, and that the it is also a CSS because $\partial(\partial \lambda_i/\partial \theta_i|_{\theta_i=\theta})/\partial \theta|_{\theta=\theta^{*w}} < 0$.

2.1. Variable worker sex ratio

This section describes the CSS of the sex ratio in the sexual caste when the fraction of females in the worker caste can vary continuously from zero to one. By Eq. (4), the CSS depends on ϑ_d and ϑ_s: the product between the reproductive values (v) of mated sexual daughters (v_d) and sons ($v_s = 1 - v_d$) and their relatedness ($p_{d,w}$ & $p_{s,w}$) to the average worker

$$\vartheta_d = p_{d,w} v_d$$
$$\vartheta_s = p_{s,w} v_s.$$
(8)

Following Taylor (1988) and Crozier and Pamilo (1996), the reproductive values can be given by the left eigenvector of the gene flow matrix

$$\begin{vmatrix} p_{d,m} & p_{d,f} \\ p_{s,m} & p_{s,f} \end{vmatrix},$$
(9)

with $p_{i,j}$ being the genetic relatedness coefficient of i to j with subscripts (m) denoting mother, (f) father, (d) daughter, (s) son, and (w) worker.

The relatedness coefficients $p_{d,w}$ and $p_{s,w}$ of Eq. (8) represent the relatedness to an average worker, which implies that the sex ratio of the sexual caste produced by the colony [Eq. (4)] is given by the average worker preference. This form of worker control may arise from two different forms of behaviour of individual workers. In the first form, each worker adheres to its own preference in the control of the sex ratio, whereas in the second form, all workers adhere to the average worker

preference. It is not obvious which of the two forms of worker control is most likely to evolve. The latter form is expected to be energetically most beneficial to the colony because it contains no conflicts among workers since they agree on the same sex ratio. But, the evolutionary stability of this form of worker control is sensitive to cheaters that follow their own preferences. Cheaters cannot influence the evolutionary stability of the former form of worker control where all individuals follow their own preferences. However, this form might have a lower fitness at the colony level if too much energy is used in worker conflicts over the sex ratio. The evolutionary dynamics of this system is not modelled in this paper, where I assume that the sex ratio of the sexual caste is determined as an average of all worker preferences.

In most cases, a genetic relatedness coefficient $p_{i,j}$ can be interpreted as the probability that a gene sampled at random in i is identical by descent to a gene in j, which is also the proportion of i's genes that are identical by descent to genes in j (Crozier and Pamilo, 1996). The relatedness coefficient may also be defined as $p_{i,j} = c_{i,j}/c_{i,i}$, where $c_{i,j}$ and $c_{j,j}$ are coefficients of consanguinity with $c_{i,j}$ being defined as the probability that two homologous genes drawn randomly, one from i and the other from j, are identical by descent (see e.g., Bulmer, 1994). Note, however, that the w in the $p_{i,w}$ coefficient refers to an average worker as defined by the fraction of the workers that are respectively females (daughters) and males (sons).

If male and female workers are equally efficient in rearing offspring, the genetic relatedness coefficients of Eq. (8) can be expressed as

$$
\begin{aligned}
p_{d,w} &= \theta_w p_{d,d} + \phi_w p_{d,s} \\
p_{s,w} &= \theta_w p_{s,d} + \phi_w p_{s,s},
\end{aligned}
\tag{10}
$$

where θ_w and $\phi_w = 1 - \theta_w$ are the proportion of the workers that are females and males. Then, when the complete genome of an individual is either haploid or diploid and there is free recombination for the entire diploid genome, it can be seen that we may use the probability interpretation of the relatedness coefficient and combine the coefficients like independent probabilities to obtain

$$
\begin{aligned}
p_{d,d} &= p_{d,m} p_{m,d} + p_{d,f} p_{f,d} \\
p_{d,s} &= p_{d,m} p_{m,s} + p_{d,f} p_{f,s} \\
p_{s,s} &= p_{s,m} p_{m,s} + p_{s,f} p_{f,s} \\
p_{s,d} &= p_{s,m} p_{m,d} + p_{s,f} p_{f,d}.
\end{aligned}
\tag{11}
$$

In eusocial diploids, where females and males have a copy of half of the genes in both their mother and father, all these latter probabilities are 1/2. Consequently, $p_{d,w} = p_{s,w} = 1/2$, $v_d = v_s = 1/2$, and $\vartheta_d = \vartheta_s = 1/4$. The equilibrium investment in females of the sexual caste of diploids is then one-half, i.e., $\theta^{css} = 1/2$, independently of the proportion of females in the worker caste.

For male-haploids

$$
\begin{aligned}
&p_{d,m} = 1/2 \quad && p_{s,m} = 1 \quad && p_{d,d} = 3/4 \\
&p_{d,f} = 1/2 \quad && p_{s,f} = 0 \quad && p_{d,s} = 1/4 \\
&p_{m,d} = 1/2 \quad && p_{f,d} = 1 \quad && p_{s,s} = 1/2 \\
&p_{m,s} = 1/2 \quad && p_{f,s} = 0 \quad && p_{s,d} = 1/2.
\end{aligned}
\tag{12}
$$

Hence, $v_d = 2/3$ and $v_s = 1/3$ in male-haploids and, thus, it follows that $\vartheta_d = \theta_w/3 + 1/6$ and that $\vartheta_s = 1/6$. Consequently, by Eq. (4), the equilibrium investment in females of the sexual caste of male-haploid eusocials is a function of the proportion of females in the worker caste:

$$
\theta^{css} = \frac{\theta_w + 1/2}{\theta_w + 1}.
\tag{13}
$$

For hymenoptera-like cases, where all workers are females, this investment is 3/4 as shown by Trivers and Hare (1976). If instead the proportion of worker females is 1/2 and 0, the investment in sexual females is 2/3 and 1/2, respectively.

2.2. Variable ploidy level

To include selection on the ploidy level, let sexual reproduction occur between a single female and a single male, and let there be free recombination for the diploid loci of the genome. Let the genomic ploidy level be defined by the fraction of the loci that is diploid in the female ($0 \leq h \leq 1$), and the fraction that is diploid in the male ($0 \leq m \leq 1$). Let one of the homologous sets of genes in each sex be complete containing a gene copy at all loci, while the other set contains a gene copy at the fractions h and m of the loci present in the female and the male. Let a sexual female transmit a complete gene set to sons and a h-fractional set to daughters, and let a sexual male transmit a complete set to daughters and a m-fractional set to sons. This genome is haploid when $h = 0$ and $m = 0$, it is diploid when $h = 1$ and $m = 1$, male-haploid when $h = 1$ and $m = 0$, and female-haploid when $m = 1$ and $h = 0$.

The ploidy-level model can be described as a two-dimensional diagram, where the ploidy level of the male ($0 \leq m \leq 1$) and the female ($0 \leq h \leq 1$) can vary independently of one another. In Witting (1997), it is instead assumed that the male is diploid ($m = 1$) when the female is less than diploid ($0 \leq h < 1$), and that the female is diploid ($h = 1$) when the male is less than diploid ($0 \leq m < 1$).

Both ploidy-level models described here, have two variants dependent upon whether it is always the same loci, or a random collection of loci, that are diploid in the individuals with partial diploid genomes. When in all the partial diploid individuals of a variant it is the same fraction of the genome that is diploid it is a fixed portion of the genome that has diploid inheritance. When instead in all the partial diploid individuals of a variant it is only the percentage of the genome with diploid inheritance that is fixed, it is a random portion of the genome that has diploid

inheritance. Witting (1997) dealt only with the latter case, while both variants are considered here.

The terms of Eqs. (8) and (9) are independent of the degree to which it is always the same loci that have diploid inheritance. Thus, when the terms are defined as functions of h and m, we find that the gene flow matrix of Eq. (9) is

$$\begin{vmatrix} h/(1+h) & 1/(1+h) \\ 1/(1+m) & m/(1+m) \end{vmatrix}, \tag{14}$$

and that the reproductive values of mated sexual daughters and sons are

$$
\begin{aligned}
v_d &= (1+h)/(2+h+m) \\
v_s &= (1+m)/(2+h+m).
\end{aligned} \tag{15}
$$

2.2.1. Random portion of genome with diploid inheritance

The relatedness coefficients between parents and offspring

$$
\begin{aligned}
p_{d,m} &= h/(1+h) & p_{s,m} &= 1/(1+m) \\
p_{d,f} &= 1/(1+h) & p_{s,f} &= m/(1+m) \\
p_{m,d} &= h/(1+h) & p_{f,d} &= 1/(1+m) \\
p_{m,s} &= 1/(1+h) & p_{f,s} &= m/(1+m),
\end{aligned} \tag{16}
$$

are also independent of the mode of diploid inheritance. And for the case with a random portion with diploid inheritance, we can use the probability interpretation of the relatedness coefficients under the assumption of independence, i.e., we can combine Eqs. (11) and (16) to obtain the relatedness coefficients

$$
\begin{aligned}
\hat{p}_{d,d} &= \frac{1}{1+h}\left(\frac{h^2}{1+h} + \frac{1}{1+m}\right) \\
\hat{p}_{d,s} &= \frac{1}{1+h}\left(\frac{h}{1+h} + \frac{m}{1+m}\right) \\
\hat{p}_{s,s} &= \frac{1}{1+m}\left(\frac{1}{1+h} + \frac{m^2}{1+m}\right) \\
\hat{p}_{s,d} &= \frac{1}{1+m}\left(\frac{h}{1+h} + \frac{m}{1+m}\right),
\end{aligned} \tag{17}
$$

where ˆ denotes a random portion with diploid inheritance. Thus, from Eqs. (8), (10), (15), and (17)

$$
\hat{\vartheta}_d = \frac{\theta_w\left[\frac{1-m}{1+m} - \frac{h(1-h)}{1+h}\right] + \frac{h}{1+h} + \frac{m}{1+m}}{2+h+m}
$$

$$\hat{\vartheta}_s = \frac{\theta_w\left[\frac{m(1-m)}{1+m} - \frac{1-h}{1+h}\right] + \frac{1}{1+h} + \frac{m^2}{1+m}}{2+h+m}. \tag{18}$$

From Eq. (4), the investment in sexual females at the classical equilibrium is $\hat{\theta}^{css} = \hat{\vartheta}_d/(\hat{\vartheta}_d + \hat{\vartheta}_s)$ and, thus, from Eq. (18)

$$\hat{\theta}^{css} = \hat{\alpha}/\beta, \tag{19}$$

with

$$\hat{\alpha} = \theta_w \left[\frac{1-m}{1+m} - \frac{h(1-h)}{1+h}\right] + \frac{h}{1+h} + \frac{m}{1+m}$$

$$\beta = \theta_w(h-m) + 1 + m. \tag{20}$$

This equation gives the equilibrium investment in females of the sexual caste as a function of the proportion of female workers (θ_w) and the ploidy level of the genome (m, h). Again $\hat{\theta}^{css} = 1/2$ for termite-like cases ($m = 1$, $h = 1$ and $0 \le \theta_w \le 1$), and $\hat{\theta}^{css} = 3/4$ for hymenoptera-like cases ($m = 0, h = 1$ and $\theta_w = 1$).

2.2.2. Fixed portion of genome with diploid inheritance

When, for a given variant, the portion of the genome with diploid inheritance is fixed, the assumption in Eq. (11) of independence is no longer valid. With a fixed portion we need to treat the loci with diploid and haploid inheritance separately. For example, to obtain the probability that a randomly chosen gene from one daughter can be found in another full-sib daughter ($p_{d,d}$), we have that the probability that the gene came from the father is $h/(1 + h)$, in which case the probability of diploid inheritance is m while the probability of haploid inheritance is $1 - m$. In the latter case, the gene is always identical among full-sib daughters, while for the former case of diploid inheritance the probability that the gene is found also in another full-sib daughter is only 1/2. In this way, we find that the relatedness coefficients among offspring are

$$\tilde{p}_{d,d} = \frac{1}{1+h}\left(\frac{2+h-m}{2}\right)$$

$$\tilde{p}_{d,s} = \frac{1}{1+h}\left(\frac{h+m}{2}\right)$$

$$\tilde{p}_{s,s} = \frac{1}{1+m}\left(\frac{2+m-h}{2}\right) \tag{21}$$

$$\tilde{p}_{s,d} = \frac{1}{1+m}\left(\frac{m+h}{2}\right),$$

with ˜ denoting a fixed portion with diploid inheritance. Then, from Eqs. (8), (10), (15), and (21), we find

$$
\begin{aligned}
\tilde{\vartheta}_d &= \frac{\theta_w(1-m) + \frac{h+m}{2}}{2+h+m} \\
\tilde{\vartheta}_s &= \frac{\theta_w(h-1) + 1 + \frac{m-h}{2}}{2+h+m},
\end{aligned}
\tag{22}
$$

and, thus, the investment in sexual females at the classical equilibrium is

$$
\tilde{\theta}^{css} = \tilde{\alpha}/\beta,
\tag{23}
$$

with

$$
\tilde{\alpha} = \theta_w(1-m) + (h+m)/2,
\tag{24}
$$

and β given by Eq. (20). While the worker sex ratio and degree of sexual reproduction asymmetry are unaffected by the within-population selection described here, these traits might evolve by selection at the between-population level.

3. Between-population selection

For a spatially structured species with reproductively isolated populations will the relative gene replication rate not only depend on the interactions within the different populations, but also upon the interactions between populations. Especially when the evolutionary process is considered on the time-scale of long-term evolution, can we for spatially structured species expect that reproductively isolated populations will arise from time to time, allowing for evolutionary divergence between populations. Between-population selection, based on insignificant mixing of genes between populations, may then occur if subsequent hybrid colonies in a hybrid-zone of adjacent populations have decreased fitness, or if the overall habitat is spatially structured with extirpation and re-colonisation of populations in local habitats. For both of these cases, is it expected that the relative gene replication rates between populations will depend on the population dynamic growth rate. In the former case, because it is the growth rate that determines the growth of the different populations. In the latter case, because the persistence probability of a population in a local habitat, and the potential that a population has to colonise new and empty habitats, is expected to depend on the population dynamic growth rate.

Between-population differences in the sexual sex ratio is likely to occur if the average worker sex ratio and/or ploidy-level asymmetry starts to differ between isolated populations. This is because the CSS of within-population selection for the sexual sex ratio depends on the population average of the worker sex ratio and the sexual reproduction asymmetry. And between-population differences in the sexual sex ratio induce between-population differences in the population dynamic

growth rate, generating between-population selection on the underlying variation, i.e., on the between-population variation in worker sex ratio and sexual reproduction asymmetry.

For cases with insignificant mixing between populations, it is shown in the appendix that the long-term evolutionary equilibrium of within- and between-population selection on the sex ratios and sexual reproduction asymmetry can be found by applying between-population selection across the complete set of populations at the CSSs of within-population selection. This conclusion holds even though between-population selection may equilibrate at a faster rate than within-population selection, generating between-population selection among populations that have not yet reached their within-population CSS.

3.1. No pair bond

Following the appendix, the long-term equilibrium may be determined by an optimisation of the growth rate λ over the complete set of populations at the CSSs $(\theta_i = \theta = \theta^{css})$ of within-population selection. For the hymenoptera-like case, where there is no pair bond between sexual males and females, the growth rate λ in the number of eusocial colonies at CSS is

$$\lambda = \dot{n}_\theta \theta|_{\theta=\theta^{css}}. \tag{25}$$

Note that $\lambda_{\theta=1}/\lambda_{\theta=0.5} = 2$, where $\lambda_{\theta=1}$ is λ for a sexual caste with only females, and $\lambda_{\theta=0.5}$ is λ for an even investment sex ratio. This two-fold difference in λ is the two-fold cost of the male (Maynard Smith, 1968), a cost that is included in the between-population selection for a female biased sex ratio, as described also in models of local mating (see e.g., Sober and Wilson, 1998).

As the population dynamic growth rate is a function of θ^{css}, it follows that the growth rate is determined by the worker sex ratio and the ploidy level of the genome. When between-population selection favours the variant with the highest λ, it induces selection not only on the investment in sexual females (θ^{css}), but also on the ploidy level (m and h) and on the proportion of females in the worker caste (θ_w). For cases where the portion of the genome with diploid inheritance is either fixed or random, the between-population selection gradient on the ploidy level and the proportion of female workers is

$$\frac{\partial \lambda}{\partial x} = \frac{\partial \lambda}{\partial \theta} \frac{\partial \theta}{\partial x}\bigg|_{\theta=\theta^{css}}, \tag{26}$$

with

$$\frac{\partial \theta}{\partial x}\bigg|_{\theta=\theta^{css}} = \left[\beta \frac{\partial \alpha}{\partial x} - \alpha \frac{\partial \beta}{\partial x}\right]/\beta^2, \tag{27}$$

$x \in \{\theta_w, h, m\}$, $\theta^{css} \in \{\hat{\theta}^{css}, \tilde{\theta}^{css}\}$ and $\alpha \in \{\hat{\alpha}, \tilde{\alpha}\}$ dependent upon whether the portion of the genome with diploid inheritance is random or fixed. An evolutionary stable attractor of the long-term equilibrium of between-population selection is

given by the selection optimum defined by $\partial\lambda/\partial x|_{x=x^{**}+\rho} < 0$ and $\partial\lambda/\partial x|_{x=x^{**}-\rho} > 0$ with $x \in \{\theta, \theta_w, h, m\}$.

Combining Eqs. (20), (24), (26), and (27), and examining the models with a fixed and a random portion with diploid inheritance, we obtain the selection surface in Table 2, a surface that is independent of the relative energetic investment in a sexually reproducing male and female offspring. For the three-dimensional trait-space ($0 \le \theta_w \le 1, 0 \le h \le 1$, and $0 \le m \le 1$), this table shows the parameter space

Table 2 The selection surface on the fraction of female workers (θ_w) and the fractions of the genome that is diploid in the female (h) and the male (m), for the no pair bond case (hymenoptera-like) with a random and fixed genomic portion with diploid inheritance

	Selection gradients, No pair bond				
	Random portion of diploid inheritance				
	$\theta_w = 0$	$\theta_w = .25$	$\theta_w = .50$	$\theta_w = .75$	$\theta_w = 1$
$\partial\lambda/\partial\theta_w|_{\theta=\theta^{css}}$	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]
$\partial\lambda/\partial h|_{\theta=\theta^{css}}$	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]
$\partial\lambda/\partial m|_{\theta=\theta^{css}}$	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]
	Fixed portion of diploid inheritance				
	$\theta_w = 0$	$\theta_w = .25$	$\theta_w = .50$	$\theta_w = .75$	$\theta_w = 1$
$\partial\lambda/\partial\theta_w|_{\theta=\theta^{css}}$	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]
$\partial\lambda/\partial h|_{\theta=\theta^{css}}$	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]
$\partial\lambda/\partial m|_{\theta=\theta^{css}}$	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]	[selection surface grid]

Each selection surface grid plots h (vertical axis, 0 to 1) against m (horizontal axis, 0 to 1).

Note. Each small square of plusses, minuses, and zeros represents the selection surface in the two-dimensional space of h and m, with $+$ indicating selection for an increase, $-$ selection for a decrease, and 0 no selection in the corresponding parameter θ_w, h, or m. The lower left corner of each square represents the haploid genome, the upper right corner the diploid, the upper left corner the male-haplod, and the lower right corner the female-haploid genome.

where the three traits θ_w, h and m are selected to increase ($+$), to decrease ($-$), or to remain stable (0).

Witting (1997) is based on a random portion with diploid inheritance and complete sexual reproduction as defined by a diploid genome in at least one of the two sexes. In Table 2, complete sexual reproduction is given by the right hand columns and the top rows of the two-dimensional ploidy-level space $0 \leq h \leq 1$ and $0 \leq m \leq 1$. The table confirms the result that for most initial conditions there is selection for a male-haploid genome and a workers caste with only female offspring. However, if initially both the fraction of female workers is sufficiently high ($\theta_w > 0.72 \wedge h = 0 \wedge m = 1$) and the genome is sufficiently biased toward the female-haploid genome ($h < 0.33 \wedge m = 1 \wedge \theta_w = 1$) there can be selection for a female-haploid genome and a worker caste with only female offspring.

Table 2 also shows that a change in the mode of inheritance from a random to a fixed portion of the genome with diploid inheritance induces only a minor change in the results. The most significant change is the absence of selection for a female-haploid genome when the genomic portion with diploid inheritance is fixed. Again, for nearly all initial conditions, there is selection for a male-haploid genome and a worker caste with only female offspring. The only two exceptions are the initial conditions $0 \leq h < 1 \wedge m = 1 \wedge \theta_w = 1$ and $h = m = 1 \wedge \theta_w = 0$. In the former case, there is no selection on h, which implies that mutations may cause h to drift neutrally between zero and one. However, if h drifts to one, then, there is selection for the male-haploid genome and the female-dominated workers caste. The latter case ($h = m = 1 \wedge \theta_w = 0$) is also an unstable equilibrium. Here, m may drift below one, which will induce selection for an increase in θ_w, and once θ_w has increased above zero there is again selection for the male-haploid genome and a female-dominated worker caste.

According to Eqs. (2)–(27), the worker sex ratio and ploidy level are influenced only by between-population selection, while the sexual sex ratio is influenced by the combined action of between-population and within-population selection. The relative forces of the two types of selection on the sexual sex ratio will, among other things, depend on the population structure. At one limit of the spectrum, we have species that are so sub-structured that each worker sex ratio and ploidy-level variant forms its own population with no migration to other populations. In this case, it is between-population selection that determines the evolutionary setting of the sexual sex ratio. At the other limit, we have species where there are no population boundaries and the species is made up of one panmictic population. In this case, it is within-population selection that determines the sex ratio of the sexual caste. Natural species are likely to be situated in-between these two extremes having a sexual sex ratio that, at least to some extend, is influenced both by between-population and within-population selection.

By Eq. (25), the relative investment in sexual females is 1 at the equilibrium of between-population selection. And, for the case with complete sexual reproduction, we find by Eqs. (19) and (23) that the relative investment is 3/4 at the equilibrium of within-population selection, given the equilibrium conditions $\theta_w^{**} = 1$, $h^{**} = 1$ and $m^{**} = 0$. Thus, dependent upon the relative strengths of

between-population and within-population selection the equilibrium investment in sexual females may vary between 3/4 and 1.

These results change drastically when the assumption of complete sexual reproduction is relaxed, and we need to consider the selection pressure over the complete two-dimensional ploidy-level space. Here, we first note that the diploid genome is always evolutionary unstable in m. The only potential exception is when the portion of the genome with diploid inheritance is fixed and $\theta_w = 0$. But if, in this case, m drifts below one, there is selection for an increase in θ_w, and with $\theta_w > 0$ there is selection for a decline in m. And with $m < 1$ there is always selection for $\theta_w = 1$. And with $\theta_w = 1$ there is always selection for $m = 0$. And with $\theta_w = 1$ and $m = 0$ there is selection for $h = 0$. Thus, for the hymenoptera-like case the model will not maintain sexual reproduction. When partial and asexual reproduction is allowed, we expect instead selection toward a haploid genome, asexual reproduction, and a worker caste with only 'female' offspring. This result holds independently of whether the genomic portion with diploid inheritance is fixed or not.

3.2. Pair bond

For termite-like cases, where there is a pair bond between the sexual male and female, we find that the population dynamic growth rate λ is

$$\lambda = \dot{n}_\theta \theta|_{\theta=\theta^{css}} \quad \text{for} \quad \theta \le \dot{n}_\phi/(\dot{n}_\theta + \dot{n}_\phi)$$
$$\lambda = \dot{n}_\phi \phi|_{\phi=\phi^{css}} \quad \text{for} \quad \phi \le \dot{n}_\phi/(\dot{n}_\theta + \dot{n}_\phi). \tag{28}$$
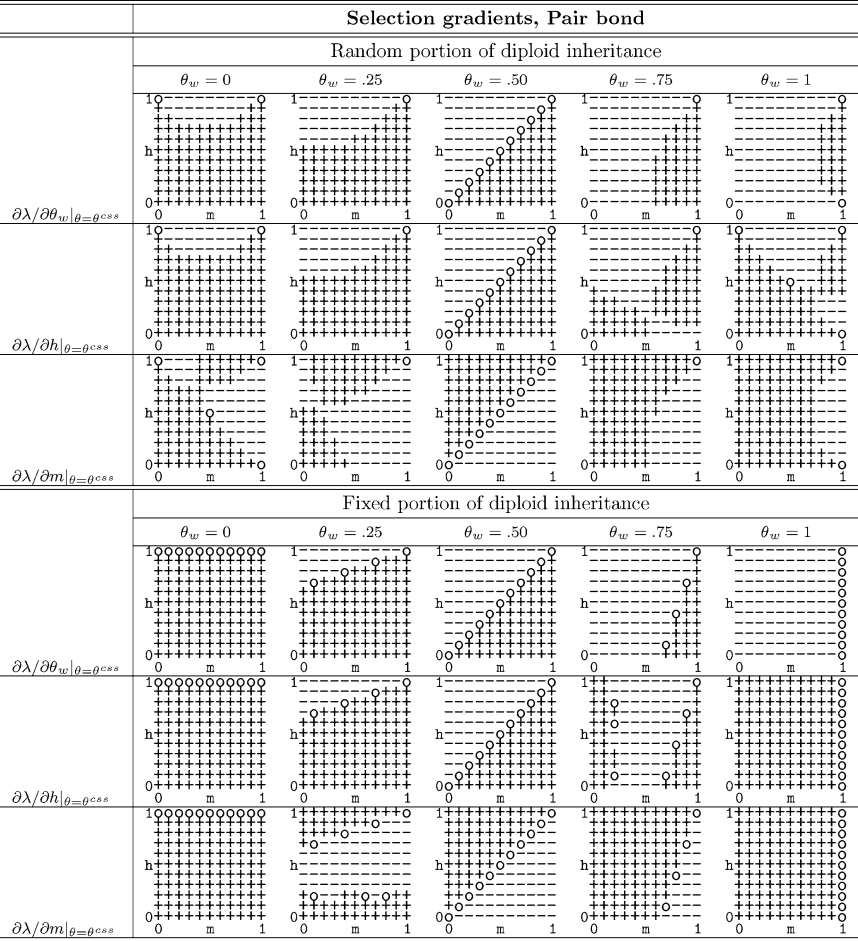
Here, there is a cost to sexually reproducing males only when the numerical sex ratio is male biased $[\theta \le \dot{n}_\phi/(\dot{n}_\theta + \dot{n}_\phi)]$ and it is the number of females that constrain λ. When instead the numerical sex ratio is female biased, and it is the number of males available for pair formation that constrain λ, there is a cost to the sexually reproducing females. At equilibrium, the numerical sex ratio is even so that all sexual individuals can find a mate.

The between-population selection gradient is then

$$\partial\lambda/\partial\theta|_{\theta=\theta^{css}} = \dot{n}_\phi \quad \text{for} \quad \theta < \dot{n}_\phi/(\dot{n}_\theta + \dot{n}_\phi)$$
$$\partial\lambda/\partial\theta|_{\theta=\theta^{css}} = -\dot{n}_\theta \quad \text{for} \quad \theta > \dot{n}_\phi/(\dot{n}_\theta + \dot{n}_\phi). \tag{29}$$

Combining this with Eqs. (20), (24), (26), and (27), and examining the models with a fixed and a random portion of the genome with diploid inheritance, for the symmetrical case with equal energetic investment in a sexual male and female, we obtain the selection surface in Table 3. For most initial conditions with complete sexual reproduction and a random portion with diploid inheritance, we have evolution toward a diploid genome and a worker caste where the fraction of female offspring is neutrally stable, being able to vary continuously from zero to one. However, if initially both the fraction of female workers is sufficiently high ($\theta_w > 0.72 \wedge h = 0 \wedge m = 1$) and the genome is sufficiently biased toward the

Table 3 The selection surface on the fraction of female workers (θ_w) and the fractions of the genome that is diploid in the female (h) and the male (m), for the pair bond case (termite-like) with a random and fixed genomic portion with diploid inheritance and a symmetrical energetic investment in a male and female sexual offspring

	Selection gradients, Pair bond				
	Random portion of diploid inheritance				
	$\theta_w = 0$	$\theta_w = .25$	$\theta_w = .50$	$\theta_w = .75$	$\theta_w = 1$
$\partial\lambda/\partial\theta_w\vert_{\theta=\theta^{css}}$					
$\partial\lambda/\partial h\vert_{\theta=\theta^{css}}$					
$\partial\lambda/\partial m\vert_{\theta=\theta^{css}}$					
	Fixed portion of diploid inheritance				
	$\theta_w = 0$	$\theta_w = .25$	$\theta_w = .50$	$\theta_w = .75$	$\theta_w = 1$
$\partial\lambda/\partial\theta_w\vert_{\theta=\theta^{css}}$					
$\partial\lambda/\partial h\vert_{\theta=\theta^{css}}$					
$\partial\lambda/\partial m\vert_{\theta=\theta^{css}}$					

Each cell contains a selection-surface plot with vertical axis h (ranging 0 to 1) and horizontal axis m (ranging 0 to 1).

Note. For details see Table 2.

female-haploid genome ($\theta_w = 1 \wedge h < 0.33 \wedge m = 1$), there can be selection for a female-haploid genome and a worker caste of only female offspring. Likewise, if initially both the fraction of female workers is sufficiently low ($\theta_w < 0.28 \wedge h = 1 \wedge m = 0$) and the genome is sufficiently biased toward the male-haploid genome ($\theta_w = 0 \wedge h = 1 \wedge m < 0.33$) there can be selection for a male-haploid genome and a worker caste of only male offspring.

Table 3 also shows that a change in the mode of inheritance from a random to a fixed genomic portion with diploid inheritance induces only a minor change in the results. The most significant change is the lack of selection for a male-haploid

and a female-haploid genome when the genomic portion with diploid inheritance is fixed. Again, for nearly all initial conditions, there is selection for a diploid genome where the worker caste may contain both female and male offspring. However, when $m = 1$ and initially the worker caste contains only female offspring, we find that h is neutrally stable and that the ploidy level may drift toward the female-haploid genome. Likewise, when $h = 1$ and the worker caste contains only male offspring, we find that m is neutrally stable and that the ploidy level may drift toward the male-haploid genome.

For the above-mentioned equilibria of between-population selection the relative investment in sexual females is one-half. By inserting the corresponding equilibrium values for h, m and θ_w into Eqs. (19) and (23), it is easily seen that the equilibrium of within-population selection on the relative investment in sexual females is also one-half. Thus, for the termite-like case with complete sexual reproduction and symmetrical energetic investment in a male and female offspring, there is no equilibrium conflict between within- and between-population selection.

These results become more complex when the assumption of complete sexual reproduction is relaxed, and we need to consider selection over the complete two-dimensional ploidy-level space. For this situation, Fig. 1 illustrates the evolutionary attractor of between-population selection when the genomic portion with diploid inheritance is either random or fixed. This attractor is defined by the within-population selection equilibrium $\theta^{css} = 1/2$ and the evolutionary attractor criterion associated with Eq. (26). Unlike the case with no pair bond, with a pair bond the evolutionary attractor is not a single combination of θ_w, m, and h. It is instead a surface upon which the equilibrium trait values may drift by neutral mutations. When the genomic portion with diploid inheritance is fixed, the equilibrium surface includes almost the entire ploidy-level space, while the equilibrium surface with a random portion of diploid inheritance includes approximately half of the possible ploidy levels, including the haploid, the diploid, the male-haploid, and the female-haploid genome. For all ploidy levels with equilibrium-states, the equilibrium-state of the diploid genome includes all possible worker sex ratios, while the equilibrium-state of all other ploidy levels includes only a single worker sex ratio. For the latter cases the ploidy level at equilibrium-state is symmetrical for $\theta_w^{**} = 1/2$, male-haploid biased for $\theta_w^{**} < 1/2$, and female-haploid biased for $\theta_w^{**} > 1/2$. And for all the equilibrium contours in Fig. 1, there is no conflict over the sexual sex ratio. In all cases, the equilibrium ratio is 1/2 for both within- and between-population selection.

The results mentioned above refer to the case with a symmetrical energetic investment in a male and female offspring. When instead the energy that is invested in a female sexual offspring increases relative to the investment in a male sexual offspring, the general result is that the equilibrium becomes increasingly biased toward the male-hapoid genome and a worker caste with only female offspring. Likewise, when the energy that is invested in a male sexual offspring increases relative to the investment in a female sexual offspring the equilibrium becomes increasingly biased toward the female-haploid genome and a worker caste with only male offspring. Table 4 illustrates this change by showing the selection surface of Table 3 when the energetic investment in two sexual male offspring is the same as the investment in one sexual female offspring.
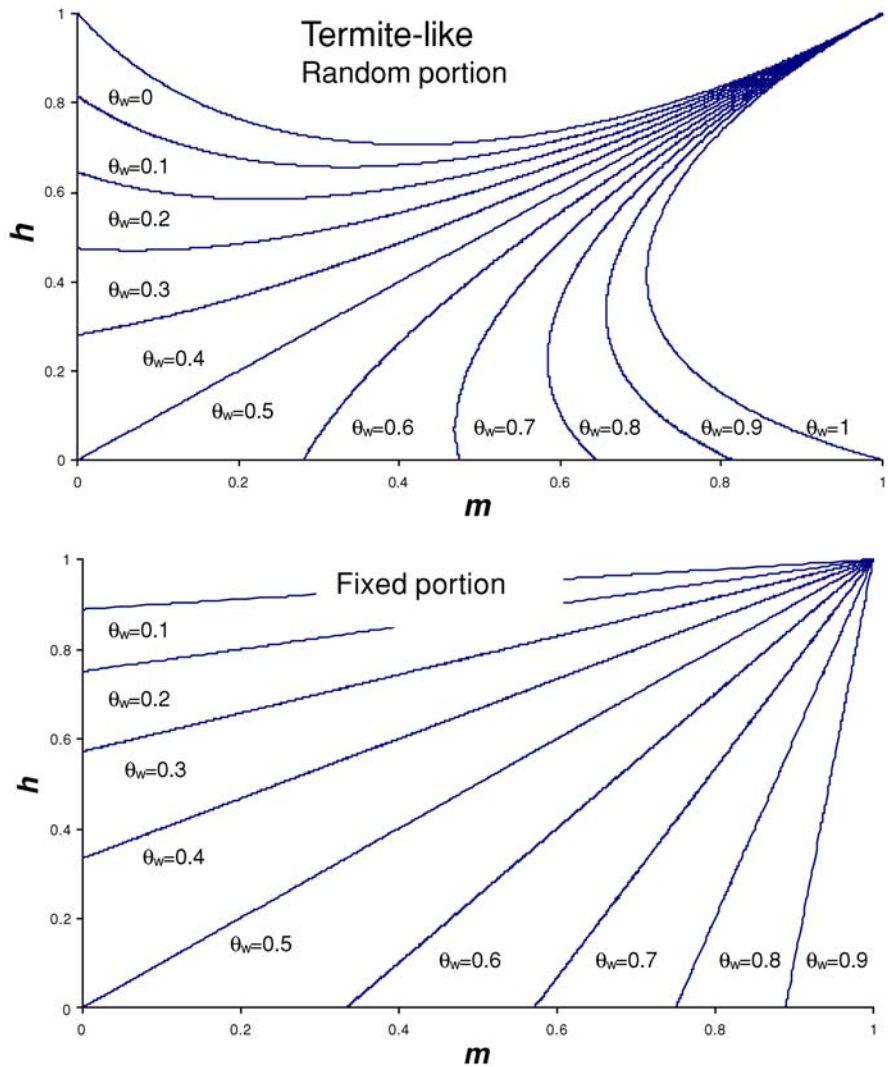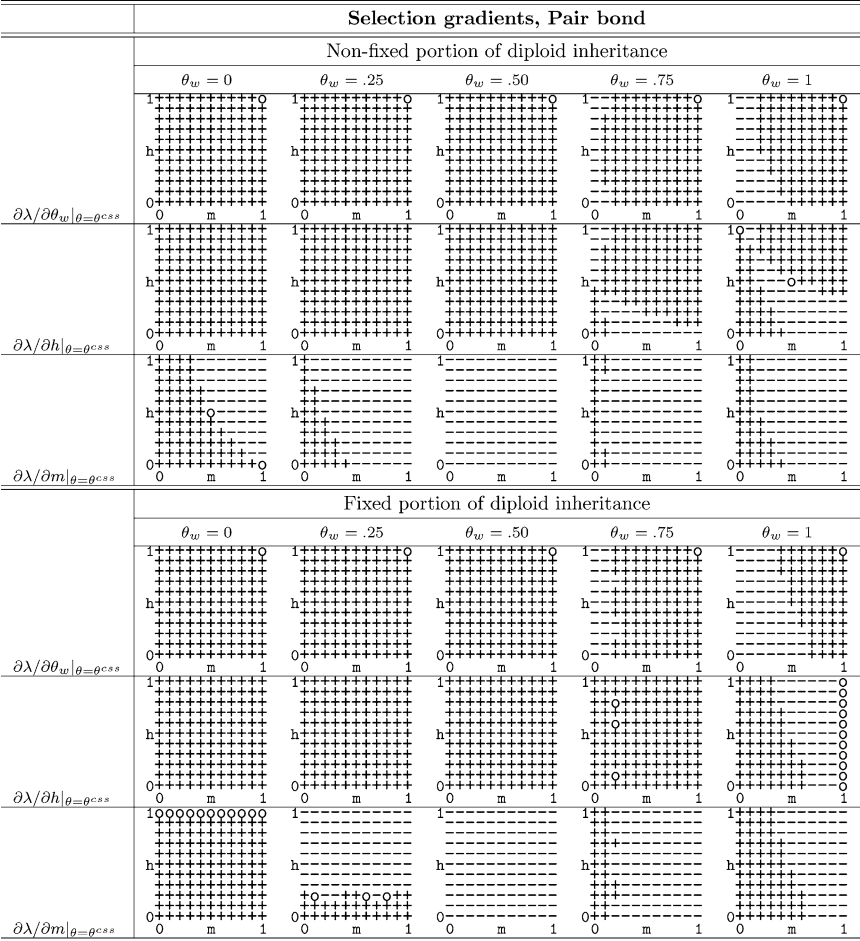
Fig. 1 The evolutionary equilibrium surface for the worker sex ratio and the ploidy level in the pair bond case (termite-like) where the energetic investment in a sexual male and female offspring is symmetrical. The upper and lower figures show respectively the cases with a random and fixed portion of the genome with diploid inheritance. The surface is illustrated by equilibrium contours for different worker sex ratios ($0 \leq \theta_w \leq 1$). h and m are the fractions of the genome in respectively the female and the male that are diploid instead of haploid.

3.3. One-step mutations between ploidy-levels

So far I have treated the ploidy level as a quantitative trait with continuous variation between the ploidy-levels of the diploid genome the male-haploid genome, the female-haploid genome, and the haploid genome. The obvious alternative

Table 4 The selection surface on the fraction of female workers (θ_w) and the fractions of the genome that is diploid in the female (h) and the male (m), for the pair bond case (termite-like) with a random and fixed genomic portion with diploid inheritance and the energetic investment in a female sexual offspring being twice the investment in a male sexual offspring

	Selection gradients, Pair bond				
	Non-fixed portion of diploid inheritance				
	$\theta_w = 0$	$\theta_w = .25$	$\theta_w = .50$	$\theta_w = .75$	$\theta_w = 1$
$\partial\lambda/\partial\theta_w\|_{\theta=\theta^{css}}$					
$\partial\lambda/\partial h\|_{\theta=\theta^{css}}$					
$\partial\lambda/\partial m\|_{\theta=\theta^{css}}$					
	Fixed portion of diploid inheritance				
	$\theta_w = 0$	$\theta_w = .25$	$\theta_w = .50$	$\theta_w = .75$	$\theta_w = 1$
$\partial\lambda/\partial\theta_w\|_{\theta=\theta^{css}}$					
$\partial\lambda/\partial h\|_{\theta=\theta^{css}}$					
$\partial\lambda/\partial m\|_{\theta=\theta^{css}}$					

Note. For details see Table 2.

possibility is sexual reproduction with discrete one-step mutations between the diploid genome, the male-haploid genome and the female-haploid genome. The discrete model is a sub-model of the continuous model described in the previous sections, with the long-term equilibrium of within- and between-population selection being given by between-population selection across the complete set of populations at the CSSs of within-population selection.

For the diploid genome ($m = 1$ & $h = 1$), we find that $\hat{\alpha}$ and $\tilde{\alpha}$ of Eqs. (20) and (24) reduce to one, and that β reduces to two, both independently of the worker

sex ratio. Thus, the female investment at the CSS of the diploid genome is $\theta^{css} = 1/2$. For the male-haploid genome ($m = 0$ & $h = 1$) the female investment is

$$\theta^{css} = \frac{\theta_w + 1/2}{\theta_w + 1}, \tag{30}$$

while it is

$$\theta^{css} = \frac{1}{2(2 - \theta_w)}, \tag{31}$$

for the female-haploid genome ($m = 1$ & $h = 0$).

3.3.1. No pair bond

With between-population selection on the ploidy level being defined by $\lambda = \dot{n}_\theta \theta|_{\theta=\theta^{css}}$, it follows that male-haploid populations with $\lambda \propto \frac{\theta_w + 1/2}{\theta_w + 1}$ are selected to increase at the expense of diploid populations with $\lambda \propto 1/2$, unless $\theta_w = 0$ a case where the two variants are selectively neutral with respect to one another because they have the same population dynamic growth rate λ. Furthermore, male-haploid populations are selected to increase at the expense of female-haploid populations, which have $\lambda \propto \frac{1}{2(2-\theta_w)}$. Diploid populations are also selected over female-haploid populations, unless $\theta_w = 1$ a case where the two variants are selectively neutral with respect to one another. Thus, given sufficient time we expect a male-haploid genome, and as $\partial \theta^{css}/\partial \theta_w > 0$ across male-haploid populations it follows that the female fraction in the worker caste of male-haploid eusocials is expected to converge toward one in the long run.

3.3.2. Pair bond

Let the ratio between the energetic investment in a sexual female offspring and a sexual male offspring be $x = \epsilon_\theta / \epsilon_\phi$. The between-population selection criterion of Eq. (28) may then be rewritten as

$$\begin{aligned} \lambda &= \theta|_{\theta=\theta^{css}}/x \quad \text{for} \quad \theta \leq x/(x+1) \\ \lambda &= 1 - \theta|_{\theta=\phi^{css}} \quad \text{for} \quad \theta \geq x/(x+1), \end{aligned} \tag{32}$$

given that the survival to the age of reproduction is the same for a sexual male and female. Thus, male-haploid populations will increase at the expense of diploid populations when $\theta^{css} \leq x/(x+1)$ and $\theta^{css}/x > 1/2$, which may be rewritten as

$$(x-1)/(2-x) < \theta_w \leq (x-1)/2, \tag{33}$$

given Eq. (30). Thus, as for $0 < x \leq 2$, $(x-1)/(2-x) < (x-1)/2$ only when $x < 1$ and $(x-1)/2 < 0$, it follows that there is no selection for a male-haploid genome when $x \leq 2$. When instead the energetic investment in a sexual female is two to three time the investment in a sexual male (i.e., when $2 < x < 3$), there can be

selection for a male-haploid genome when $\theta_w < (x-1)/2$. However, as $\partial\lambda/\partial\theta_w > 0$ for $m = 0$, there is between-population selection for $\theta_w \to 1$ in cases with a male-haploid genome and, thus, back transitions to the diploid genome may be expected whenever θ_w has increased beyond $(x-1)/2$. If instead the investment is strongly female biased with $x \geq 3$, the $(x-1)/2$ ratio is larger than one, which implies that there is between-population selection for a male-haploid genome for all θ_w.

Female-haploid populations will increase at the expense of diploid populations when $\theta^{css} \geq x/(x+1)$ and $\theta^{css} < 1/2$, which may be rewritten as

$$(3x-1)/2x \leq \theta_w < 1, \tag{34}$$

given Eq. (31). Thus, as $(3x-1)/2x < 1$ only when $x < 1$, it follows that there is no selection for a female-haploid genome when the energetic investment in a sexual female is larger than the investment in a male, i.e., when $x \geq 1$. If instead $1/3 < x < 1$, there is between-population selection for a female-haploid genome if $(3x-1)/2x \leq \theta_w$. However, as $\partial\lambda/\partial\theta_w < 0$ for $h = 0$, there is between-population selection for $\theta_w \to 0$ in cases with a female-haploid genome and, thus, back transitions to the diploid genome may be expected whenever θ_w has decreased below $(3x-1)/2x$. If instead the investment is strongly male biased with $x < 1/3$, the $(3x-1)/2x$ ratio is smaller than zero, which implies that there is between-population section for a female-haploid genome for all θ_w.

4. Discussion

Assuming complete sexual reproduction with diploid individuals in at least one of the two sexes, that the genomic portion with diploid inheritance in partial diploid individuals is random, and that the energetic investment in a male and female offspring is the same, Witting (1997) showed (i) that the absence of a pair bond between sexual males and females in eusocial species (as in hymenoptera) induces between-population selection for a male-haploid genome and a complete female biased worker caste, and (ii) that a pair bond (as in termites) induces between-population selection for a diploid genome and a worker caste with male and female offspring. These results were confirmed here, and it was shown: That they apply also if the genomic portion with diploid inheritance in partial diploid individuals is fixed. And that they apply both to ploidy levels that vary continuously as quantitative traits and to ploidy levels that vary discretely between the diploid genome, the male-haploid genome, and the female-haploid genome.

Furthermore, the male-haploid genome was predicted from the absence of a pair bond independently of the relative energetic investment in a male and female offspring. The diploid genome associated with a pair bond, however, does depend on a relative symmetrical investment in a sexual male and female offspring. If the energetic investment in a female sexual offspring is more that three times the investment in a male sexual offspring, the pair-bond case allows for the long-term evolution of a male-haploid genome and a worker case with only female offspring. If instead, the energetic investment in the male is three time the investment in the female, long-term evolution would proceed towards a female-haploid genome and

a worker caste with only male offspring. Pair formation may though be expected mainly when there is no overall fitness cost to the male, which requires that the male must provide some fitness gain that approximately outweighs his cost. If this gain is provided by an ecological process that is symmetrically divided between the sexual male and female we may expect that the energetic requirement of the male is relatively similar to that of the female. In such cases, the individuals of the two sexes are likely to require an approximately even energetic investment by the parents generating selection for the diploid genome.

4.1. Sexual reproduction

Seen in isolation the proposed model will generally not maintain sexual reproduction when evolution toward haploid and asexually reproducing organisms is allowed. With no pair bond there is selection towards asexual reproduction unless sexual reproduction is maintained by another mechanism. With a pair bond sexual reproduction may be maintained, although it need not be between diploid individuals.

The proposed mechanism is though unlikely responsible for the maintenance of sexual reproduction in eusocial species with pair bonds, as it seems more likely that it is the same mechanism that maintains sexual reproduction in both diploid and male-haploid eusocials. The proposed model is thus best seen as a mechanism that may influence the degree of sexual reproduction asymmetry, more than it may affect the evolution of sexual reproduction *per se*. In a larger theoretical framework, where the proposed model is superimposed upon the models of Witting (1997, 2002, 2003), it is selection by density-dependent competitive interactions that select for both eusocial colonies and for sexual reproduction, while the present model selects for sex ratios of workers and sexuals, and for degrees of sexual reproduction asymmetry.

4.2. Genetic constraints

For the proposed partial ploidy-level model, it may seem that many gametes may meet with gametes with which a viable individual cannot be formed. A zygote formed by two sub-haploid gametes, e.g., is very unlikely viable. The energy wasted on such zygotes may induce selection for mechanisms that will prevent their formation. Such a mechanism was implicitly assumed for the quantitative model in this paper, where the haploid gametes of the female form zygotes with the sub-haploid gametes of the male, and the haploid gametes of the male form zygotes with the sub-haploid gametes of the female.

The genomic portion with diploid inheritance is fixed when a sub-haploid gamete is formed from the incomplete chromosomes of the partial diploid individuals. Thus, for the model where the genomic portion with diploid inheritance is random, it may seem to be difficult to ensure that the genes that go into the sub-haploid gamete is taken at random from the entire genome of the partial diploid individual. Random sampling may though occur when there is free recombination

among the loci of the diploid portion of the genome, and all gametes are initially formed from the complete chromosomes, with sub-haploid gametes being formed secondarily by degeneration of genes within the gamete. Alternatively, diploid individuals may be formed from partial diploid zygotes by duplicating the genes of the complete chromosomes into the unoccupied loci of the incomplete chromosomes. Then, haploid gametes may be formed in the usual way, and sub-haploid gametes may be formed secondarily by gene degeneration. Although all individuals in the latter model might be diploid, the model allows for partial diploid inheritance with the diploid portion being selected at random.

This paper is based on a game-theoretical model assuming implicit that genetic constraints will not set limits to the predicted long-term equilibria. And at least for the case with a random portion with diploid inheritance, it seems likely that autosomal genes can code for the model. When the portion with diploid inheritance is random, the rate by which an autosomal gene is copied into the future through sexual reproduction is affected by the fraction of the genome that is haploid instead of diploid. This is because the randomly chosen portion with diploid inheritance fall back on the gene as a probability by which that particular gene is copied though haploid or diploid inheritance. This seems not to be the case when the portion with diploid inheritance is fixed. In the latter case, a gene at a particular locus is copied either through haploid or through diploid inheritance and, thus, the fraction of the genome with diploid inheritance may not affect the rate by which the gene is transmitted through sexual reproduction. These concerns do not apply to the model with discrete ploidy-levels.

So far I have assumed autosomal inheritance with complete recombination among the diploid portions of the genome. Given this assumption, it was shown that between-population selection can affect the relatedness coefficients among offspring through evolutionary modifications of the ploidy level. Another way that between-population selection may change the relatedness coefficients among offspring is through evolutionary changes in the fraction of the genome that has sex-linked instead of autosomal inheritance. Many termites have sex-linked genomes where up to more than 50% of the genome has sex-linked instead of autosomal inheritance (e.g., Syren and Luykx, 1977; Rowell, 1987; Crozier and Pamilo, 1996; Thorne, 1997). For the case with a symmetrical energetic investment in a sexual male and female offspring, it is shown in the appendix that there is at least two ways by which between-population selection may explain sex-linked genomes in eusocial diploid species. If between-population selection is defined by a pair bond between sexual males and females the fraction of the genome that is sex-linked is evolutionary neutral, i.e., dependent upon initial conditions it may take any value between zero and one. If instead between-population selection is defined by the two-fold cost of the male the most likely evolutionary equilibrium is a completely sex-linked genome.

4.3. Level of selection

An essential component that separates the proposed model from more traditional sex ratio models for eusocial species is the additional level of between-population selection. As apparent from the results, for hymenoptera-like cases, the strength

of between-population selection relative to the strength of within-population selection could be reflected in the sex ratio of the sexual caste. For 40 species of monogynous ants listed by Crozier and Pamilo (1996), the investment sex ratio is $\phi/\theta = 0.5 \pm 0.2$ (S.E.). This sex ratio is less female biased than the least female biased prediction of between-population selection (1/3 for a panmictic species), which indicates that the force of between-population selection is likely low compared with within-population selection.

Although this study is the first that analyse a joint selection for worker sex ratios and ploidy-level asymmetry in eusocial species, there have been earlier attempts to explain why there are no male workers in eusocial hymenoptera (e.g., Alexander, 1974; West-Eberhard, 1975; Starr, 1985; Kukuk et al., 1989; Kerr, 1990). Based on the earlier studies Crozier and Pamilo (1996, p. 64) conclude that "there has been no genetic bias against the evolution of male workers in the hymenoptera." The consensus has been that male workers are absent in hymenoptera, not because there is selection against them, but because they lacked the pre-adaptation necessary to become efficient workers. The present study suggests instead that between-population selection against male workers is indeed expected in hymenoptera, but not in termites. It is clear that a lack of pre-adaptation for the worker task is not a general character of males; male workers exist in other eusocial species, like termites.

In traditional sex ratio models for eusocial species, it is the phenotypic constraints of the ploidy level and the worker sex ratio that determine the sex ratio of the sexual caste. In the proposed model, it is instead the ecological constraints on the sex ratio of the sexual caste, as defined by the interactions among sexual individuals, that determine the worker sex ratio and the ploidy level. At first, it may seem contradictory that it is possible to obtain conclusions that appear diametrically opposite to the traditional conclusions by a model that incorporates the classical models. But the hint is that the different causalities operate at different levels of selection. Selection at the higher between-population level operates on the predictions of the classical sex ratio models, where in the long run it selects the most optimal phenotypic constraints from a wider set of classical models that cover the complete range of worker sex ratios and ploidy-level asymmetries.

But could the proposed two-level selection concept support a more traditional view where the sexual sex ratio, the worker sex ratio, and the interactions among sexuals are predicted from the ploidy level. It is unlikely that traditional sex ratio theory alone would explain worker sex ratios and sexual interactions from ploidy levels simply because all these traits are assumptions of that theory. An additional level of selection may therefore be needed to get such a hypothesis to work. But in relation to between-population selection by the ploidy level, we note that the classical sex ratio equilibrium is independent of the two types of sexual interactions considered here. Thus, even if it could be shown that the relationship between the classical sex ratio equilibrium and the between-population fitness profile would depend on the ploidy level, this relationship cannot generally be expected to impose selection on the sexual interactions because the traditional equilibrium is independent of these interactions. So, to explain sex ratios and interactions among sexual males and females from ploidy levels, it seems that we need to invoke a completely different model concept than considered here.

4.4. Existence versus history

This paper analysed selection causes for the existence of co-variance between life-history traits in eusocial species and did not consider their history of evolution. This is because historical analysis is neither necessary nor sufficient to identify the historical constraints that have shaped the process of natural selection (Reeve and Sherman, 2001). Only studies of the fitness consequences of the traits in question are needed, but such studies can generally not be tested historically, but only against existing populations.

However, if evolution is shaped by a deterministic type of natural selection (Witting, 2003), where past selection causes are responsible also for the evolutionary maintenance of life-histories in existing species, it may be possible to determine the historical order by natural selection models that explain the co-variance between the life-history traits of existing species. A parsimonious interpretation of the proposed model would then suggest that eusociality could have evolved prior to the evolution of asymmetrical sexual reproduction. This view is in general agreement with the lack of strong evidence for the Hamiltonian hypothesis that asymmetrical sexual reproduction poses strong selection for eusocial reproduction (Trivers and Hare, 1976; Seger, 1983; Grafen, 1986; Frank and Crespi, 1989; Gadagkar, 1991), with the apparent positive taxonomic correlation between eusociality and asymmetrical reproductive systems, and with the observation that sex-linked genomes apparently have evolved on several occasions in eusocial termites (Crozier and Luykx, 1985; Rowell, 1987). But parsimonious causality is not necessarily guaranteed in natural selection systems, and the observation that eusociality has evolved perhaps 12 times in male-haploid hymenoptera (Crozier and Pamilo, 1996) points in the other direction.

Duffy et al. (2000) noted that comparative statistical tests for determining the origins of eusociality is confounded by the ancient origins of eusociality (Hölldobler and Wilson, 1990; Choe and Crespi, 1997) and by the paucity of robust phylogenies. If eusociality is more easily lost than gained, estimation will be biased toward the finding of multiple origins, when multiple losses in descendants from a single eusocial ancestor are more likely (Olmland, 1997; Duffy et al., 2000). And the historical uncertainty on the male-haploid genome may be even larger than the historical uncertainty on eusociality, as it is normally assumed that the male-haploid genome evolved prior to the evolution of the eusocial colony. Conclusions on the chronological order of evolution may therefore, as noted by Crespi (1996, p. 263), be "premature or misleading for almost all groups of social insects."

4.5. Conclusion

Confronting the Hamiltonian view that asymmetrical sexual reproduction selects for eusocial colonies in hymenoptera and termites (Hamilton, 1964, 1972; Lacy, 1980, 1984), this study suggests that it instead are the interactions among the sexual males and females in eusocial colonies that select for asymmetrical sexual reproduction. Here, it is intriguing to note that there is between-population selection for the absence of a pair bond between the sexual male and female (compare Eqs. (25) and (28)). Constraints on the sexual interactions, as represented by the

two sub-models in this paper, may therefore ultimately explain the evolutionary differences that this paper has considered between hymenoptera and termite-like cases.

Appendix

Two-level selection framework

Within-population selection on the relative investment in sexual females, θ, is given by a two-dimensional fitness profile

$$\lambda_i = f(\theta_i, \theta), \tag{A.1}$$

where the population dynamic growth rate λ of the ith variant depends on the trait value of that variant (θ_i) and on the average trait value in the population (θ). The evolutionary equilibrium $\partial \lambda_i / \partial \theta_i |_{\theta_i = \theta} = 0$ denoted θ^{*w}, is an Evolutionary Stable Strategy (ESS) when the equilibrium variant θ^{*w} is more fit in the equilibrium population than any other variant $\theta \neq \theta^{*w}$, i.e., when $f(\theta^{*w}, \theta^{*w}) > f(\theta, \theta^{*w})$, or when for the case of equality $f(\theta^{*w}, \theta^{*w}) = f(\theta, \theta^{*w})$ the equilibrium variant θ^{*w} is more fit in any other population $\theta \neq \theta^{*w}$ than those population variants, i.e., when $f(\theta^{*w}, \theta) > f(\theta, \theta)$ (Maynard Smith and Price, 1973; Maynard Smith, 1982). The ESS is a Continuously Stable Strategy (CSS) when $\partial(\partial \lambda_i / \partial \theta_i |_{\theta_i = \theta})/\partial \theta |_{\theta = \theta^{*w}} < 0$, and an evolutionary repellor when $\partial(\partial \lambda_i / \partial \theta_i |_{\theta_i = \theta})/\partial \theta |_{\theta = \theta^{*w}} > 0$ (Eshel and Motro, 1981; Eshel, 1983; Taylor, 1989; Christiansen, 1991). For the present study, the equilibrium θ^{*w} is a CSS, denoted θ^{css} (see Eq. (6)). A long-term convergence to the CSS can generally be expected independently of the genetic structure for a wide range of genetic assumptions (Eshel and Feldman, 1984; Liberman, 1988; Matessi and Di Pasquale, 1996; Eshel et al., 1997, 1998).

By Eq. (2), there are no within-population selection on θ_w, and the two ploidy-level parameters m and h. Hence, these parameters may drift neutrally within the different populations, while θ is determined by within-population selection. The fraction θ^{css}, however, depends on θ_w, m and h

$$\theta^{css} = g(\theta_w, m, h), \tag{A.2}$$

with g being a selection function that is specified in the main text of the paper.

The population dynamic growth rate λ, obtained by Eq. (A.1) at the limit $\theta_i \to \theta$, depends on θ so that between-population variation in θ generates between-population selection on θ. The three parameters θ_w, m and h have no direct influence on λ, implying that there is no direct between-population selection on these parameters. However, by inserting Eq. (A.2) into Eq. (A.1), the relationship between λ and θ defines a relationship between λ and θ_w, m, and h, given that θ is at θ^{css}. Thus, there is indirect between-population selection on θ_w, m and h. And with no frequency-dependent interactions among populations, a joint non-trivial evolutionary equilibrium for within- and between-population selection on the four parameters θ, θ_w, m and h would be given by an optimum to λ, provided that $\theta = \theta^{css}$.

The between-population fitness profile on $x \in \{\theta_w, m, h\}$ is therefore given by Eq. (A.1) taken at the limit $\theta_i(x) = \theta(x) = \theta^{css}(x)$, where

$$\lambda = f[\theta^{css}(x), \theta^{css}(x)], \tag{A.3}$$

converts the between-population differences in θ^{css} caused by the between-population differences in $x \in \{\theta_w, m, h\}$ into between-population differences in λ. Hence, the evolutionary equilibrium x^{**} is given by $\partial\lambda/\partial x|_{\theta=\theta^{css}} = 0$, with the equilibrium being an evolutionarily stable attractor when $\partial\lambda/\partial x|_{\theta=\theta^{css}=x^{**}+\rho} < 0$ and $\partial\lambda/\partial x|_{\theta=\theta^{css}=x^{**}-\rho} > 0$, where subscript $x^{**} + \rho$ indicates a small positive, and $x^{**} - \rho$ a small negative, perturbation of the evolutionary equilibrium x^{**}.

Evolution toward an attractor x^{**} can be expected when evolution at the within-population scale is faster than between-population evolution. Then, we may expect that between-population selection occurs between populations that have evolved to CSSs so that the above described optimisation process may approximate the overall evolutionary dynamics. More generally, between-population selection may occur at the time-scale of population dynamics that generally is faster than a mutation limited convergence toward a CSS. But even then evolution may be expected to convert toward the joint equilibrium x^{**}.

To see this, let between-population selection occur between a mother population x and a variant population x_i, where the variant population is defined as a population that due to mutation and drift deviates from the mother population in the trait $x \in \{\theta_w, m, h\}$. As the variant population arose from the mother population and as the varying traits have no direct influence on λ, there is no direct between-population selection before the sex ratio of the sexual caste has evolved in at least one of the two population. And as between-population evolution is assumed here to be faster than within-population evolution, let within-population evolution in θ occur only in one of the two populations before the outcome of between-population selection is determined, and let initially the sexual female fraction be at some unspecified CSS. Then, as the mother population $\theta^{css}(x)$ is situated at the CSS, within-population evolution on θ can occur only in the variant population where selection will carry that population toward the CSS $\theta^{css}(x_i)$. Hence, although we cannot expect the variant population to have evolved to the CSS before between-population selection will exclude one of the two populations, we find that a variant population can invade and exclude the mother population only if $\lambda(\theta^{css}(x_i)) > \lambda(\theta^{css}(x))$. If exclusion occurs we have a case where the new mother population cannot generally be at a CSS, and here we can expect four situations

$$
\begin{aligned}
&\text{a)}\ \lambda(\theta^{css}(x)) > \lambda(\theta_{t_i}(x)) = \lambda(\theta_{t_i}(x_i)), &&\Rightarrow \theta(x) \to \theta^{css}(x)\\
&\text{b)}\ \lambda(\theta^{css}(x)) < \lambda(\theta_{t_i}(x)) = \lambda(\theta_{t_i}(x_i)), &&\text{not possible}\\
&\text{c)}\ \lambda(\theta^{css}(x_i)) < \lambda(\theta_{t_i}(x)) = \lambda(\theta_{t_i}(x_i)), &&\Rightarrow x_i \text{ cannot invade}\\
&\text{d)}\ \lambda(\theta^{css}(x_i)) > \lambda(\theta_{t_i}(x)) = \lambda(\theta_{t_i}(x_i)), &&\Rightarrow x_i \text{ exclude } x,
\end{aligned}
\tag{A.4}
$$

where (a) and (b) relate to the case with within-population evolution in the mother population, (c) and (d) relate to the case with within-population evolution

in the variant population, and $\lambda(\theta_{t_i})$ gives the population dynamic growth rate at the time t_i where the variant population x_i arose from the mother population x. Of these possibilities (b) is not possible because the only populations that can have become fixed as mother populations are populations that have a present λ that is lower than or equal to their λ at the CSS. And (c) induces no change because the mother population excludes the variant population. The overall dynamics is therefore described by (a) and (d). Here (d) allows for the invasion and exclusion of the mother population by populations that have a $\lambda(\theta^{css})$ that is larger than $\lambda(\theta^{css})$ for the original population in CSS, and (a) excludes the variant population while the mother population evolves towards it's CSS. Hence, given sufficient time we may expect the mother population to reach a new CSS that has a λ that is larger than the λ of the original population in CSS. The process may then be repeated from a mother population in CSS, and over a longer time-scale we may expect the evolutionary process to convert towards the overall equilibrium x^{**}, defined by the nearest optimum in λ given $\theta = \theta^{css}$.

Sex-linked genomes in diploid eusocials

This section examines whether between-population selection can alter the fraction of the genome that has sex-linked inheritance. I assume that the genome is diploid, that the energetic investment in a sexual male and female offspring is symmetrical, that there is free recombination among autosomal genes, that there is no crossing over between sex-linked genes, and that the fraction of the genome with sex-linked inheritance is κ. Following Leinaas (1983), in this case, the relatedness coefficients among offspring are

$$p_{s,s} = p_{d,d} = 1/2 + \kappa/4$$
$$p_{s,d} = p_{d,s} = 1/2 - \kappa/4. \tag{A.5}$$

Then, by Eqs. (8) and (10), and $v_d = v_s = 1/2$, we find that

$$\vartheta_d = [2 + \kappa(2\theta_w - 1)]/8$$
$$\vartheta_s = [2 - \kappa(2\theta_w - 1)]/8. \tag{A.6}$$

Thus, the investment in sexual females at the classical equilibrium $\theta^{css} = \vartheta_d/(\vartheta_d + \vartheta_s)$ is

$$\theta^{css} = \frac{2 + \kappa(2\theta_w - 1)}{4}. \tag{A.7}$$

For the case where between-population selection is defined by the cost of the male, the between-population selection gradients are

$$\partial\lambda/\partial\theta_w = \dot{n}_\theta \kappa/2$$
$$\partial\lambda/\partial\kappa = \dot{n}_\theta(\theta_w/2 - 1/4). \tag{A.8}$$

This implies that there are two evolutionary equilibria:

$$\kappa^{**} \ = \ 0$$
$$\theta^{**} \ = \ 1/2 \qquad\qquad\qquad\qquad\qquad\qquad (A.9)$$
$$0 \leq \theta_w^{**} \ < 1/2,$$

that is evolutionarily unstable at the limit $\theta_w^{**} = 1/2$, and

$$\kappa^{**} = 1$$
$$3/4 \leq \theta^{**} \leq 1 \qquad\qquad\qquad\qquad\qquad\qquad (A.10)$$
$$\theta_w^{**} = 1,$$

that is the evolutionary attractor for most initial conditions. Thus, if the ancestor is a diploid species with an even sex ratio, the expected equilibrium for the case with no pair bond between sexual males and females is a genome with complete sex-linked inheritance.

For the alternative case where between-population selection is defined by a pair bond between sexual males and females, it can be seen that the evolutionary equilibrium is

$$0 \leq \kappa^{**} \leq 1$$
$$\theta^{**} \ = \ 1/2$$
$$\theta_w^{**} \ = \ 1/2. \qquad\qquad\qquad\qquad\qquad\qquad (A.11)$$

That is, if there is a pair bond between sexual males and females, dependent upon initial conditions, the genomic fraction with sex-linked inheritance may take any value between zero and one.

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