The evolution of morphological castes under decoupled control

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Abstract

Eusociality, where units that previously reproduced independently function as one complex entity, is a phenomenon of major interest in evolutionary biology. Obligately eusocial societies are characterised by morphologically differentiated castes and reduced conflict. We explore conditions under which morphological castes may arise in the social Hymenoptera and the factors constraining their evolution. Control over offspring morphology and behaviour may often be decoupled. Queens and provisioners can influence offspring morphology directly, through the nutrition they provide, while offspring control their own behaviour as adults. Queens and provisioners may, however, influence worker behaviour indirectly, if offspring modify their behaviour in response to their morphology. Our results suggest that the evolution of a morphologically differentiated worker caste depends on the prior presence of a behavioural caste: specialist worker morphology will be mismatched with behaviour unless some offspring already choose to work. A mother's certainty about her offspring's behaviour is also critical – less certainty results in greater mismatch. We then show how under decoupled control, morphologically differentiated castes should be less and less likely to be lost through evolution as they become more specialized. We show how worker productivity in the absence of a morphological trait can affect the likelihood of that trait being favoured by natural selection. We also comment on the evolutionary irreversibility of eusociality.

1. Introduction

Eusociality, where some individuals in a social group forfeit their own reproduction to help others to reproduce, is a phenomenon of major interest in evolutionary biology. Division of labour is most extreme in so-called obligate eusocial groups, where workers are not able to functionally replace reproductives and reproductives cannot produce reproductive offspring without help from a worker caste (see also Crespi and Yanega, 1995). These groups are characterised by morphologically differentiated castes and reduced conflict over reproduction (Bourke, 2011; Quinones and Pen, 2017; Boomsma and Gawne, 2018). In contrast, in facultatively eusocial groups, either reproductives cannot produce reproductive offspring without help from a worker caste (Crespi and Yanega, 1995), or workers are not able to functionally replace reproductive roles, but not both. In this instance, caste differences tend to be mainly behavioural (Boomsma and Gawne, 2018), and the functional constraints on caste members are typically the result of ecological conditions and life history traits (e.g. mating opportunities or swarm founding) rather than morphology. Finally, cooperatively

Figure 1. The two morphological worker castes of the turtle ant Cephalotes varians; (A) the soldier, or major worker, sporting the impressive head armour it uses to seal the nest entrance and (B) the much smaller minor worker which conducts all the foraging duties for the nest. Photo ©Alex Wild, used with permission.

breeding groups are those where workers can functionally replace reproductives and reproductives are capable of producing reproductive offspring without help from a worker caste (Crespi and Yanega, 1995). Different authors define these categories in slightly different ways, and the above working definitions are provided for clarity.

Morphological castes are startlingly diverse, ranging from simple differences in body size (Trible and Kronaeur, 2017; Kerr et al, 2019) to elaborate task-specific morphologies in taxa such as turtle ants, in which the head armour of soldiers is shaped so as to seal the nest entrance (Powell, 2016; Figure 1). Greater morphological specialisation tends to be found in larger groups (Bourke, 1999; Bourke, 2011). This is thought to reflect reduced reproductive conflict and increased efficiency returns from task specialisation at larger group sizes (Bourke, 1999; Bourke, 2011).

Decoupling of control over offspring morphology and behaviour

Eusocial groups exhibiting morphological caste are characterised by a shift away from individual control. This is to say that individuals often have limited control over their own morphologies. Morphology is instead primarily controlled by either the queen (and if present, the King) or the workforce at large (Wade, 2001; Schwander et al, 2008; Korb, 2008; Russell and Lummaa, 2009). This is most clearly seen in the social insects, in particular the bees, wasps and ants, which include a significant majority of eusocial organisms. These taxa have a holometabolic life history, in which exoskeletal development occurs in a controlled environment prior to adult emergence from the pupa (Anderson, 1972). The controlled environment is often a nest where young are

provisioned and cared for by the mother or workforce (Peters et al, 2017). The use of a nest is ancestral for all social Hymenoptera (Boomsma and Gawne, 2018). Combined with a holometabolic life history, nests give provisoners a huge amount of control over the development of immature offspring by enabling them to manipulate the environment in which offspring develop and the provisions that offspring receive (Reinhold, 2002; Karsai and Hunt, 2002; Schwander et al, 2008; Kovacs et al, 2010; Brand and Chapusiat, 2012). While the importance of nest use in driving eusociality is widely accepted (Hunt, 2007; Nowak et al, 2010; Boomsma and Gawne, 2018), its role in enabling elevated maternal control over development, and hence a greater degree of maternal manipulation, has received less attention.

If we consider individuals to be fitness maximisers (Lehmann and Rousset, 2020), we would expect those controlling phenotype to manipulate it, and hence caste, to their own benefit (Michener and Brothers, 1974; Alexander 1974; Dawkins, 1976; Kapheim et al 2015). Previous work addressing the evolution of such maternally influenced traits has focused predominantly on the ability of individuals to resist manipulation by provisioners (Keller and Nonacs, 1993; Wenseleers et al., 2003; Uller and Pen, 2011), and on how provisioners that can manipulate both offspring behaviour and morphology might influence the origin of eusociality (Craig, 1979; Gonzalez-Forero, 2015; Gonzalez-Forero and Pena, 2021; Rodrigues and Gardner, 2021; Liu et al, 2022). Our focus in this paper, however, is not the origin of eusociality or helping behaviour, but the evolution of morphological castes, and we consequently aim to characterise when manipulation of offspring phenotype by provisioners will be favoured by selection. It has previously been noted that there may be costs as well as benefits to manipulating offspring, such as manipulator error resulting in offspring

death (Wenseleers et al., 2003). We aim to identify key factors which influence the costs and benefits of manipulation and provide insight into how these factors might shape the evolution of morphological castes in the social Hymenoptera. To do so we assume a state of split control, with provisioners controlling the morphology of offspring but offspring retaining control of their behavioural phenotype. We believe this assumption to be generally representative of the facultatively eusocial, cooperatively breeding, and solitary Hymenoptera (Hunt, 2007; Kapheim et al, 2011; Brand and Chapusiat, 2012; Kapheim et al 2015), from which obligate eusociality evolved. The terminology surrounding eusociality can be confusing, with different authors advocating different usages. For the purposes of this paper, “behavioural worker caste” refers to all individuals in a group that behave as workers irrespective of their morphology. The term “morphological worker caste” refers to all the individuals in a group that possess specialist worker morphology, irrespective of whether they behave as workers or reproductives. Specialist worker morphology enhances individuals’ ability to carry out worker functions while decreasing their fitness as reproductives. We consider a “worker caste” to be present in a group if there is either a behavioural worker caste or a morphological worker caste.

We will start by considering a singly mated, solitary, female hymenopteran. We assume that this female controls the morphology of her offspring, but that her offspring control their own behaviour, so that control over behaviour and morphology is decoupled. To begin with, we will also assume that any individuals which become workers will remain workers (behavioural caste is immutable) and that the mother produces an equal sex ratio. In this situation, a simple implementation of Hamilton’s rule (Hamilton, 1964; Grafen, 1985) indicates that a focal daughter, being equally

related to her siblings and her offspring (r=0.5), would favour becoming a worker when she would be more productive as a worker than if she dispersed as a reproductive. In contrast, because the relatedness of a mother to her offspring (r=0.5) is twice her relatedness to her grand-offspring (r=0.25), we would expect the mother to favour her daughter becoming a worker, and hence her imposing a worker caste through altering the environment she provides for offspring development, when workers are only half as productive as reproductives. The productivity of a worker relative to a reproductive is therefore critical for the arisal of a worker caste (Charnov, 1978; Bourke and Ratnieks, 1999; Reuter and Keller, 2001) and we would expect the mother to favour imposing a worker caste - perhaps by manipulating daughter morphology - before her daughter would favour being a member of it, i.e. at a lower reproductive/worker productivity ratio (Michener and Brothers, 1974; Alexander 1974; Dawkins, 1976; Craig, 1979; Kapheim et al 2015). Inducing morphological specialization in daughters, so that they themselves will be more productive if they choose to become workers, is an obvious mechanism by which mothers could impose a worker caste. Accordingly, we might expect the first workers to be morphologically specialised. In fact, however, comparative data suggest that behavioural castes always precede the evolution of morphological castes in the social insects (Boomsma, 2013; Peters et al, 2017; Boomsma and Gawne, 2018), indicating that the evolution of a morphological worker caste is somehow reliant on the prior presence of a behavioural worker caste (Supplementary materials Part 1).

Productivity in the absence of specialist morphology

Across the social Hymenoptera, worker productivity varies widely (Michener, 1964; Jeanne et al., 2022), depending on factors such as group size (Michener, 1964;

Jeanne et al., 2022), time constraints (Lucas and Field, 2013) and environmental constraints (Bourke, 1999; Jeanne et al., 2022) due to seasonal variations in resource availability (Poitrineau et al., 2009). Variation in worker productivity can occur between species (Field and Toyoizumi, 2020) but also within them over time (Michener, 1964; Jeanne et al., 2022). The increase in worker productivity that a specialist worker morphological trait represents for a given worker will often depend on baseline worker productivity (worker productivity without that morphological trait). To illustrate, consider a small worker whose primary function is nest defence. If a large worker is twice as likely to successfully repel an attack on the nest, then as the frequency of attacks increases, the difference in number of attacks successfully repelled by a large and small worker will also increase. We might then expect large worker size to be most likely to evolve when attacks are most frequent, i.e. when workers engaging in nest defence would be most productive.

Summary

To summarize, there is significant evidence in the nest building Hymenoptera that provisioners can control the morphology of offspring (Reinhold, 2002; Karsai and Hunt, 2002; Schwander et al, 2008; Kovacs et al, 2010; Brand and Chapusiat, 2012). Provisioners (queens or the workforce) should favour daughters becoming workers at a lower worker productivity than daughters themselves, so that we might expect the first workers be morphologically specialised. Yet the evidence suggests that daughters choose to become workers evolutionarily before morphological castes arise. Here, we provide a possible explanation for this paradox. Drawing on the relationship between form and function, we propose a simple model illustrating the relationship between the evolution of morphological caste and the certainty the individual controlling

morphology has over the behaviour of individuals occupying that caste. We then use this model to explore how worker productivity in the absence of specialist morphology might influence the benefit that morphology provides, and hence the likelihood of that morphology evolving.

2. The Model

We imagine a bivoltine life cycle such as that of many temperate zone cooperatively breeding bees and wasps (e.g. Seger, 1983; Field et al., 2010; Couchoux & Field 2019). A single female reproductive founds a nest then provisions a first brood of offspring (B1) herself. A fraction of the female offspring from this B1 brood will immediately disperse as reproductives and found new nests, while the remainder stay and help raise a second brood (B2) of their mother's offspring. The females from the second brood all disperse as reproductives. Daughters from B1 which stay and help represent a behavioural worker caste. While in many small colony cooperatively breeding bees and wasps, behavioural castes are mutable, with worker takeover being common, we will start by assuming that they are immutable and that once an individual becomes a worker it will remain a worker.

2.1. The role of dispersal

We wish to determine when it will be beneficial for a mother (queen) to impart a novel morphological trait $\boldsymbol{m}$ onto a daughter in B1, for example through the nutrition she provides the daughter during immature development. We are primarily interested in traits that provide a fitness benefit to the mother when imparted on offspring of one behavioural caste but a fitness cost to the mother when imparted to the other caste. Examples might be enlarged ovaries – benefitting reproductives but representing wasted investment on workers - and sterilisation – detrimental to reproductives but beneficial to the mother when imparted to workers as it avoids colony provisions being used to raise the offspring of workers (with which the mother shares lower relatedness). We model the expected fitness per unit investment a mother will receive

from a given daughter in the presence f' and absence f of morphological trait m (Table 1).

Table 1. Parameters used in our models.

	With morphological trait m	Without morphological trait m ("baseline value")
Fitness a worker daughter will provide to the mother	v'_w	v_w
Fitness a reproductive daughter will provide to the mother	v'_r	v_r
Cost to mother of producing a daughter	c'	c
Probability a daughter disperses (independent of morphology)	d	d
Expected fitness per unit investment a daughter will provide to the mother	f'	f
Probability a daughter disperses when trait m decreases the likelihood of daughters staying as workers.	$1-(1-d)(1+a)$	d
Probability a daughter disperses when trait m increases the likelihood of daughters staying as workers.	$d(1-a)$	d

Equation 1:

$$f' = \frac{(1-d)v'_w + dv'_r}{c'}, \qquad f = \frac{(1-d)v_w + dv_r}{c}$$

Trait m will be selected for when;

Equation 2:

$$f' > f$$

Thus the expected fitness per unit investment a mother will receive from a given daughter is dependent on the probability of that daughter dispersing as a reproductive d, as well as on the cost of producing the daughter. Since m here is considered to be a novel trait, we assume that daughters do not respond to the presence of the trait behaviourally, and have the same probability of dispersing with or without the trait (Table 1).

Substituting Equation 1 into Equation 2 we obtain the parameter space where we expect trait $\boldsymbol{m}$ to be selected for (Figure 2):

Equation 3:

$$\boldsymbol{d}[\boldsymbol{c}(\boldsymbol{v}'_{\boldsymbol{r}} - \boldsymbol{v}'_{\boldsymbol{w}}) + \boldsymbol{c}'(\boldsymbol{v}_{\boldsymbol{w}} - \boldsymbol{v}_{\boldsymbol{r}})] + \boldsymbol{c}\boldsymbol{v}'_{\boldsymbol{w}} - \boldsymbol{c}'\boldsymbol{v}_{\boldsymbol{w}} > \mathbf{0}$$

When $\boldsymbol{m}$ is a trait conferring specialist worker morphology, we would expect it to increase the fitness the mother receives from workers per unit cost more than the fitness she receives from reproductives per unit cost ($\frac{\boldsymbol{v}'_{\boldsymbol{w}}}{\boldsymbol{c}'} - \frac{\boldsymbol{v}_{\boldsymbol{w}}}{\boldsymbol{c}} > \frac{\boldsymbol{v}'_{\boldsymbol{r}}}{\boldsymbol{c}'} - \frac{\boldsymbol{v}_{\boldsymbol{r}}}{\boldsymbol{c}}$). When no daughters from B1 disperse as reproductives ($\boldsymbol{d} = \mathbf{0}$), a trait which increases the fitness a mother receives from a worker per unit cost ($\frac{\boldsymbol{v}'_{\boldsymbol{w}}}{\boldsymbol{c}'} - \frac{\boldsymbol{v}_{\boldsymbol{w}}}{\boldsymbol{c}} > \mathbf{0}$) will always be selected for. More generally, there will be a negative linear relationship between probability of dispersal and the likelihood of trait $\boldsymbol{m}$ being favoured (Figure 2): the smaller the proportion of B1 daughters that disperse as reproductives, the more likely that it is advantageous for a mother to impart worker morphology, because morphology will less often be mismatched with behaviour. Because we are primarily interested in worker morphology which decreases the fitness per unit cost of a reproductive daughter, and behaviour here is considered independent of morphology, we do not expect such specialist worker morphology to evolve without the prior evolution of helping behaviour: if all B1 daughters become reproductives, trait $\mathbf{m}$ inevitably reduces offspring fitness.

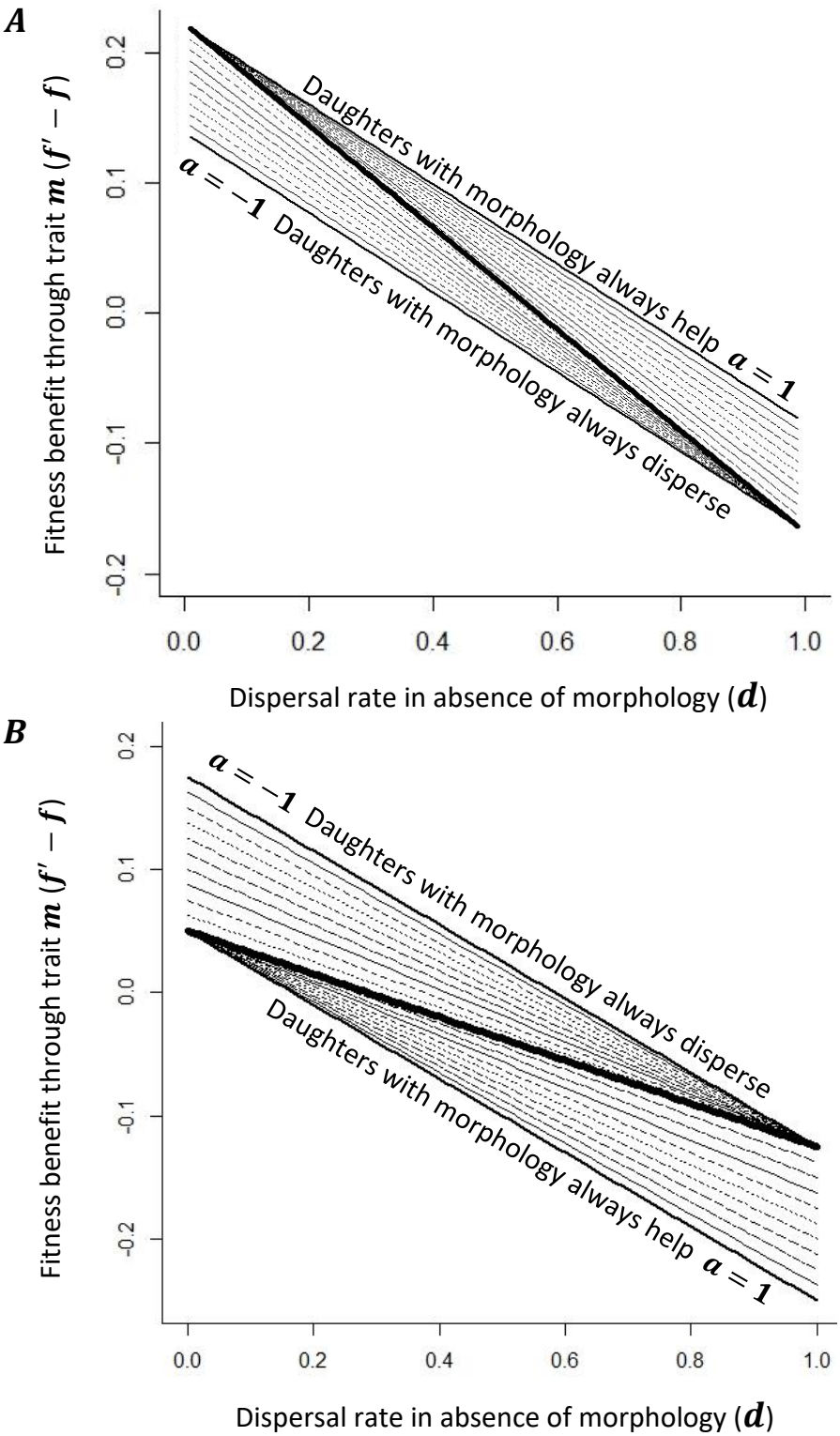

*Figure 2. The linear relationship between the net fitness increase a provisioner will receive from imparting morphological trait $\boldsymbol{m}$ onto a daughter ($\boldsymbol{f}' - \boldsymbol{f}$), and the baseline probability of a daughter dispersing (see Table 1 for parameter definitions). We have plotted this for $-\mathbf{1} \leq \boldsymbol{a} \leq \mathbf{1}$ at 0.1 increments. The thick central lines represent $\boldsymbol{a} = \mathbf{0}$ and hence Equation 3. **A** Daughters with trait $\boldsymbol{m}$ give more fitness as workers than reproductives ($\boldsymbol{v}'_{\boldsymbol{w}} > \boldsymbol{v}'_{\boldsymbol{r}}$) for parameter values ($\boldsymbol{v}'_{\boldsymbol{w}} = 0.55$, $\boldsymbol{v}'_{\boldsymbol{r}} = 0.5$, $\boldsymbol{v}_{\boldsymbol{w}} = 0.7$, $\boldsymbol{v}_{\boldsymbol{r}} = 1$, $\boldsymbol{c}' = 0.6$, $\boldsymbol{c} = 1$). **B** Daughters with trait $\boldsymbol{m}$ give less fitness as workers than reproductives ($\boldsymbol{v}'_{\boldsymbol{w}} < \boldsymbol{v}'_{\boldsymbol{r}}$) for parameter values ($\boldsymbol{v}'_{\boldsymbol{w}} = 0.6$, $\boldsymbol{v}'_{\boldsymbol{r}} = 0.7$, $\boldsymbol{v}_{\boldsymbol{w}} = 0.7$, $\boldsymbol{v}_{\boldsymbol{r}} = 1$, $\boldsymbol{c}' = 0.8$, $\boldsymbol{c} = 1$).*

2.2. Behaviour as a response to morphology

In the previous section, morphological evolution responds to behaviour, and worker morphology cannot evolve without the prior presence of a behavioural worker caste. Next, we consider the possibility that individuals can respond plastically to their morphology (El Mouden and Gardner, 2008), by choosing to disperse as reproductives or not. Morphological traits may not always be novel, and if we assume that trait $\boldsymbol{m}$ was historically present in our population, it seems likely that B1 daughters will have evolved to alter their dispersal decisions in response to the trait's presence. To model this new situation, we introduce parameter $\boldsymbol{a}$ (Table 1; Figure 3), which represents the effect of trait $\boldsymbol{m}$ on the probability of B1 daughters dispersing. When $\boldsymbol{a} > \mathbf{0}$, daughters with trait $\boldsymbol{m}$ are more likely to stay as workers, and when $\boldsymbol{a} = \mathbf{1}$ they always stay. Conversely, when $\boldsymbol{a} < \mathbf{0}$, daughters with trait $\boldsymbol{m}$ are more likely to disperse as reproductives, and when $\boldsymbol{a} = -\mathbf{1}$ they always disperse (Figure 3). Incorporating parameter $\boldsymbol{a}$ gives us the following equation:

Equation 4:

$$\boldsymbol{f} = \frac{(\mathbf{1}-\boldsymbol{d})\boldsymbol{v_w} + \boldsymbol{d}\boldsymbol{v_r}}{\boldsymbol{c}},$$

$$\boldsymbol{f'} = \begin{cases} \dfrac{[\mathbf{1}-\boldsymbol{d}(\mathbf{1}-\boldsymbol{a})]\boldsymbol{v'_w} + \boldsymbol{d}(\mathbf{1}-\boldsymbol{a})\boldsymbol{v'_r}}{\boldsymbol{c'}}, & \boldsymbol{a} \in \{\mathbf{0} \leq \boldsymbol{a} \leq \mathbf{1}\} \\ \dfrac{(\mathbf{1}-\boldsymbol{d})(\mathbf{1}+\boldsymbol{a})\boldsymbol{v'_w} + [\mathbf{1}-(\mathbf{1}-\boldsymbol{d})(\mathbf{1}+\boldsymbol{a})]\boldsymbol{v'_r}}{\boldsymbol{c'}}, & \boldsymbol{a} \in \{-\mathbf{1} \leq \boldsymbol{a} \leq \mathbf{0}\} \end{cases}$$

When $\boldsymbol{a} = \mathbf{0}$, the presence of trait $\boldsymbol{m}$ has no effect on the dispersal decisions of daughters, and Equation 4 reduces to Equation 1. When daughters can respond to the presence of morphological traits ($\boldsymbol{a} \neq \mathbf{0}$), mothers obtain a degree of indirect control over daughter behaviour through manipulating their morphology. The extent of this control is represented by the magnitude of $\boldsymbol{a}$. In order to determine when $\boldsymbol{m}$ will be

favoured by selection now that daughters can respond to it behaviourally, we can substitute Equation 4 into Equation 2 and rearrange to give the parameter space where we expect trait $\boldsymbol{m}$ to evolve as:

Equation 5:

$$\mathbf{0} < \begin{cases} \boldsymbol{d}[\boldsymbol{c}(\mathbf{1}-\boldsymbol{a})(\boldsymbol{v}_r'-\boldsymbol{v}_w') + \boldsymbol{c}'(\boldsymbol{v}_w-\boldsymbol{v}_r)] + \boldsymbol{c}\boldsymbol{v}_w' - \boldsymbol{c}'\boldsymbol{v}_w, & \boldsymbol{a} \in \{\mathbf{0} \leq \boldsymbol{a} \leq \mathbf{1}\} \\ \boldsymbol{d}[\boldsymbol{c}(\mathbf{1}+\boldsymbol{a})(\boldsymbol{v}_r'-\boldsymbol{v}_w') + \boldsymbol{c}'(\boldsymbol{v}_w-\boldsymbol{v}_r)] + \boldsymbol{c}(\mathbf{1}+\boldsymbol{a})(\boldsymbol{v}_w'-\boldsymbol{v}_r') + \boldsymbol{c}\boldsymbol{v}_r' - \boldsymbol{c}'\boldsymbol{v}_w, & \boldsymbol{a} \in \{-\mathbf{1} \leq \boldsymbol{a} \leq \mathbf{0}\} \end{cases}$$

We again find a linear relationship between $\boldsymbol{d}$, the baseline probability of dispersal, and the likelihood of trait $\boldsymbol{m}$ evolving (Figure 2). The relationship is again negative when $\boldsymbol{m}$ confers specialist worker morphology, but the gradient is now dependant on the value of $\boldsymbol{a}$. When $\boldsymbol{a}$ is less than zero (daughters with trait $\boldsymbol{m}$ are more likely to disperse), our y intercept is also dependant on $\boldsymbol{a}$, such that $\boldsymbol{a}$ is moderating the relationship between baseline dispersal and the likelihood of trait $\boldsymbol{m}$ evolving (Figure 2). This is because $\boldsymbol{a}$ causes the realised dispersal choices of daughters to correlate with their morphologies, altering the degree of mismatch between form and function. Parameter $\boldsymbol{a}$ therefore introduces a mechanism through which mothers can use their control over daughter morphology to influence daughter behaviour, and consequently moderate the certainty a mother has about how an individual daughter will behave.

To take an example, trait $\boldsymbol{m}$ might represent a simple reduction in the size of B1 daughters. Smaller daughters will be cheaper to produce (Brand and Chapusiat, 2012), so that if worker performance is independent of size (e.g. Couchoux and Field, 2019), the fitness per unit investment received by a mother from a worker will increase. However, we might also expect trait $\boldsymbol{m}$ to decrease the fitness per unit investment from daughters that disperse as reproductives: reproductives must found

new nests and lay eggs, and smaller reproductives may perform less well with these tasks (Couchoux and Field, 2019). If there has historically been variation in the size of daughters independent of trait $\boldsymbol{m}$, perhaps environmentally induced, it seems plausible that daughters will have already evolved to alter their dispersal decisions according to their size, with smaller daughters being more likely to stay as workers (Brand and Chapusiat, 2012). Our value of $\boldsymbol{a}$ in this instance would be positive (since daughters with trait $\boldsymbol{m}$ are more likely to stay as workers), and so long as $\boldsymbol{v'_w} > \boldsymbol{v'_r}$, trait $\boldsymbol{m}$ will be favoured by selection over a larger range of values of $\boldsymbol{d}$ than if daughters are unable to respond plastically to morphology (see Figure 2A). Conversely, if $\boldsymbol{v'_w} < \boldsymbol{v'_r}$, so that even with trait $\boldsymbol{m}$ daughters are less productive as workers than reproductives, a positive value of $\boldsymbol{a}$ will reduce the likelihood of trait $\boldsymbol{m}$ evolving (Supplementary materials Part 3, Figure 2B). Note that specialist worker morphology, which decreases the fitness per unit cost of a reproductive daughter, can now be selected for even when all offspring disperse ($\boldsymbol{d} = \mathbf{1}$) and daughters with trait *m* are more likely to stay ($\boldsymbol{a} > 0$; Figure 2). However, it seems unlikely that this combination will exist: daughters are unlikely to have evolved the ability to respond to the presence of trait $\boldsymbol{m}$ in a population where no daughters stay as workers in its absence.

We can extend this idea of maternal certainty over offspring behaviour to instances where workers have the possibility of inheriting the queen role by considering time spent as an inheriting worker as equivalent to time spent as a reproductive (Supplementary materials Parts 1 and 2). This changes the proportion of time a mother expects a daughter to spend as a worker or reproductive for a given probability of dispersal (Toyoizumi and Field, 2014). Thus the likelihood of a mismatch between

form and function when a mother imparts specialist worker morphology onto a daughter also changes, making specialist worker morphology less likely to be favoured. However, since time spent as a reproductive or inheriting worker still depends on the probability of dispersal ($\boldsymbol{d}$), the qualitative nature of the relationship between dispersal and the parameter space where we might expect to see the evolution of specialist morphology remains similar (Figure S1).

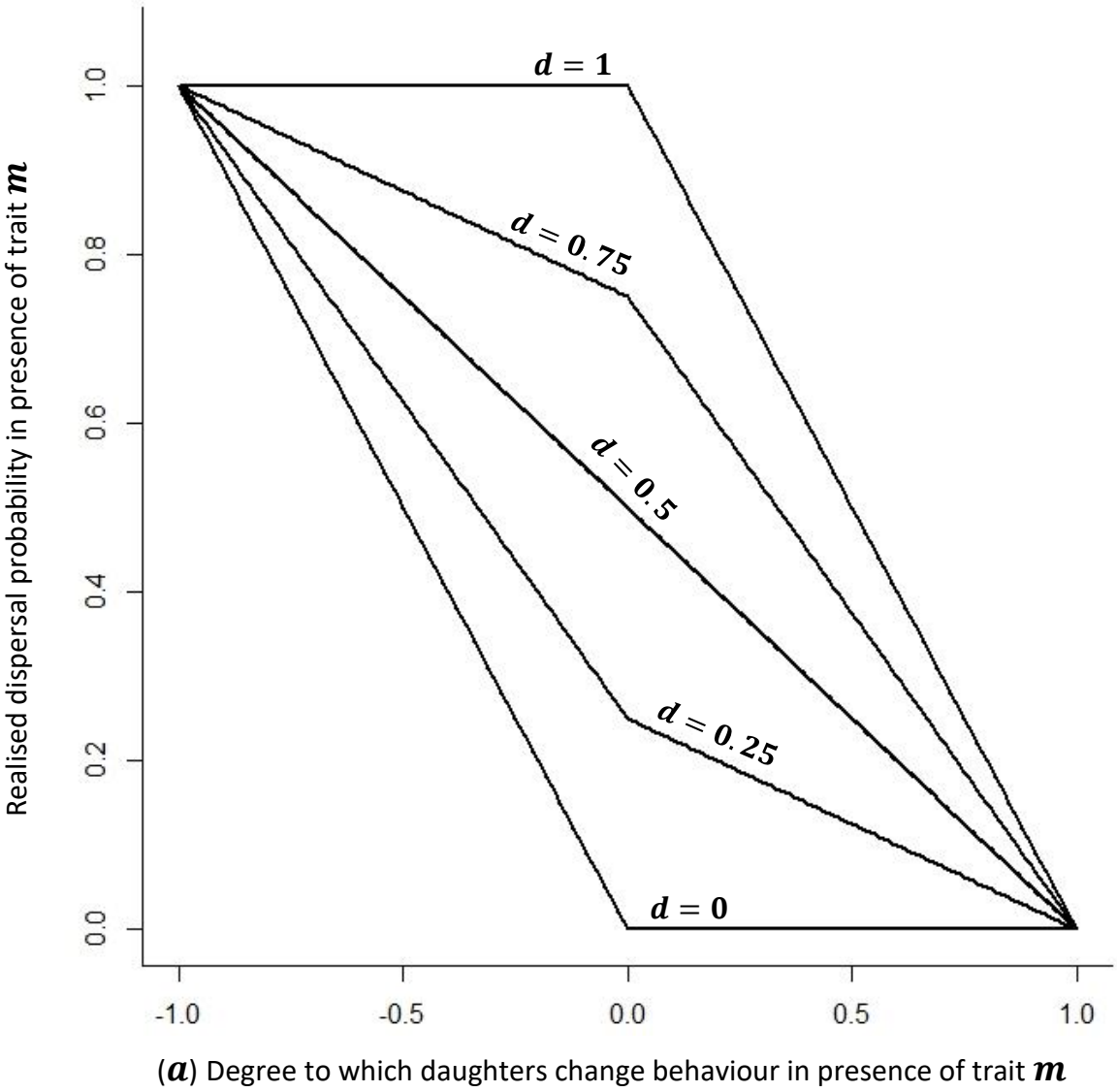

Figure 3. The relationship between $\boldsymbol{a}$, the degree to which daughters change their dispersal behaviour in the presence of trait $\boldsymbol{m}$, and realised offspring dispersal. Different lines represent different values of baseline dispersal (dispersal in the absence of trait $\boldsymbol{m}$; $\mathbf{0} \leq \boldsymbol{d} \leq \mathbf{1}$) in 0.25 increments. When $\boldsymbol{a} > \mathbf{0}$ daughters are more likely to work, when $\boldsymbol{a} < \mathbf{0}$ daughters are more likely to disperse (Table 1).

2.3. Trait benefit as a function of baseline productivity

The fitness represented by a worker offspring bearing trait $\boldsymbol{m}$ ($\boldsymbol{v'_w}$) is likely to be correlated with the fitness represented by a worker that lacks trait $\boldsymbol{m}$ ($\boldsymbol{v_w}$): trait $\boldsymbol{m}$ represents a single modification of worker morphology, leaving the remaining morphology unchanged. Thus, when the productivity of a worker without trait $\boldsymbol{m}$ changes we expect the productivity of workers with trait $\boldsymbol{m}$ to change as well, so that selection on trait $\boldsymbol{m}$ will depend on $\boldsymbol{v_w}$. Now it may be the case that the fitness benefit conferred by trait $\boldsymbol{m}$ varies with $\boldsymbol{v_w}$ such as in the relationship $\boldsymbol{v'_w = 2v_w}$, where trait $\boldsymbol{m}$ doubles the fitness represented by a worker. Again taking the example of worker size, this would be the case if a large worker is twice as productive as a small worker. The difference in productivity between large and small workers (the fitness benefit of being large) would then be equal to the productivity of a small worker. We use changes in productivity and fitness interchangeably here, but note that the productivity and fitness benefit of a worker trait may not always be equivalent, for example when the mortality of immature offspring also changes in the presence of a morphological trait (Cant and Field, 2001; Couvillon and Dornhaus, 2010). Substituting $\boldsymbol{v'_w}$ for $\boldsymbol{2v_w}$ in Equation 5 we can rearrange to give the following:

Equation 6:

$$\boldsymbol{0} < \begin{cases} \boldsymbol{v_w(d[\,c' + (a-1)2c] + 2c - c') + d[cv'_r(1-a) - c'v_r],} & \boldsymbol{a \in \{0 \le a \le 1\}} \\ \boldsymbol{v_w\big(d\big[\,c' - (1+a)2c\big] + 2c(1+a) - c'\big) + [1-(1-d)(1+a)]cv'_r - dc'v_{r,}} & \boldsymbol{a \in \{-1 \le a \le 0\}} \end{cases}$$

As discussed above, when $\boldsymbol{v'_w = 2v_w}$ we tend to see a strong positive relationship between $\boldsymbol{v_w}$ and the likelihood of trait $\boldsymbol{m}$ being favoured by selection (Figure 4). However, Equation 6 also highlights how this is not always the case. If our value of $\boldsymbol{a}$ is very low ($\boldsymbol{a < -0.5}$; Figure 4), so that daughters are more likely to disperse if they have trait m, or if the cost of producing a daughter with trait $\boldsymbol{m}$ ($\boldsymbol{c' - c}$) is very large

($\boldsymbol{c'} > \mathbf{2}\boldsymbol{c}$), then we can in fact generate negative relationships between $\boldsymbol{v_w}$ and the likelihood of trait $\boldsymbol{m}$ being selected for, despite setting $\boldsymbol{v'_w} = \mathbf{2}\boldsymbol{v_w}$ (Supplementary materials Part 3).

More generally we find that if there is a positive relationship between the productivity benefit of a specialist worker trait and baseline worker productivity; so long as the increased benefit provided by the trait remains proportionally greater than the cost of producing it, and if the trait does not significantly increase the likelihood of daughters dispersing, an increase in baseline worker productivity will lead to increased selection for that trait (Supplementary materials Part 3).

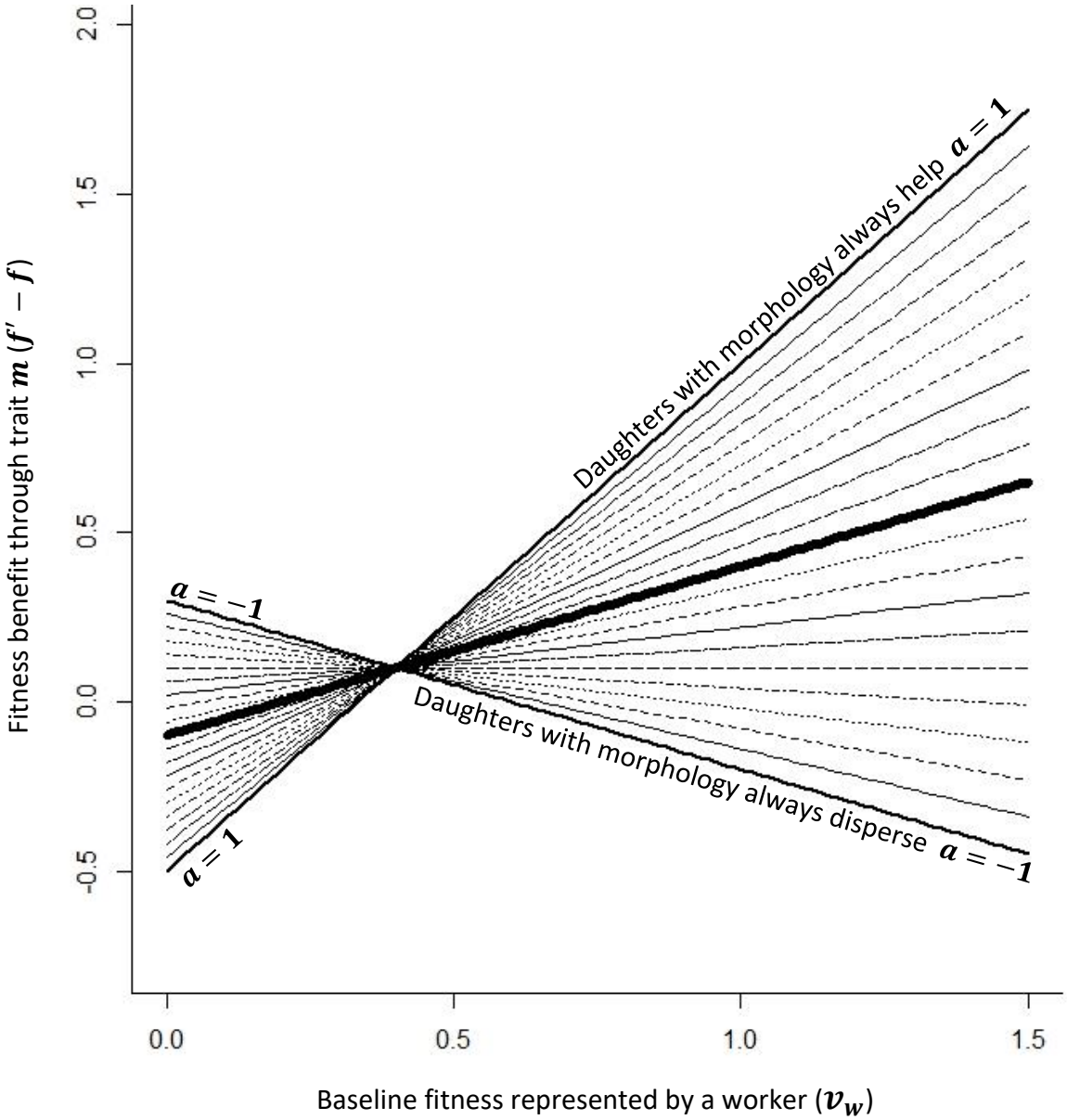

Figure 4.The relationship between the fitness of a worker in the absence of a trait and the likelihood of that trait being selected, when workers with that trait are twice as productive as those without it ($\boldsymbol{v}'_{\boldsymbol{w}} = \mathbf{2}\boldsymbol{v_w}$). We have plotted this for $-\mathbf{1} \leq \boldsymbol{a} \leq \mathbf{1}$ at 0.1 increments with parameter values ($\boldsymbol{v}'_{\boldsymbol{r}}$ = 0.8, $\boldsymbol{v_r}$ = 1, $\boldsymbol{d}$ = 0.5, $\boldsymbol{c}'$ = 1, $\boldsymbol{c}$ = 1). The thick central line represents $\boldsymbol{a} = \mathbf{0}$.

3. Discussion

Our analysis shows that unless a behavioural worker caste has already evolved, a new morphological trait that increases worker fitness but decreases the fitness of reproductives cannot invade, for the simple reason that all offspring will be reproductives. This may seem obvious, but it means that although we might expect queens to use their control over offspring morphology to impose worker behaviour at a lower threshold benefit/cost ratio than the threshold at which offspring themselves would work voluntarily, worker behaviour will not evolve unless the worker's own threshold has already been reached. Our analysis can therefore explain why behavioural castes always precede morphological castes in the social Hymenoptera (Boomsma, 2013; Peters et al, 2017; Boomsma and Gawne, 2018). We have primarily considered queens as being the provisioners controlling the morphology of offspring. However, once a behavioural caste has been established as we see in the social Hymenoptera, it becomes increasingly common for the workforce to instead control offspring morphology (Cameron and Robinson, 1990; Inoue et al., 1996; O'Donnell and Jeanne, 1993; Giray et al., 2005). The worker productivity at which the workforce favours offspring helping will depend on the number of times the queen has mated and also on the sex ratio of offspring produced (Reuter and Keller, 2001). However, we would still expect to see a disparity between workforce and offspring over the worker productivity at which helping is preferred (Stubblefield and Charnov, 1986).

More importantly, our findings suggest that in the social Hymenoptera, where it is likely that provisioners control offspring morphology while offspring control their own behaviour (Reinhold, 2002; Karsai and Hunt, 2002; Kapheim et al, 2011; Kovacs et al, 2010; Brand and Chapusiat, 2012; Kapheim et al, 2015), the certainty that

provisioners have about offspring dispersal decisions is a key constraint on the evolution of increasingly differentiated morphological castes (Equation 3). Reduced certainty results in greater mismatch between form and function. These conclusions are expected to hold even when behavioural castes are mutable (Supplementary materials Part 2). It is important to emphasise that the certainty provisioners have over offspring dispersal decisions can be increased through mechanisms other than a direct offspring response to morphology, for example where there is seasonal variation in offspring dispersal. A clear example of this is in temperate cooperatively breeding bees and wasps, where daughters from the first brood (B1) are more likely to become helpers than daughters from the second brood (B2), which always disperse as reproductives (section 2.1). Provisioners therefore have greater certainty about second brood daughter behaviour. The ability for offspring to adjust their dispersal decisions as a response to their morphology can also give provisioners a significant degree of indirect control over the behaviour of female offspring and allow morphological traits to be selected for at lower baseline rates of dispersal than we might otherwise expect (Equation 5).

Baseline worker productivity can affect the likelihood of specialist morphology evolving

We have shown that the baseline productivity of workers (in the absence of specialised morphology) can be important in determining when specialist morphology is likely to evolve. The gain in worker productivity (and hence provisioner fitness) provided by a morphological trait may vary as a function of baseline worker productivity, an example being a trait that increases worker size, where larger workers are always twice as productive as smaller workers. In this case, when smaller workers

have a productivity value of 5, larger workers would have a productivity of 10 (5 greater), but when smaller workers have a productivity value of 7, larger workers have a productivity of 14 (7 greater). A trait causing larger worker size will then be most likely to evolve when baseline worker productivity is high, since this is when larger workers provide the largest gain. Generally, if the extra fitness provided by a specialised morphological trait increases with baseline worker productivity (linearly or otherwise), the trait is most likely to be favoured when baseline productivity is high - unless that trait is especially costly (Supplementary materials Part 3). In practice, determining the relationship between morphology and productivity can be complex, with morphological traits not always enhancing all worker tasks equally, and epistasis for fitness (Bank, 2022) often making the extraction of simple empirical correlations difficult (Gimm et al, 2005; Kugonza et al, 2011; Wen et al 2015).

Decoupled control, reversibility, and loss of conflict between offspring and provisioners

We now extend our analysis by considering how it relates to the evolutionary reversibility of morphological castes. It has previously been suggested that the presence of a morphologically specialised worker caste, in particular a sterile worker caste, represents a state of irreversibility wherein the worker caste can no longer be lost evolutionarily (Boomsma 2013; Boomsma and Gawne 2018). Our analysis suggests a mechanism that could underlie reduced reversibility: with decoupled control, morphological castes become less likely to be lost as they become more specialised, and conflict between offspring and provisioners may disappear.

After a worker caste has evolved, it might be lost when the environment changes so that worker productivity decreases. Indeed, phylogenetic work shows that the largely behavioural worker caste seen in sweat bees has frequently been lost (Wcislo and Danforth, 1997), probably when bees entered environments where the season was too short for workers to be productive (Lucas and Field, 2013). Once a morphological worker caste is present, however, we expect workers to evolve to respond to their morphology when making decisions about their behaviour (section 2.2). Figure 5 illustrates the implications of this. For simplicity, we focus on the case when offspring with specialist worker or reproductive morphology are equally costly to produce – an example might be where worker morphology simply involves mandibles shaped specifically for defensive or foraging tasks. Initially, offspring prefer to disperse at higher worker productivities than provisioners prefer – productivities at which provisioners, because they are more closely related to the queen's offspring than to her grand-offspring, would prefer them to work (Figure 5A; see Introduction). With each additional morphological specialisation, however, the behavioural caste that an offspring chooses to join should depend more and more on its morphology: offspring themselves will incur larger and larger costs if they mismatch their behaviour to their morphology. The effect is almost ratchet-like: each additional morphological specialism reduces the fitness of daughters that mismatch their behaviour to their morphology by dispersing, so that worker productivity must drop progressively lower for offspring with worker morphology to nevertheless prefer dispersal (Figure 5B).

In contrast, because provisioners control offspring morphology, the worker productivity at which provisioners prefer offspring to disperse remains constant (figure 5): if the fitness that provisioners obtain from workers with specialist worker morphology falls

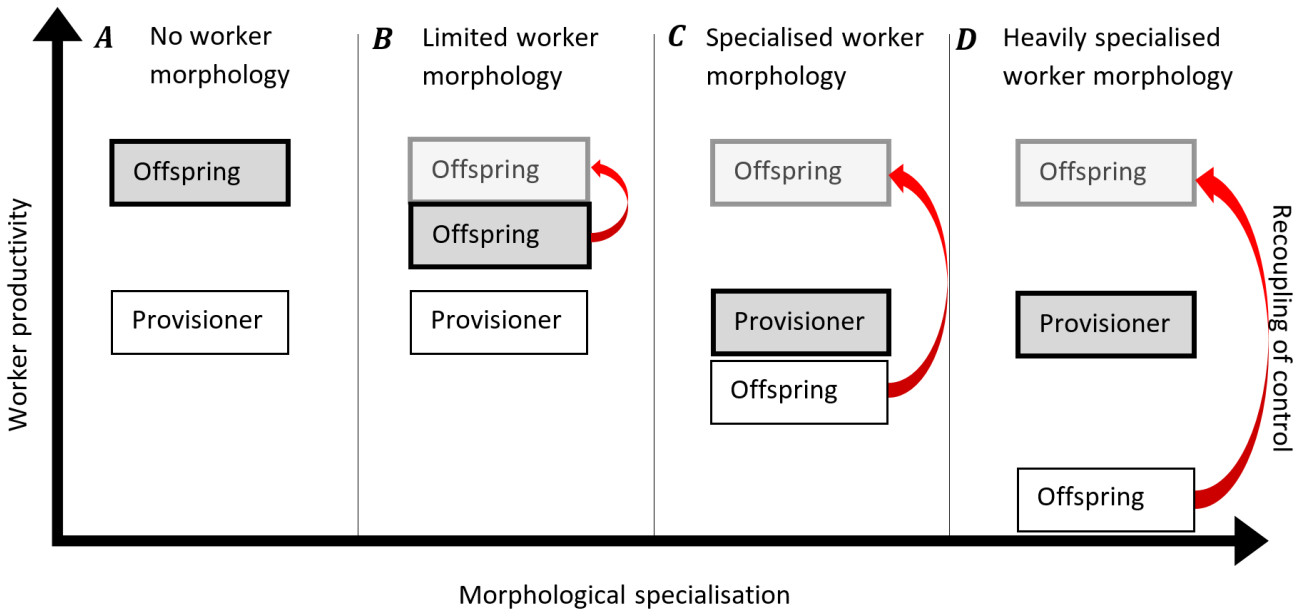

Figure 5. The relationship between the level of worker morphological specialisation and the threshold worker productivity at which offspring dispersal is favoured by two parties, offspring and provisioners. Preferences under decoupled control are represented by shaded (bold-edged) and unshaded boxes. The worker productivities at which offspring will begin to disperse, so that the worker caste is lost, are represented by shaded/bold-edged boxes. Red arrows linked to faded boxes indicate the possibility that offspring regain control of their morphology, recoupling it with control of behaviour, so that they do not incur mismatch costs when dispersing.

below what they obtain from dispersers with reproductive morphology, provisioners are expected to impart reproductive morphology – offspring should respond to this by dispersing, thus avoiding any mismatch. Eventually, once morphological castes are sufficiently specialised, the ratchet-like effect will mean that the worker productivity at which offspring with worker morphology themselves prefer dispersal drops below that at which provisioners prefer their offspring to disperse (Figure 5C). It should then be provisioners, not offspring, that first cause the loss of a worker caste during evolution, should worker productivity drop sufficiently. The worker caste is then no longer 'self-enforced' by the offspring and can instead be considered to be 'manipulator enforced' by the provisioner. At this point, realised conflict between offspring and provisioners over dispersal is lost, with both parties preferring the same outcome (the dispersal of offspring).

If at any point individual offspring are able to regain control of their morphology during evolution (recoupling control over morphology and behaviour), as seems to be the case in stingless bees (Meliponini) and a few other obligately eusocial taxa (Ishay and Landau, 1972; Wenseleers et al., 2003; Kaptein et al, 2005; Mas and Kolliker, 2008), the threshold worker productivity required for a worker caste to be lost becomes wholly determined by individual offspring (returning the worker caste to being ‘self-enforced’; red arrows in Figure 5). Offspring can then choose whether to work or disperse as reproductives without incurring costs through mismatching morphology and behaviour. This too represents a loss of realised conflict over dispersal, since now only one party is able to influence the outcome, this time resulting in dispersal being preferred at a higher level of worker productivity. The apparently offspring-controlled caste determination seen in the Meliponini (Wenseleers et al, 2003; Wenseleers and Ratnieks, 2004) could therefore represent a vulnerability to selection for loss of the worker caste, although so long as other aspects of meliponine life history remain, such as swarm founding that requires workers, such a reversal seems unlikely.

Extreme worker traits and evolutionary irreversibility

It is useful to consider where extreme morphological specializations such as worker sterility might appear in the above sequence (Figure 5). The very high costs of mismatch that such specializations entail means that they should either be associated with a recoupling of control over morphology and behaviour, such that mismatch can be avoided, or with a manipulator enforced worker caste. This is because, if control has not been recoupled and mismatch cannot be avoided, we would expect less

extreme specialisations, with lower costs of mismatch, to evolve before extreme traits like sterility – when provisioners are less certain about offspring behaviour. These less extreme traits might be sufficient on their own to cause the worker caste to become manipulator enforced (Figure 5C). Additional, more extreme morphological specialisations such as sterility would not then further reduce the likelihood of a worker caste being lost, since the point at which workers themselves might prefer to disperse would already have been passed (Figures 5C and 5D).

In the previous section, we suggested that the worker caste is less likely to be lost as it becomes more specialized. We here consider more generally what evolutionary 'irreversibility' means in the context of eusociality (Boomsma and Gawne, 2018). If reproductives are dependent on help from a worker caste to produce reproductive offspring – for example if the life cycle requires swarm founding - then that worker caste (morphologically specialised or otherwise) cannot be lost evolutionarily following a reduction in worker productivity, without resulting in extinction (Crespi and Yanega, 1995). It might then seem reasonable to consider the worker caste evolutionarily irreversible at this point. Irreversibility for the worker caste is then conditional on the capabilities of individuals of the reproductive caste, not on how morphologically specialised the worker caste itself has become. However, the capabilities of individuals in the reproductive caste could change – for example if the environment changes so that swarm founding is no longer essential. Likewise, if workers are unable to functionally replace reproductives in producing both male and female reproductive offspring, so long as worker capabilities remaining unchanged the reproductive caste cannot be lost evolutionarily without resulting in extinction. Thus, both of the criteria for obligate eusociality (Crespi and Yanega, 1995) must be maintained for eusociality to

be considered evolutionarily irreversible, at least at a given point in time: workers must be unable to functionally replace reproductives, and reproductives must be unable to produce reproductive offspring without help from a worker caste. We note that while being strongly correlated with morphological specialisation (Bourke, 2011; Quinones and Pen, 2017; Boomsma and Gawne, 2018), both criteria could in principle be maintained entirely through ecological conditions and life history traits, such as when workers lack mating opportunities (inability for workers to functionally replace reproductives) and swarm founding is favoured (reliance of reproductives on the worker caste to produce reproductive offspring).

The prevalence of decoupled control

While we have focused primarily on the evolution of a morphological worker caste in the facultatively eusocial and cooperatively breeding Hymenoptera, the relationships we have discussed underlying the evolution of morphological traits will hold for any level of social organisation so long as our assumptions regarding the immutability of morphology and split control are met (Supplementary materials Part 2). Relaxing these assumptions represents a possible future extension of our ideas and would greatly generalise our results, though it seems likely that the key linear relationships we identify involving behavioural certainty and baseline productivity will remain important. Shared control seems especially likely in progressively provisioning taxa, with substantial evidence that offspring begging influences provisioning decisions in obligately eusocial Hymenoptera (Ishay and Landau, 1972; Creemers et al, 2003; Kaptein et al, 2005; den Boer and Duchateau, 2006; Mas and Kolliker, 2008; He et al, 2016). However, evidence for offspring resistance to provisioner manipulation in the

Hymenoptera is limited outside of obligately eusocial species (Ishay and Landau, 1972; Wenseleers and Ratnieks, 2003; Kaptein et al, 2005; Mas and Kolliker, 2008; Gonzalez-Forero, 2015). Begging behaviours in solitary, cooperatively breeding, or facultatively eusocial progressively provisioning taxa have not to our knowledge been reported, suggesting that our assumption of queen control over morphology but offspring control of behaviour is reasonable before morphological castes evolve. It is possible, however, that the absence of begging outside the obligately eusocial Hymenoptera instead reflects a disparity in the volume of research conducted.

3.1. Conclusions

(1) There is strong evidence for the evolution of a morphological worker caste being reliant on the presence of a behavioural worker caste in the social Hymenoptera. (2) We suggest that maternal certainty of offspring dispersal decisions is one of the main constraints on the evolution of a morphological worker caste in the facultatively eusocial and cooperatively breeding Hymenoptera. (3) The decoupling of control over morphology and behaviour could be a key factor maintaining a morphological worker caste in the facultatively eusocial and cooperatively breeding Hymenoptera, and can lead to reduced conflict between offspring and provisioners. (4) The productivity of workers in the absence of specialist worker morphology can affect the likelihood of specialist morphology being favoured by selection.

Bibliography

Alexander, R. D. (1974). The Evolution of Social Behavior. *Annual review of ecology and systematics, 5*, 325-383. doi:https://doi.org/10.1146/annurev.es.05.110174.001545

Anderson, D. T. (1972). The development of holometabolous insects. In S. J. Counce, & C. H. Waddington (Eds.), *Developmental systems: Insects* (Vol. 1, pp. 165-242). Academic Press.

Bank, C. (2022). Epistasis and adaptation on fitness landscapes. *Annual Review of Ecology, Evolution, and Systematics, 53*, 457-479. doi:https://doi.org//10.1146/annurev-ecolsys-102320-112153

Boomsma, J. J. (2013). Beyond promiscuity: mate-choice commitments in social breeding. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 368*, 20120050. doi:https://doi.org//10.1098/rstb.2012.0050

Boomsma, J. J., & Gawne, R. (2018). Superorganismality and caste differentiation as points of no return: how the major evolutionary transitions were lost in translation. *Biological Reviews of the Cambridge Philosophical Society, 93*, 28-54. doi:https://doi.org/10.1111/brv.12330

Bourke, A. F. (1999). Colony size, social complexity and reproductive conflict in social insects. *Journal of evolutionary biology, 12*, 245-257. doi:https://doi.org/10.1046/j.1420-9101.1999.00028.x

Bourke, A. F. (2011). *Principles of social evolution.* Oxford University Press. doi:https://doi.org//10.1093/acprof:oso/9780199231157.001.0001

Bourke, A. F., & Ratnieks, F. L. (1999). Kin conflict over caste determination in social Hymenoptera. *Behavioral Ecology and Sociobiology, 46*, 287-297. doi:https://doi.org//10.1007/s002650050622

Brand, N., & Chapuisat, M. (2012). Born to be bee, fed to be worker? The caste system of a primitively eusocial insect. *Frontiers in zoology, 9*, 35. doi:https://doi.org//10.1186/1742-9994-9-35

Cameron, S. A., & Robinson, G. E. (1990). Juvenile hormone does not affect division of labor in bumble bee colonies (hymenoptera: apidae). *Annals of the Entomological Society of America, 83*, 626-631. doi:https://doi.org//10.1093/aesa/83.3.626

Cant, M. A., & Field, J. (2001). Helping effort and future fitness in cooperation animal societies. *Proceedings. Biological Sciences / the Royal Society, 268*, 1959-1964. doi:https://doi.org//10.1098/rspb.2001.1754

Charnov, E. L. (1978). Evolution of eusocial behavior: offspring choice or parental parasitism? *Journal of Theoretical Biology, 75*, 451-465. doi:https://doi.org//10.1016/0022-5193(78)90356-9

Couchoux, C., & Field, J. (2019). Parental manipulation of offspring size in social groups: a test using paper wasps. *Behavioral Ecology and Sociobiology, 73*, 36. doi:https://doi.org//10.1007/s00265-019-2646-3

Couvillon, M. J., & Dornhaus, A. (2010). Small worker bumble bees (Bombus impatiens) are hardier against starvation than their larger sisters. *Insectes sociaux, 57*, 193-197. doi:https://doi.org//10.1007/s00040-010-0064-7

Craig, R. (1979). Parental manipulation, kin selection, and the evolution of altruism. *Evolution, 33*, 319. doi:https://doi.org//10.2307/2407622

Creemers, B., Billen, J., & Gobin, B. (2003). Larval begging behaviour in the ant Myrmica rubra. *Ethology Ecology & Evolution, 15*, 261-272. doi:https://doi.org//10.1080/08927014.2003.9522671

Crespi, B. J., & Yanega, D. (1995). The definition of eusociality. *Behavioral Ecology, 6*, 109-115. doi:https://doi.org//10.1093/beheco/6.1.109

Dawkins, R. (1976). *The Selfish Gene.* Oxford University Press.

den Boer, S. P., & Duchateau, M. J. (2006). A larval hunger signal in the bumblebee Bombus terrestris. *Insectes sociaux, 53*, 369-373. doi:https://doi.org//10.1007/s00040-006-0883-8

El Mouden, C., & Gardner, A. (2008). Nice natives and mean migrants: the evolution of dispersal-dependent social behaviour in viscous populations. *Journal of Evolutionary Biology, 21*, 1480-1491. doi:https://doi.org//10.1111/j.1420-9101.2008.01614.x

Field, J., & Toyoizumi, H. (2020). The evolution of eusociality: no risk-return tradeoff but the ecology matters. *Ecology Letters, 23*, 518-526. doi:https://doi.org//10.1111/ele.13452

Giray, T., Giovanetti, M., & West-Eberhard, M. J. (2005). Juvenile hormone, reproduction, and worker behavior in the neotropical social wasp Polistes canadensis. *Proceedings of the National Academy of Sciences of the United States of America, 102*, 3330-3335. doi:https://doi.org//10.1073/pnas.0409560102

González-Forero, M. (2015). Stable eusociality via maternal manipulation when resistance is costless. *Journal of Evolutionary Biology, 28*, 2208-2223. doi:https://doi.org//10.1111/jeb.12744

González-Forero, M., & Peña, J. (2021). Eusociality through conflict dissolution. *Proceedings. Biological Sciences / the Royal Society, 288*, 20210386. doi:https://doi.org//10.1098/rspb.2021.0386

Grafen, A. (1985). A geometric view of relatedness. *Oxford surveys in evolutionary biology, 2*, 28-89.

Grimm, L. H., Kelly, S., Krull, R., & Hempel, D. C. (2005). Morphology and productivity of filamentous fungi. *Applied Microbiology and Biotechnology, 69*, 375-384. doi:https://doi.org//10.1007/s00253-005-0213-5

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology, 7*, 1-16. doi:https://doi.org//10.1016/0022-5193(64)90038-4

He, X. J., Zhang, X. C., Jiang, W. J., Barron, A. B., Zhang, J. H., & Zeng, Z. J. (2016). Starving honey bee (Apis mellifera) larvae signal pheromonally to worker bees. *Scientific Reports, 6*, 22359. doi:https://doi.org//10.1038/srep22359

Hunt, J. H. (2007). *The Evolution of Social Wasps.* Oxford University Press.

Inoue, T., Salmah, S., & Sakagami, S. (1996). Individual Variations in Worker Polyethism of the Sumatran Stingless Bee, Trigona (Tetragonula) minangkabau (Apidae, Meliponinae). *Japanese journal of entomology, 64*, 641-668.

Ishay, J., & Landau, E. M. (1972). Vespa larvae send out rhythmic hunger signals. *Nature, 237*, 286-287. doi:https://doi.org//10.1038/237286a0

Jeanne, R. L., Loope, K. J., Bouwma, A. M., Nordheim, E. V., & Smith, M. L. (2022). Five decades of misunderstanding in the social Hymenoptera: a review and meta-analysis of Michener's

paradox. *Biological Reviews of the Cambridge Philosophical Society, 97*, 1559-1611. doi:https://doi.org//10.1111/brv.12854

Kapheim, K. M., Bernal, S. P., Smith, A. R., Nonacs, P., & Wcislo, W. T. (2011). Support for maternal manipulation of developmental nutrition in a facultatively eusocial bee, Megalopta genalis (Halictidae). *Behavioral Ecology and Sociobiology, 65*, 1179-1190. doi:https://doi.org//10.1007/s00265-010-1131-9

Kapheim, K. M., Nonacs, P., Smith, A. R., Wayne, R. K., & Wcislo, W. T. (2015). Kinship, parental manipulation and evolutionary origins of eusociality. *Proceedings. Biological Sciences / the Royal Society, 282*, 20142886. doi:https://doi.org//10.1098/rspb.2014.2886

Kaptein, N., Billen, J., & Gobin, B. (2005). Larval begging for food enhances reproductive options in the ponerine ant Gnamptogenys striatula. *Animal Behaviour, 69*, 293-299. doi:https://doi.org//10.1016/j.anbehav.2004.04.012

Karsai, I., & Hunt, J. H. (2002). Food Quantity AffectTraits of Offspring in the Paper Wasp Polistes metricus (Hymenoptera: Vespidae). *Environmental Entomology, 31*, 99-106. doi:https://doi.org//10.1603/0046-225X-31.1.99

Keller, L., & Nonacs, P. (1993). The role of queen pheromones in social insects: queen control or queen signal? *Animal Behaviour, 45*, 787-794. doi:https://doi.org//10.1006/anbe.1993.1092

Kerr, N. Z., Crone, E. E., & Williams, N. M. (2019). Integrating vital rates explains optimal worker size for resource return by bumblebee workers. *Functional Ecology, 33*, 467-478. doi:https://doi.org//10.1111/1365-2435.13251

Korb, J. (2008). The ecology of social evolution in termites. In J. Korb, & J. Heinze (Eds.), *Ecology of social evolution* (pp. 151-174). Berlin, Heidelberg: Springer Berlin Heidelberg. doi:https://doi.org/10.1007/978-3-540-75957-7

Kovacs, J. L., Hoffman, E. A., Marriner, S. M., Rekau, J. A., & Goodisman, M. A. (2010). Environmental and genetic influences on queen and worker body size in the social wasp Vespula maculifrons. *Insectes sociaux, 57*, 53-65. doi:https://doi.org//10.1007/s00040-009-0050-0

Kugonza, D. R., Nabasirye, M., Mpairwe, D., Hanotte, O., & Okeyo, A. M. (2011). Productivity and morphology of Ankole cattle in three livestock production systems in Uganda. *Animal Genetic Resources/Ressources génétiques animales/Recursos genéticos animales, 48*, 13-22. doi:https://doi.org//10.1017/S2078633611000038

Lehmann, L., & Rousset, F. (2020). When do individuals maximize their inclusive fitness? *The American Naturalist, 195*, 717-732. doi:https://doi.org//10.1086/707561

Liu, M., West, S. A., & Wild, G. (2022). The evolution of manipulative cheating. *eLife, 11*. doi:https://doi.org//10.7554/eLife.80611

Lucas, E. R., & Field, J. (2013). Caste determination through mating in primitively eusocial societies. *Journal of Theoretical Biology, 335*, 31-39. doi:https://doi.org//10.1016/j.jtbi.2013.05.032

Mas, F., & Kölliker, M. (2008). Maternal care and offspring begging in social insects: chemical signalling, hormonal regulation and evolution. *Animal Behaviour, 76*, 1121-1131. doi:https://doi.org//10.1016/j.anbehav.2008.06.011

Michener, C. D. (1964). Reproductive efficiency in relation to colony size in hymenopterous societies. *Insectes sociaux, 11*, 317-341. doi:https://doi.org//10.1007/BF02227433

Michener, C. D., & Brothers, D. J. (1974). Were workers of eusocial hymenoptera initially altruistic or oppressed? *Proceedings of the National Academy of Sciences of the United States of America, 71*, 671-674. doi:https://doi.org//10.1073/pnas.71.3.671

Nowak, M. A., Tarnita, C. E., & Wilson, E. O. (2010). The evolution of eusociality. *Nature, 466*, 1057-1062. doi:https://doi.org//10.1038/nature09205

O'Donnell, S., & Jeanne, R. L. (1993). Methoprene accelerates age polyethism in workers of a social wasp (Polybia occidentalis). *Physiological entomology, 18*, 189-194. doi:https://doi.org//10.1111/j.1365-3032.1993.tb00467.x

Peters, R. S., Krogmann, L., Mayer, C., Donath, A., Gunkel, S., Meusemann, K., . . . Niehuis, O. (2017). Evolutionary history of the hymenoptera. *Current Biology, 27*, 1013-1018. doi:https://doi.org//10.1016/j.cub.2017.01.027

Poitrineau, K., Mitesser, O., & Poethke, H. J. (2009). Workers, sexuals, or both? Optimal allocation of resources to reproduction and growth in annual insect colonies. *Insectes sociaux, 56*, 119-129. doi:https://doi.org//10.1007/s00040-009-0004-6

Powell, S. (2016). A comparative perspective on the ecology of morphological diversification in complex societies: nesting ecology and soldier evolution in the turtle ants. *Behavioral Ecology and Sociobiology, 70*, 1075-1085. doi:https://doi.org//10.1007/s00265-016-2080-8

Powell, S., Price, S. L., & Kronauer, D. J. (2020). Trait evolution is reversible, repeatable, and decoupled in the soldier caste of turtle ants. *Proceedings of the National Academy of Sciences of the United States of America, 117*, 6608-6615. doi:https://doi.org//10.1073/pnas.1913750117

Quiñones, A. E., & Pen, I. (2017). A unified model of Hymenopteran preadaptations that trigger the evolutionary transition to eusociality. *Nature Communications, 8*, 15920. doi:https://doi.org//10.1038/ncomms15920

Reinhold, K. (2002). Maternal effects and the evolution of behavioral and morphological characters: a literature review indicates the importance of extended maternal care. *The Journal of Heredity, 93*, 400-405. doi:https://doi.org//10.1093/jhered/93.6.400

Reuter, M., & Keller, L. (2001). Sex ratio conflict and worker production in eusocial hymenoptera. *The American Naturalist, 158*, 166-177. doi:https://doi.org//10.1086/321311

Rodrigues, A. M., & Gardner, A. (2022, April). Reproductive value and the evolution of altruism. *Trends in Ecology & Evolution, 37*, 346-358. doi:10.1016/j.tree.2021.11.007

Russell, A. F., & Lummaa, V. (2009). Maternal effects in cooperative breeders: from hymenopterans to humans. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364*, 1143-1167. doi:https://doi.org//10.1098/rstb.2008.0298

Schwander, T., Humbert, J.-Y., Brent, C. S., Cahan, S. H., Chapuis, L., Renai, E., & Keller, L. (2008). Maternal effect on female caste determination in a social insect. *Current Biology, 18*, 265-269. doi:https://doi.org//10.1016/j.cub.2008.01.024

Seger, J. (1983). Partial bivoltinism may cause alternating sex-ratio biases that favour eusociality. *Nature, 301*, 59-62. doi:https://doi.org//10.1038/301059a0

Stubblefield, J. W., & Charnov, E. L. (1986). Some conceptual issues in the origin of eusociality. *Heredity, 57 (Pt 2)*, 181-187. doi:https://doi.org//10.1038/hdy.1986.108

Szathmáry, E., & Smith, J. M. (1995). The major evolutionary transitions. *Nature, 374*, 227-232. doi:https://doi.org//10.1038/374227a0

Toyoizumi, H., & Field, J. (2014). Dynamics of social queues. *Journal of Theoretical Biology, 346*, 16-22. doi:https://doi.org//10.1016/j.jtbi.2013.12.017

Trible, W., & Kronauer, D. J. (2017). Caste development and evolution in ants: it's all about size. *Journal of Experimental Biology, 220*, 53-62. doi:https://doi.org//10.1242/jeb.145292

Uller, T., & Pen, I. (2011). A theoretical model of the evolution of maternal effects under parent-offspring conflict. *Evolution, 65*, 2075-2084. doi:https://doi.org//10.1111/j.1558-5646.2011.01282.x

Wade, M. J. (2001). Maternal effect genes and the evolution of sociality in haplo-diploid organisms. *Evolution, 55*, 453-458. doi:https://doi.org//10.1554/0014-3820(2001)055[0453:megate]2.0.co;2

Wcislo, W. T., & Danforth, B. N. (1997). Secondarily solitary: the evolutionary loss of social behavior. *Trends in Ecology & Evolution, 12*, 468-474. doi:https://doi.org//10.1016/s0169-5347(97)01198-1

Wen, W., Li, K., Alseekh, S., Omranian, N., Zhao, L., Zhou, Y., . . . Fernie, A. R. (2015). Genetic determinants of the network of primary metabolism and their relationships to plant performance in a maize recombinant inbred line population. *The Plant Cell, 27*, 1839-1856. doi:https://doi.org//10.1105/tpc.15.00208

Wenseleers, T., & Ratnieks, F. L. (2004). Tragedy of the commons in Melipona bees. *Proceedings. Biological Sciences / the Royal Society, 271 Suppl 5*, S310-S312. doi:https://doi.org//10.1098/rsbl.2003.0159

Wenseleers, T., Ratnieks, F. L., & Billen, J. (2003). Caste fate conflict in swarm-founding social hymenoptera: an inclusive fitness analysis. *Journal of Evolutionary Biology, 16*, 647-658. doi:https://doi.org//10.1046/j.1420-9101.2003.00574.x

West, S. A., Fisher, R. M., Gardner, A., & Kiers, E. T. (2015). Major evolutionary transitions in individuality. *Proceedings of the National Academy of Sciences of the United States of America, 112*, 10112-10119. doi:https://doi.org//10.1073/pnas.1421402112