The evolution of morphological castes under decoupled control

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Abstract

The evolution of eusociality is regarded as a major evolutionary transition, where units that previously reproduced independently function as one complex entity. Advanced eusocial societies are characterised by morphologically differentiated castes and reduced conflict. We explore conditions under which morphological castes may arise and the factors constraining their evolution. Control over offspring morphology and behaviour may often be decoupled. Queens and provisioners can influence 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 should also be critical – less certainty results in greater mismatch. Decoupled control is important in maintaining a worker caste, and may result in reduced or no conflict between offspring and provisioners. We also show how worker productivity in the absence of a morphological trait can affect the likelihood of that trait being favoured by natural selection.

1. Introduction

The evolution of obligate eusociality (Crespi and Yanega, 1995; Boomsma, 2013; Boomsma and Gawne, 2018) has long been considered a major evolutionary transition (Szathmary and Smith, 1995; West et al, 2015), characterised by morphologically differentiated castes and reduced conflict over reproduction (Bourke, 2011; Quinones and Pen, 2017; Boomsma and Gawne, 2018). 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). Boomsma and Gawne (2018) regard irreversibility as a key component of evolutionary transitions and identify morphological castes as representing that evolutionarily irreversible step. 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).

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 by permission.

Decoupling of control over offspring morphology and behaviour

Eusocial societies 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 skeletal 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 has been noted in the past (Hunt, 2007; Nowak et al, 2010; Boomsma and Gawne, 2018), its role in enabling elevated maternal control over development 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 for individuals to resist manipulation by provisioners (Keller and Nonacs, 1993; 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; Liu et al, 2022). Here we instead consider when morphological castes will evolve assuming split control, with provisioners controlling the morphology of offspring and offspring retaining control of their behavioural phenotype. We believe this to be generally representative of the facultatively eusocial and solitary Hymenoptera (Hunt, 2007; Kapheim et al, 2011; Brand and Chapusiat, 2012; Kapheim et al 2015). In the following text, “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 morphology irrespective of whether they behave as workers or reproductives. Specialist morphology enhances their 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 the imposition of a worker caste, when workers are only half as productive as reproductives. The productivity of a worker relative to a reproductive is therefore a limiting factor in 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 (Michener and Brothers, 1974; Alexander 1974; Dawkins, 1976; Craig, 1979; Kapheim et al 2015). Accordingly we might expect the first workers to be morphologically specialised. In fact, however, behavioural castes always precede the evolution of morphological castes in the social insects (Boomsma, 2013; Peters et al, 2017; Boomsma and Gawne, 2018).

Behavioural castes are often mutable, so that individuals can switch behavioural castes over their lifetimes. The inclusion of effects such as worker takeover, through which a worker can become a reproductive, may reduce the threshold worker productivity required for a daughter to favour joining a behavioural worker caste (Field et al., 1999; Toyoizumi and Field, 2014; Price and Field, 2022). Similarly, if a daughter can help raise more reproductive sisters (r=0.75) than reproductive brothers (r=0.25) by staying as a worker, it will further lower the productivity of a worker relative to a reproductive required for the daughter to favour joining a behavioural worker caste (Trivers and Hare, 1976). The fact that we see strong evidence for behavioural worker

castes preceding morphological worker castes in the social insects (Boomsma, 2013; Peters et al, 2017; Boomsma and Gawne, 2018) therefore indicates that at least one of the following must be true: (1) the mutability of behavioural worker castes causes daughters to favour joining them at a lower worker productivity than required for mothers to favour imposing a morphological worker caste, (2) workers help raise broods which are sufficiently female biased to mean that daughters favour joining behavioural worker castes at a lower worker productivity than required for mothers to favour imposing a morphological worker caste or (3) the evolution of a morphological worker caste is somehow reliant on the prior presence of a behavioural worker caste.

On its own, the mutability of behavioural castes (explanation 1) cannot reasonably affect the argument that mothers will impose a worker caste before daughters prefer to join it. This would require workers to always immediately inherit the queen position or to produce an infinite number of offspring whenever they do (Supplementary materials Part 1). Similarly, mechanisms such as unmatedness (Godfray and Grafen, 1988; Godfray, 1990) and split sex ratios (Seger, 1983; Grafen, 1986; Gruber and Field, 2022), are unlikely to result in sex ratios that are female-biased enough to reverse the argument (Godfray and Hardy, 1990; Grafen, 1986; Boomsma and Eickwort, 1993). Even when daughters raise entirely sisters, they receive only 1.5 times the fitness benefit of raising the same number of their own offspring, less than the doubled benefit that mothers receive. Thus, we find that our proposed explanations 1 and 2, even acting in tandem, could not cause daughters to favour the arisal of a worker caste before mothers do (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). Variations in worker productivity can occur both between species (Field and Toyoizumi, 2020) but also within them over time (Michener, 1964; Jeanne et al., 2022). The increase in worker productivity that specialist worker morphological traits represent for a given worker will often change as a function of the productivity of that worker. To illustrate, consider a worker whose primary function is nest defence. If a large worker is twice as likely to successfully repel an attack on the nest when compared as a small worker, then as the frequency of attacks on the nest 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 examine our proposed explanation 3, that the evolution of a morphological worker caste is reliant on the prior presence of a behavioural worker caste. 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 likelihood of that morphology evolving.

2. The Model

We imagine a bivoltine life cycle such as that of many temperate zone small colony bees and wasps (e.g. Seger, 1983; Field et al., 2010; Couchoux & Field 2019). A single female reproductive will found a nest then produce a first brood of offspring (B1) which she will provision 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 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 the point at which it will be beneficial for a mother 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 benefit one behavioural caste and are detrimental to the other. Examples might be enlarged ovaries (benefitting reproductives) and sterilisation (benefitting workers). We model the expected fitness per unit investment a mother will receive from a given daughter in the presence $\boldsymbol{f}'$ and absence $\boldsymbol{f}$ of morphological trait $\boldsymbol{m}$ (Table 1).

Table 1. Parameters used in our models.

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

Equation 1:

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

Trait $\boldsymbol{m}$ will be selected for when;

Equation 2:

$$\boldsymbol{f' > f}$$

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 $\boldsymbol{d}$, as well as on the cost of producing the daughter. Since $\boldsymbol{m}$ 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 as reproductives 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 ($\frac{\boldsymbol{v}'_{\boldsymbol{w}}}{\boldsymbol{c}'} - \frac{\boldsymbol{v}_{\boldsymbol{w}}}{\boldsymbol{c}} > \frac{\boldsymbol{v}'_{\boldsymbol{r}}}{\boldsymbol{c}'} - \frac{\boldsymbol{v}_{\boldsymbol{r}}}{\boldsymbol{c}}$)(Fisher, 1930). 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 less often morphology is mismatched with behaviour, and the more likely that it will be advantageous for a mother to impart worker morphology. 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 $\mathbf{m}$ reduces offspring fitness.

248

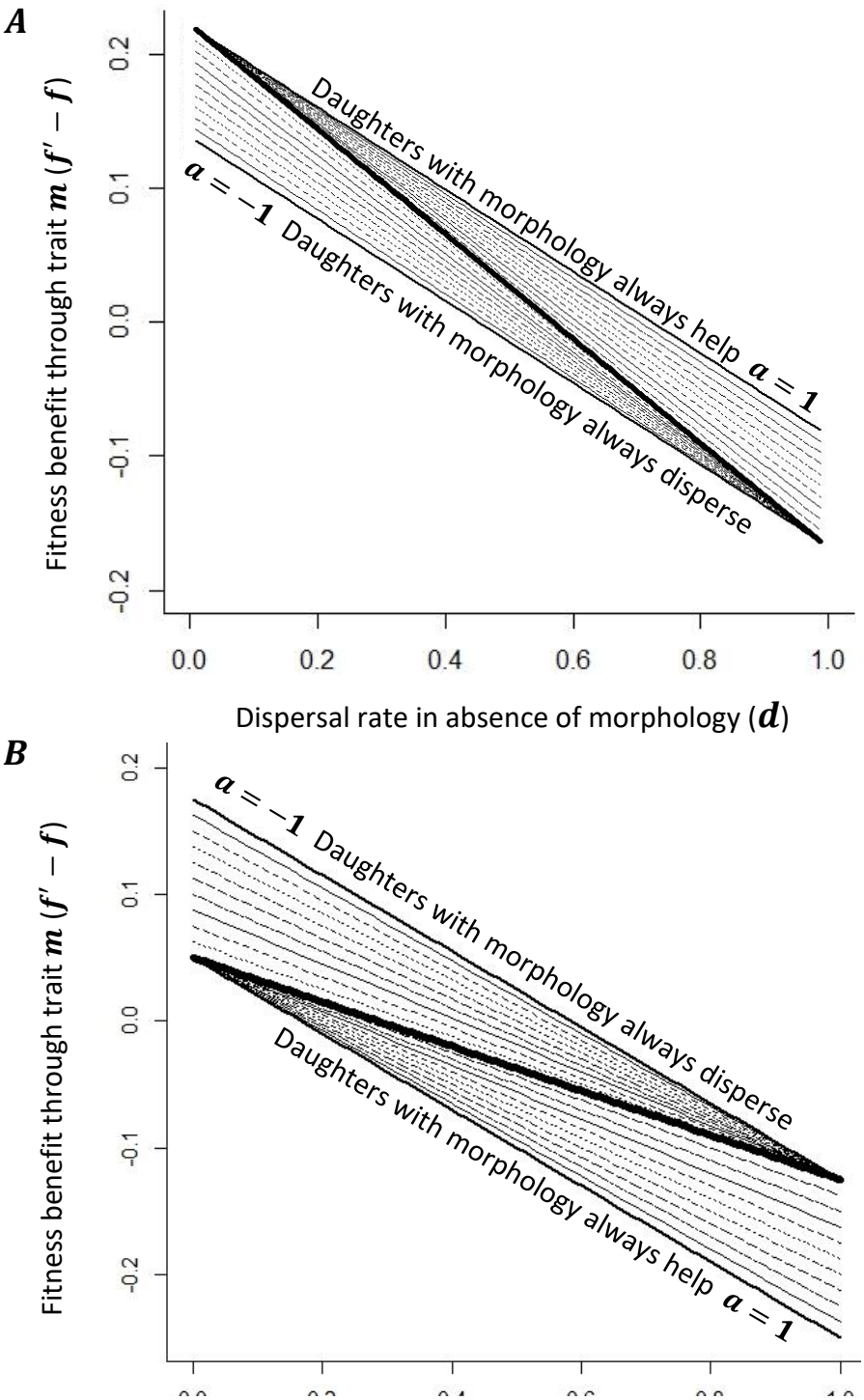

*Figure 2. The linear relationship between the net fitness increase a provisioner will receive from imparting morphological trait $\boldsymbol{m}$ onto a daughter ($\boldsymbol{f}' - \boldsymbol{f}$), and the baseline probability of a daughter dispersing (see Table 1 for parameter definitions). We have 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

The ability to respond plastically to traits can have significant impacts on individual fitness (El Mouden and Gardner, 2008). 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 indirectly obtain a degree of 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, 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 our 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.

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 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 $\boldsymbol{d}$ (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 when $\boldsymbol{d} = \mathbf{1}$ (all offspring disperse) and $\boldsymbol{a} > 0$ (Figure 2). However, it seems unlikely that daughters would have 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 Part 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).

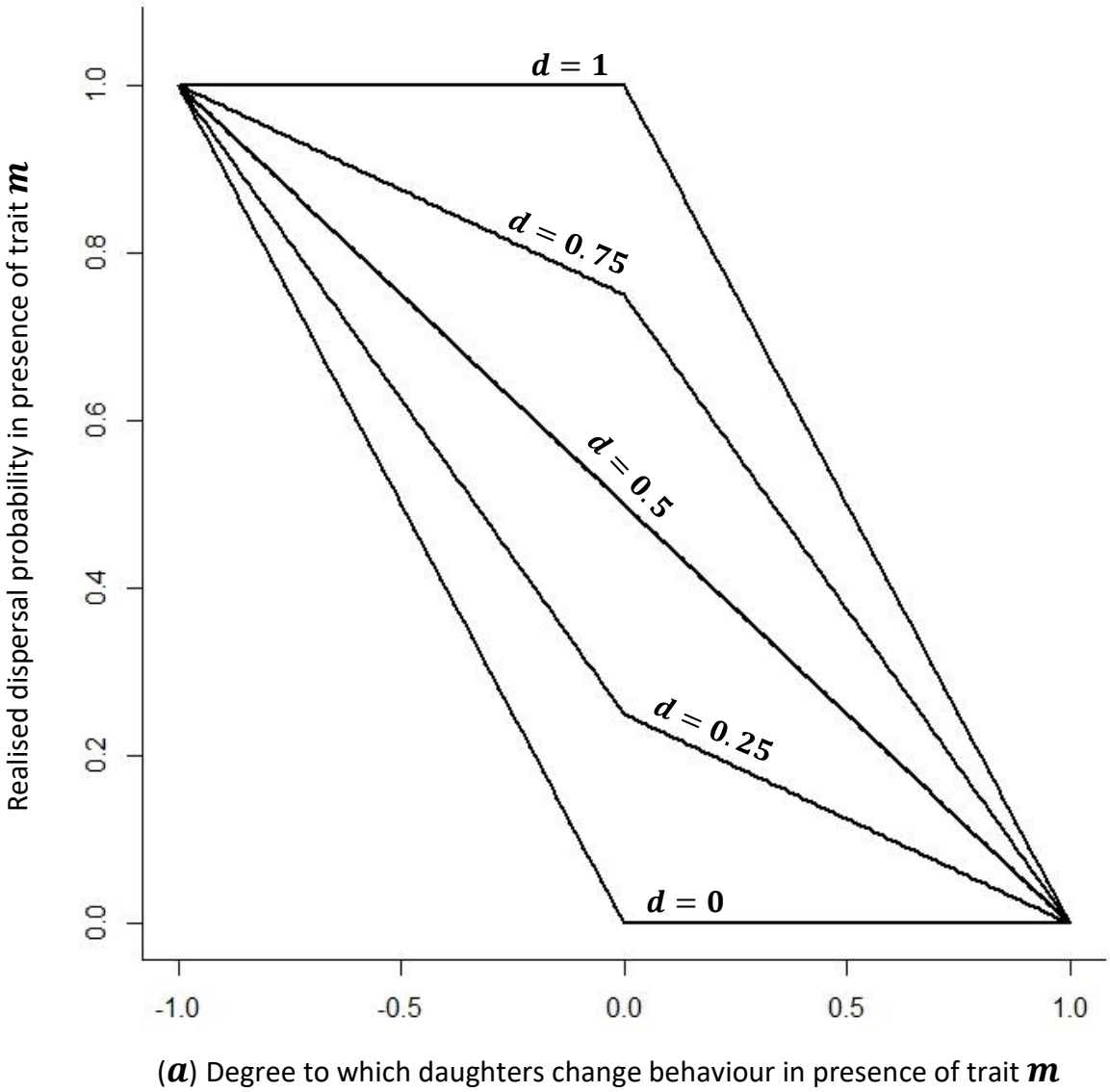

Figure 3. The relationship between a, the degree to which daughters change their dispersal behaviour in the presence of trait m, and offspring dispersal. Different lines represent different values of baseline dispersal (dispersal in the absence of trait m; $0 \leq d \leq 1$) in 0.25 increments. When $a > 0$ daughters are more likely to work, when $a < 0$ 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. Whether the relationship between size and benefit to productivity is linear (Figure 4) or increases with diminishing returns, the benefit of being a large worker ($\boldsymbol{v'_w - v_w}$) increases as the productivity of a small worker increases. We note that the productivity and fitness of a worker 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:

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

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 ($\boldsymbol{a} < -\mathbf{0.5}$; Figure 4), or the cost of producing a daughter with trait $\boldsymbol{m}$ ($\boldsymbol{c}' - \boldsymbol{c}$) 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, despite setting $\boldsymbol{v'_w} = \mathbf{2}\boldsymbol{v_w}$ (Supplementary materials Part 3).

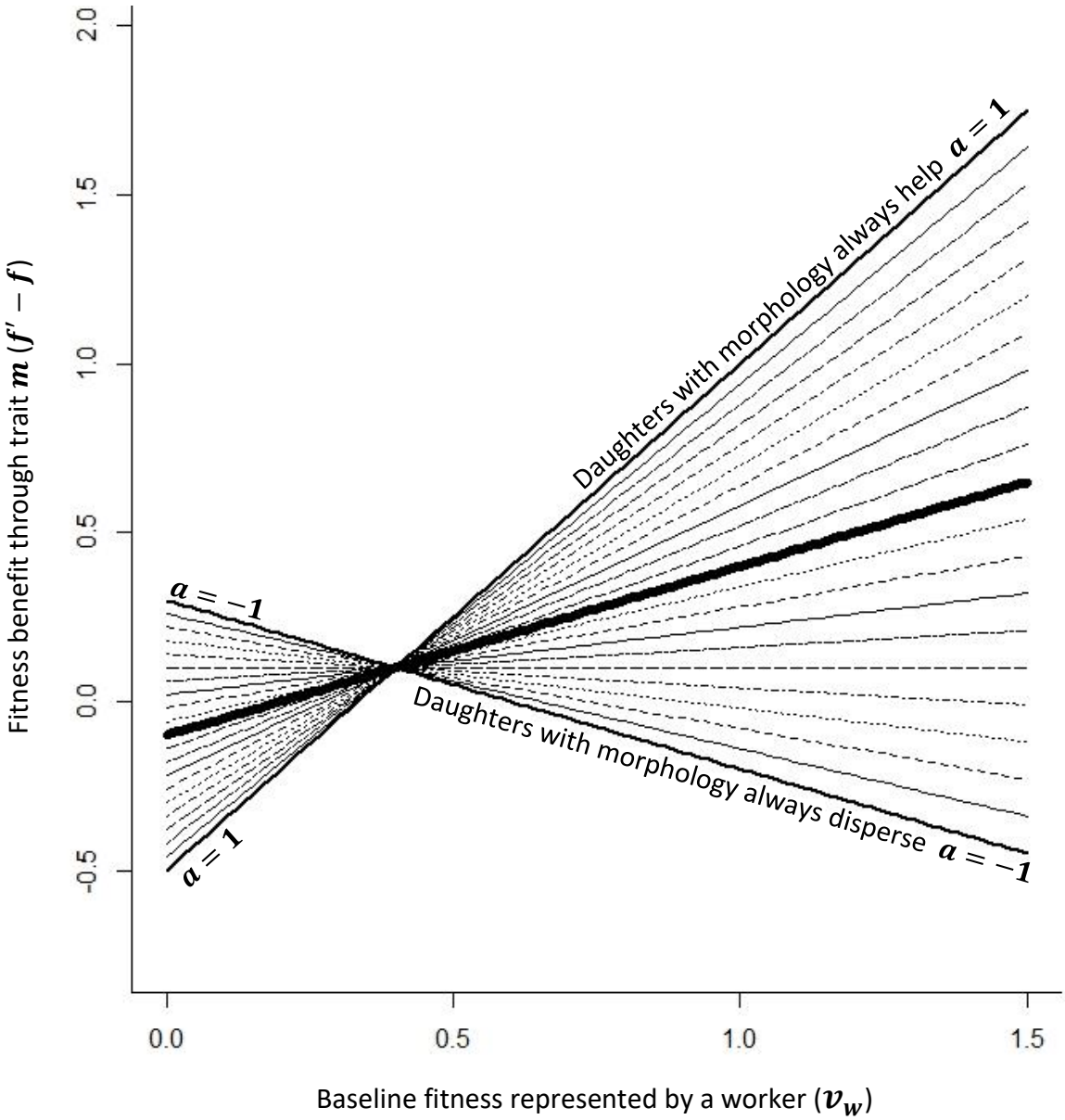

Figure 4.The relationship between the fitness of a worker in the absence of a trait and the likelihood of that trait being selected, when workers with that trait are twice as productive as those without it ($\boldsymbol{v'_w} = \mathbf{2}\boldsymbol{v_w}$). We have plotted this for $-\mathbf{1} \leq \boldsymbol{a} \leq \mathbf{1}$ at 0.1 increments with parameter values ($\boldsymbol{v'_r}$ = 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

The presence of a morphological worker caste is thought to be a key component of what qualifies eusociality as a major evolutionary transition (Boomsma, 2013). However, 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. Thus, 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 until the worker's own threshold is 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 generally 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 morphological castes, and by extension on a major evolutionary transition (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 primitively eusocial bees and wasps, where daughters from the first brood (B1) are more likely to remain at the nest as 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 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. 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 and loss of conflict between offspring and provisioners

We suggest that, 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 involves just mandibles shaped specifically for defensive or foraging tasks. Initially, offspring prefer to disperse at higher worker productivities than provisioners prefer – productivities at which provisioners would prefer them to work (Figure 5A; see Introduction. With each additional morphological specialisation the behavioural caste that an offspring chooses to join should depend more and more on its morphology: offspring 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).

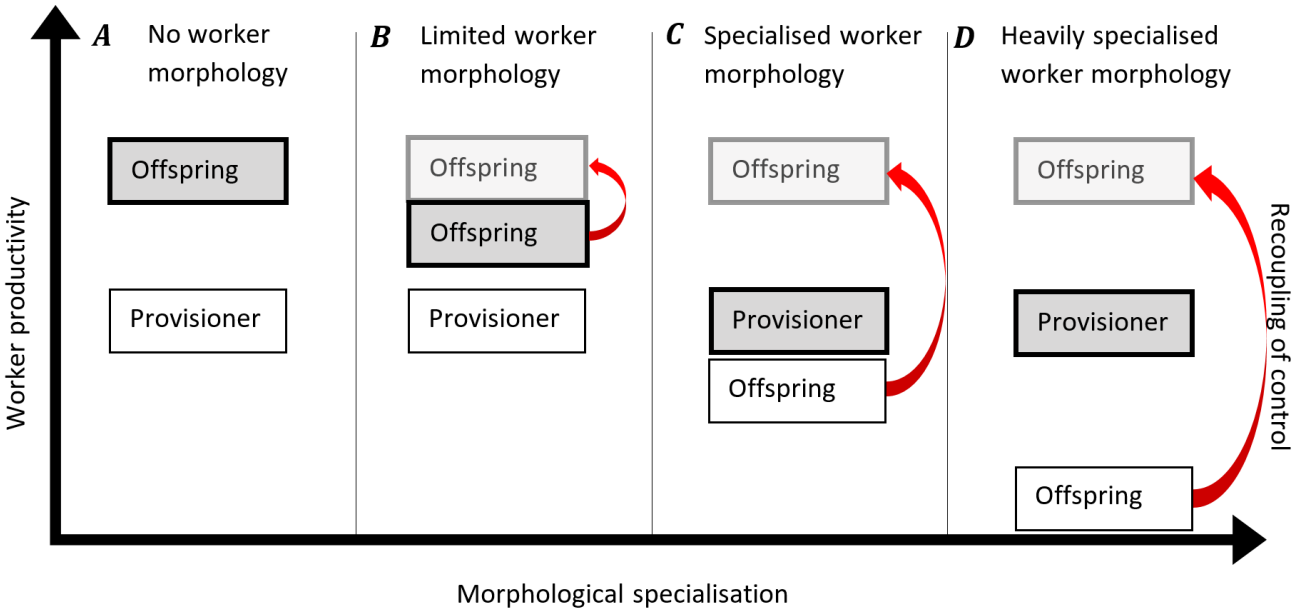

Figure 5. The relationship between the level of worker morphological specialisation and the threshold worker productivity at which offspring dispersal is favoured by two parties, offspring and provisioners. Preferences under decoupled control are represented by shaded (bold-edged) and unshaded boxes. 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.

Note, however, that 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 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 will then be provisioners, not offspring, that prefer the loss of a worker caste first during evolution. 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 (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 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. This apparently offspring controlled caste determination seen in the Meliponini (Wenseleers et al,

2003; Wenseleers and Ratnieks, 2004) could therefore represent a vulnerability to selection away from a worker caste, though other aspects of meliponine life history, such as the prevalence of swarm founding, make such a reversal unlikely.

Shared control of offspring morphology, rather than control solely by provisioners, is a possible future extension of our ideas. 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 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.

2.3.1. 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 Hymenoptera. (3) The decoupling of control over morphology and behaviour could be a key factor maintaining a morphological worker caste and could 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.

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