BIOLOGICAL ALTRUISM, EUSOCIALITY AND THE SUPERORGANISM

A critical analysis of the role of biological altruism within eusociality research

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Introduction

Today the concept of biological altruism (BA) is widely used within biological research, particularly evolutionary biology, sociobiology, and eusociality research (Cronin 1991; Dugatkin 2002; Lehmann and Keller 2006; Wilson and Wilson 2007; Ratnieks et al. 2011). Although there remains some debate over definitional issues (West et al. 2008; Wilson 2008a), the concept of BA is generally defined as a trait that causes its bearer to benefit others at a cost to itself, whereby the costs and benefits are measured as fitness consequences (Okasha 2013). This renders the concept of BA different to the common-sense notion of altruism, or what is often referred to as psychological altruism, which is necessarily to do with the intentions behind the behaviour (Sober 1994). In other words, all that is required for an individual to be altruistic (in the psychological sense) is that they behave with the *intention* to do well for another, despite the consequences. Whereas, for an individual to be considered biologically altruistic, they must exhibit a trait that causes them to benefit the fitness of others at cost to their own fitness. Thus, psychological altruism is a concept that is necessarily to do with the intentions behind behaviour, and BA is a concept that is necessarily to do with the fitness consequences of behaviour (Sober 1988).

However, the focus on fitness consequences, particularly the cost to the bearer, renders the concept of BA problematic and, even, paradoxical for evolutionary theory. A reason for this is, if natural selection typically leads to traits that increase the fitness of their bearers, how can a trait that causes a fitness cost to its bearer evolve? According to natural selection, a trait that reduces the fitness of its bearer should not be selected for. So why then, has the concept of BA become so widely used within biology? The answer to this question is that researchers believe that there are examples of BA in nature. The following are commonly conceived of as examples of BA; alarm calling in vervet monkeys (*Cercopithecus aethiops*), food sharing in vampire bats (*Desmodus rotundus*), the non-reproductive "worker" castes of eusocial insect colonies (i.e. ants, bees, termites, and wasps), and more (see Dugatkin 1997; Okasha 2013). However, it is debatable whether some of the often-cited examples are really instances of BA, this is because, for example, the cost of the trait is either short-term or only slight. This is clear in the case of food sharing in vampire bats. Food sharing regularly occurs in groups of vampire bats. Females will share food with nest mates that have failed to feed in the recent past. This is often considered as an example of BA because the female that shares food is benefitting another (the shared food ensures the survival of the bat that failed to feed) at a cost to herself by reducing her nutrition (Dugatkin 1997: 113-114; Okasha 2013). However, when studied in more detail this behaviour no longer appears to be a case of BA. It has been shown that vampire bats can recognise each other and that they typically share food with those that have given them food in the past. Thus, the food sharing behaviour appears to be an example of mutualism rather than BA; vampire bats risk the short-term costs of sharing their food in order to gain the potential benefit of receiving food in the future, if or when they fail to feed (Dugatkin 1997: 113-114).

Unlike the example of food sharing, since the inception of the concept, the non-reproductive castes of eusocial insects are widely considered as the strongest examples of BA. Eusociality is defined as colonies consisting of overlapping generations (more than one), cooperative brood care, and a reproductive division of labour where non-reproductive workers help the reproductive members (Wilson and Hölldobler 2005: 13367; Sherman et al. 1995; Crespi and Yanega 1995). The key aspect of eusociality is the reproductive division of labour; some members of the colony never reproduce but still cooperate for the colony. Thus, many authors consider the non-reproductive workers as an example of extreme BA — the workers cooperate for the colony at an extreme lifetime cost of never reproducing, or even self-sacrificing their life in the defence of the colony. The concept of BA was first introduced by J. B. S. Haldane (1932), and he argued that it is likely only possible in eusocial insects precisely due to their reproductive division of labour (Huxley 1942: 482). In other words, any behaviour of the workers that benefits the colony, even at a cost to the worker, can evolve due to the success of the reproductives (Haldane 1932: 207-210).

But authors rarely applied the concept of BA to eusocial insects after Haldane introduced it. Instead there were alternative concepts already in use. For example, the colonies-as-individuals argument and the concept of the superorganism were popular; many authors argued that eusocial colonies were higher-level individuals and consequently the non-reproductive workers were simply parts of this emergent whole, rather than being evolutionary individuals in their own right (Wheeler 1928; Emerson 1952). Another alternative was the concept of dominance, it was argued that the reproductive division of labour evolved due to the queen dominating some of her offspring into becoming non-reproductive workers (Free 1955; Free et al. 1969). It was not until the 1960s that the concept of BA was widely applied to eusocial insects, due to W. D. Hamilton (1964a, 1964b) and his theory of kin selection.

Hamilton became interested in the concept of BA in his undergraduate studies, and he devoted his PhD thesis to providing an explanation for the evolution of the trait within the framework of the Modern Synthesis (Hamilton 1996: 11-30; Segerstrale 2013: 45-77). Hamilton (1996: 20) considered the non-reproductive castes of eusocial insects as some of the strongest examples of BA. To explain the evolution of BA, Hamilton (1964a, 1964b) developed his theory of kin selection via inclusive fitness, according to which BA can evolve via selection of close relatives. Specifically, even though BA causes a cost to the fitness of its bearer if the benefits are directed to close relatives, who are likely to share the same genes, then the trait can evolve through the success of close kin — hence the term kin selection. Hamilton (1964b, 1972) conceptualised the evolution of eusociality as the evolution of BA, and used the theory of kin selection to explain its evolution.

Kin selection was considered a groundbreaking theory for evolutionary biology and has since become an integral part of evolutionary theory (West et al. 2008). It is even considered as one of the most important developments in evolutionary biology since Darwin's theory of natural selection (Queller 2001; Alonso and Schuck-Paim 2002). As a result, kin selection became the mainstream theory used to explain the evolution of eusocial insects in post-Hamiltonian eusociality research (Bourke and Franks 1995; Foster et al. 2006; Abbot et al. 2011). More importantly, the majority of authors followed Hamilton in conceptualising the evolution of eusociality as the evolution of BA (Starr 1979; Gadagkar 1990; Queller and Strassmann 1998; Wilson and Hölldobler 2005; Foster et al. 2006; Wilson 2008b; Ratnieks and Helanterä 2009; Abbot et al. 2011; Shimoji et al. 2018). For example, Ratnieks and Helanterä have pointed out that:

> The *altruism* of [eusocial] worker insects is often referred to as a Darwinian puzzle or paradox. How can natural selection, which normally favours the evolution of traits that increase an organism's reproduction, favour the reverse — *foregoing reproduction*. (Ratnieks and Helanterä 2009: 3170. Emphasis added).

The use of the concept of BA is so widespread in post-Hamiltonian eusociality research that it has resulted in an apparent conceptual monism for the description of the behaviour of the non-reproductive castes. Which, in turn, has led to the view that BA is a fundamental problem for eusociality research; i.e. the evolution of eusociality necessarily requires the evolution of BA.

Recently, J. H. Hunt (2007: 183-187) has challenged the claim that the concept of BA is a fundamental problem for eusociality research. He argued that, in fact, the widespread use of BA has impeded eusociality research because it has led to important biological factors to be ignored, e.g. phenotypic plasticity. Moreover, Hunt argued that BA is just one of multiple ways to conceptualise the non-reproductive castes, which is supported by the fact that the concept did not become widespread until after Hamilton introduced his theory of kin selection. On the other hand, F. L. W. Ratnieks and colleagues (2011), have argued that the concept of BA is a fundamental problem for eusociality research, but this went relatively unnoticed until the important work of J. B. S. Haldane (1932), Hamilton (1964a, 1964b, 1972), J. Maynard Smith (1964), and more.

Thesis objectives and methods

The aim of this thesis is to provide a critical analysis of the use of the concept of BA within eusociality research from a historical and philosophical perspective. Specifically, I will assess the following questions:

A. Is the concept of BA a correct description of the behaviour of the non-reproductive castes in eusocial insect colonies?
B. Has the widespread use of the concept of BA been problematic for eusociality research?

To do so, firstly, I will review the history and current state-of-the-art of the concept of BA and its use within eusociality research. Specifically, I will assess when and why the concept became so widespread within eusociality research, as well as the effect it has had on the field. In the first three chapters, I will challenge the following three common-place claims from the literature about the concept of BA and eusociality research:

(1) That BA *is* a fundamental issue in eusociality research
(2) That BA *has been* a fundamental issue in eusociality research since Darwin
(3) That Darwin discussed and/or developed the concept of BA and its associated paradox

Claim (1) represents the current mainstream view that the evolution of eusociality necessarily requires the evolution of BA. I will challenge the philosophical and empirical groundings for this claim, in chapter 3, in order to assess whether the concept of BA is a correct description of the behaviour of the worker castes. But before that, in chapters 1 and 2, it will be helpful to address the history of the concept in chapters 1 and 2. Claims (2) and (3) are historical claims that are often employed in order to justify claim (1), thus challenging this claims will undermine the historical grounding for the current widespread use of the concept of BA in eusociality research. Moreover, by assessing the history of the use of BA within eusociality research I will also assess whether the widespread use of the concept has been problematic for the field. For example, whether the mainstream conceptualisation of the evolution of eusociality as the evolution of BA led to the decline of viable alternatives, such as parental manipulation theory, or the superorganism.

Furthermore, the concept of BA primarily an evolutionary concept; it denotes a trait that causes a fitness cost to the bearer and fitness benefits to individuals it interacts with. It is a concept that suited the gene-centrism of the Modern Synthesis. In other words, the fact that BA could potentially describe a set of behaviours that appear to be contrary to the logic of natural selection, in terms of fitness consequences, was appealing to authors. The concept became widely used due to the success of kin selection theory. The widespread use of the concept of BA, in turn, led to the prominence of evolutionary approaches to the study of eusociality; the debate between kin selection and group selection as the best explanation for the evolution of BA in eusocial insects. However, whilst the evolutionary aspects of eusocial insect colonies are important (e.g. the transition from selection of reproductives to selection of colonies) the physiological/ontogenetic aspects are as equally important. For example, the relations and interactions between the members of the colony are important to understand the proximate causes for the functional integration that enables colony selection. Therefore, the aim of this thesis is *not* to argue against evolutionary approaches to the study of eusociality. Instead, the aim of the thesis is to provide an argument *against the current widespread use of the concept of BA within the field*.

Consequently, finally in chapters 4 and 5, I will assess in more detail the colonies-as-individuals arguments, namely the superorganism. I will argue that the superorganism, which was once very prevalent in the field, saw a radical decline due to the widespread use of the concept of BA. It has seen a recent resurgence due to the emergence of new group selection and research into the evolutionary derived (or complex) eusocial species. But currently the superorganism is also approached from an evolutionary perspective only — group selection is used to assess whether colony selection occurs within a species. In other words, authors argue that if a colony is the unit of selection then it is an evolutionary individual; i.e. a superorganism.

This is due to the prevalence of evolutionary approaches, i.e. kin selection and group selection, in eusociality research in general. However, the superorganism was originally also used from a physiological perspective. I will, therefore, develop an organizational approach — namely, the *hierarchical-organizational* approach — for the explanation of the functional/ontological aspects of colony organization, with the aim of providing further evidence against the widespread use of the concept of BA. Specifically, by using representative case studies of three eusocial insect species, I aim to show that there is no evidence that the behaviour of the workers is a case of BA.

Eusociality was once thought to be limited to insects, such as ants, bees, termites and wasps, but it has recently been discovered in a few other species such as naked mole rats and some shrimp (Duffy 1996; Wilson and Hölldobler 2005). However, I will focus on eusocial insects because, not only is eusociality much more prevalent in insects (Wilson 2008b), they have historically been the primary focus of eusociality research.

Overview of chapters

I will begin, in *chapter 1 — Altruism and eusocial insects: a brief history*, by reviewing the history of the concept of BA and eusociality research. The aim of this chapter is to trace the history of the concept of BA and to assess when and why this concept became so widespread within eusociality research. In other words, I will critically assess claim (2), ultimately arguing that it is incorrect. In section 1, I will review the history of the concept of BA. I will show that it was developed in 1932 by Haldane but I will argue that its associated paradox did not become apparent until the 1960s, due to the levels of selection debate. In section 2, I review the history of the concept of BA within eusociality research. I will argue that the concept did not become widely used until the 1960s as a result of the groundbreaking theory of kin selection developed by Hamilton. I will assess why Hamilton applied kin selection theory to eusocial insects. I will argue that he applied kin selection to eusocial insects because he rejected the colonies-as-individuals argument, which was previously prevalent. I argue that Hamilton rejected the colonies-as-individuals argument because he already considered eusocial insects as examples of BA. I will argue that Hamilton applied the concept of BA to eusocial insects due to the Sturtevant-Hamilton problem of sterility. I argue that the concept of BA became so widespread within eusociality research due, in part, to a lack of re-assessment of the Sturtevant-Hamilton problem of sterility. I do so by comparing the use of the concept of BA in pre- and post-Hamiltonian eusociality research. I conclude by arguing that the widespread use of the concept of BA is problematic for eusociality research for multiple reasons, which I explore in later chapters. Mainly, it led to a conceptual monism and lack of research into alternatives (chapters 3, 4, and 5), some of which were prevalent prior to Hamilton. Moreover, it has led to inaccurate historiographies of the field (chapter 2), and multiple definitions of the concept in use (chapter 5), both of which reinforce the widespread use of the concept.

In *chapter 2 — Biological altruism: history justified by theory, theory justified by history*, I will critically assess claim (3) — that Darwin discussed and/or developed the concept of BA. I will argue that, not only is this claim inaccurate, but that it is the result of the current widespread use of the concept of BA. I begin, in section 1, by reviewing Darwin's argument for the evolution of morality in *The Descent of Man*, and his treatment of the evolution of eusociality in *On the Origin of Species*, both of which are typically cited by authors who argue for claim (3). I argue that Darwin's concept of morality is not the same as the concept of BA. More importantly, Darwin's "special difficulty" with eusocial insects was not the concept of BA; instead, this "special difficulty" referred to the problem of how individuals that do not reproduce (the worker castes) evolved physiological and behavioural traits that are different to the reproductive castes. Thus, I will argue that Darwin did not discuss or develop the concept of BA (even under an alternative name). I then assess why claim (3) emerged, and argue that it was a result of the current conceptual monism of BA. In other words, because of the current mainstream view that evolution of BA is necessary for eusociality to evolve, many authors typically view the history of eusociality research from the same perspective. To further support this argument, in section 2, I will argue that Darwin's solution to the "special difficulty" and his argument for the evolution of eusociality are also invoked by authors in the current debate over the evolution of eusociality. Specifically, some authors have claimed that Darwin argued for group selection, whereas others have claimed that it was an early version of kin selection via worker BA. However, I argue that, not only are both interpretations inaccurate, but that they have the effect of adding historical weight to current theoretical perspectives. Consequently, I conclude that, within post-Hamiltonian eusociality research, current theoretical perspectives have affected historical claims on the concept of BA and, in turn, the resulting inaccurate historical claims have been used by researchers in order to justify their current theoretical perspectives.

In *chapter 3 — Evolutionary theories of eusociality: is BA fundamental?*, I will assess the current role of BA in eusociality research. Specifically, I will assess claim (1) — that BA is a fundamental problem for eusociality research. In section 1, I address some definitional issues with the concept of BA. I will argue that the focus on the explanatory models of BA (kin selection and group selection), and a lack of focus on the concept itself, has led to multiple definitions in use. Firstly, I argue the "weak BA" (the definition preferred in group selection models) is not true BA because it defines the fitness consequences relatively — with respect to the focal individual's group. Even though weak BA reduces the fitness of its bearer within its group, it can only evolve by increasing the absolute fitness of its bearer (via group selection), thus it is a form of mutualism rather than true BA. Secondly, I argue that the mainstream definition, preferred by kin selection theorists, is potentially vacuous because it defines BA in terms of fitness consequences alone: a trait that causes negative selection to the focal individual and positive selection to individual(s) that it interacts with. However, I argue that other traits, particularly coercion, could also fit this definition; coercion could cause negative selection on the focal individual and positive selection to another (i.e. the coercer). Therefore, I will propose a definition of BA with the added clause that the cause of the fitness consequences must derive from a trait possessed by the focal individual. In section 2, I will review the mainstream theories for the evolution of eusociality, kin selection and group selection (MLS2), and the role of BA within them. Specifically, I will examine whether the concept of BA (according to the definition I propose) is necessarily required by either of the theories to explain eusociality. Additionally, I will assess if there is any evidence to support the application of BA to eusociality. I will argue that only kin selection is applicable with the concept of BA, whereas group selection is only compatible with weak BA. But, I will highlight that there is a lack of empirical evidence to support the application of BA to the non-reproductive castes, in fact, recent evidence supports the alternative claim that offspring are coerced into the non-reproductive worker castes via parental manipulation. Thus, I will argue, similarly to Hunt, that the concept of BA is not a fundamental problem for eusociality research, contrary to claim (1). Moreover, that in fact, current evidence suggests that it is an incorrect description of the non-reproductive castes.

In *chapter 4 — The superorganism: from the past to the present*, I will assess in more detail an alternative to the concept of BA, namely the superorganism argument. Specifically, I will review the history and current state-of-the-art of the superorganism concept. Due to certain organizational properties — such as the reproductive division of labour, extreme cooperation, polymorphism, etc. — eusocial insect colonies have long been considered as biological individuals in their own right. I will highlight how the concept of the superorganism was originally approached from an evolutionary and a physiological perspective. In other words, it was used to argue that eusocial insect colonies are higher-level biological individuals in the fullest sense of the term. I will then assess the decline of the concept in the 1960s, highlighting the prominent role of kin selection and the concept of BA in its decline. I will then introduce the notion on eusociality complexity spectrum. This is the notion that there is qualitative differences in colony organization across eusocial insects; whereby in the large colonies of the most complex species (typically the evolutionary derived species), colony organization and cohesiveness are the result of a network of interactions among the members. I then argue that research into complex eusocial insects, as well as the emergence of new group selection, led to the revival of the superorganism in post-Hamiltonian eusociality research. However, the concept is currently understood using an evolutionary perspective of biological individuality. Consequently, today the concept is used to denote colonies that are units of selection; i.e. evolutionary superorganisms. Finally, I will assess why the superorganism is no approached from a physiological perspective of biological individuality, as was done so historically. I will argue that this is the result of the problem of hierarchy. It is often presupposed that top-down hierarchical control does not occur in the large colonies of the most complex eusocial insect species. Thus, this led to the mainstream view that colony cohesiveness is the result of flat self-organization in complex species. As a result, current explanatory approaches that focus on the physiological and proximate causes for colony cohesiveness (i.e. the actual organization) are centred around the concept of self-organization — which I will refer to as the self-organization (SO) approach. Finally, I will conclude that whilst the evolutionary notion of the superorganism is useful, particularly for an etiological perspective, it cannot assess the organizational differences across colonies of different species.

Consequently, in *chapter 5 — Revising the superorganism: the hierarchical-organizational approach to complex eusociality*, I will argue the presupposition that hierarchical control does not occur in the large colonies of complex eusocial insects needs to be reassessed. I argue that this claim should be assessed theoretically and empirically rather than assumed *a priori*. To do so I will develop an alternative organizational approach (the *hierarchical-organizational* approach) that assesses if there is hierarchical organization within complex colonies, that "modulates" (i.e. regulates and controls on) the self-organized dynamics within the colony system; i.e. this approach will be able to assess if colony organization is the result of self-organization only or *also* and *mainly* due to hierarchical regulation and control. I will also argue that this approach would be better suited to assess the issue of whether complex eusocial insect colonies should be considered biological individuals or not. This is because if there are colonies with hierarchical organization then an argument can be made that the colony is in "control" rather than the insects that instantiate it, i.e. the colony organization is not solely the result of self-organization but a higher-level organization that exerts top-down control on its parts. In other words, if there is evidence of hierarchical-organization within colonies of eusocial insects, then this would be evidence for the superorganism from a physiological-like perspective, as well as an evolutionary perspective of biological individuality. In section 1, I review a recent physiological approach to colony individuality, namely the "social physiological" approach. I argue that whilst the "social physiology" approach is interesting, it may not be suitable for assessing the different types of individuality at the colony level across eusocial insects because it focuses primarily at the genetic level. Consequently, I further develop the *hierarchical-organizational* approach in order to assess the types of colony individuality across species of eusocial insects. In section 2, I apply this approach to three representative case studies from across the eusocial insect complexity spectrum: *Megalopta genalis*, *Vespula vulgaris*, and *Apis mellifera*. Finally, in section 3, I assess the different types of colony individuality, if applicable, in the three case studies. I conclude that it is likely that colonies of the most simple eusocial insect species (e.g. *M. genalis*), that exhibit facultative eusociality, are not superorganisms in any sense. Colonies of species in the mid-range of the complexity spectrum (e.g. *V. vulgaris*), are likely to be evolutionary superorganisms because they are units of selection, but not physiological-like superorganisms because they exhibit only a minimal form of hierarchical-organization. But colonies of the most complex species (e.g. *A. mellifera*) are likely to be superorganisms in the fullest sense, i.e. evolutionary and physiological-like individuals, due to their hierarchical-organization. In section 4, I will highlight how the superorganism argument provides a further evidence against the claim that the non-reproductive castes in eusocial insects are example of BA.

Finally, in the *conclusions*, I will summarise how I addressed the main research questions within the thesis: has the widespread use of BA been problematic for eusociality research? Is BA the correct description of the non-reproductive castes? I will show that the widespread use of BA has been problematic for eusociality research. Firstly, because the widespread use of BA led to inaccurate historiographies of the concept. Many authors have often viewed the history of eusociality research to be centred around the problem of BA, due to the current conceptual monism of BA in post-Hamiltonian eusociality research. I argued that this is not only a problem of historical accuracy, the claim that BA has been a fundamental problem for eusociality research since Darwin had the effect of reinforcing the current widespread use of the concept. Moreover, the widespread use of the concept of BA, and the subsequent inaccurate historiographies of eusociality research, led to a lack of focus on possible alternatives. Alternatives such as the superorganism, coercion, parental manipulation, phenotypic plasticity, etc. should receive more attention by current researchers. The conceptual monism of BA was also problematic because it resulted in multiple definitions of the concept in use. Because of the view that BA was necessarily required for the evolution of eusociality, authors typically altered the concept to fit their theoretical models rather than seeking alternatives. Not only has the widespread use of the concept of BA been problematic for eusociality research, I will conclude that it is likely to be an incorrect description of the behaviour of the non-reproductive castes. I argue that only kin selection is compatible with the concept of BA that I proposed; group selection is only compatible with weak BA, which is a form of mutualism, not BA. However, I argue that there is a lack of evidence that eusociality evolved due to worker BA. Recent evidence supports the parental manipulation perspective; that eusociality evolved due to parental coercion. Furthermore, based on the findings in chapter 5 – where I developed the hierarchical-organizational approach (HO) to assess the development and maintenance of the actual organization within colonies – I will argue that it is clear that members of the colony develop into the non-reproductive worker role due to coercion and hierarchical control; they do not do so because of a trait that they possess (i.e. BA) that causes them to attempt to increase their inclusive fitness by becoming non-reproductive workers. Finally, I will address some implications of this thesis.

Chapter 1 — Altruism and eusocial insects: a brief history

Introduction

Biological altruism (BA) is generally understood as a trait that causes an individual to benefit others at a cost to itself, whereby the costs and benefits are measured in terms of fitness consequences (Okasha 2013). Today, the concept of BA is widely used within evolutionary biology, sociobiology and particularly eusociality research. Eusociality is defined as colonies consisting of overlapping generations (more than one), cooperative brood care, and a reproductive division of labour where non-reproductive workers help the reproductive members (Wilson and Hölldobler 2005: 13367; Sherman et al. 1995; Crespi and Yanega 1995). It is commonly argued that the non-reproductive castes of eusocial colonies are the most extreme examples of biological altruism because they do not reproduce their own offspring, but they help others to do so (Gadagkar 1990; Cronin 1991; Hamilton 1996; Lehmann and Keller 2006). BA is paradoxical for evolutionary theory, however, because a trait that causes a cost to its bearer should not be selected for under natural selection (Gadagkar 1990; Cronin 1991). Thus, because the worker castes of eusocial colonies typically never reproduce and work for the benefit of the reproductives within their colonies, they are often viewed as strong examples of this paradox; how did the worker castes evolve if they do not reproduce? The use of the concept of BA within eusociality research is so widespread that the evolution of eusociality is often equated with the evolution of BA (Hamilton 1972; Starr 1979; Gadagkar 1990; Queller and Strassmann 1998; Dugatkin 2002; Wilson and Hölldobler 2005; Foster et al. 2006; Wilson 2008b; Ratnieks et al. 2011). This view has led to three independent but related claims, being made within the literature about BA and its role within eusociality research:

(1) That BA *is* a fundamental issue in eusociality research

(2) That BA *has been* a fundamental issue in eusociality research since Darwin

(3) That Darwin discussed and/or developed the concept of BA and its associated paradox

Claim (1) is related to the main aim of this thesis — i.e. the challenge the widespread use of the concept of BA within eusociality research — and claims (2) and (3) are used to give historical weight to claim (1). Consequently, it will be useful to critically explore claims (2) and (3) in order to assess the historical groundings for the current widespread use of BA within eusociality research. Therefore, in this chapter and the next, I will explore claims (2) and (3) in order to provide a stronger argument against claim (1) throughout this thesis.

The aim of this chapter is to trace the history of the concept of BA and to assess when and why this concept became so widespread within eusociality research. In other words, I will critically assess claim (2), ultimately arguing that it is incorrect. I will begin, in *section 1*, by providing a history of the concept of BA, when it emerged, and how it differs from the original psychological notion of altruism. In doing so, I will also highlight how the concept of altruism, within biology, went from a general term used for social behaviour that was interchangeable with cooperation and morality to what we know today as biological altruism, which is essentially about fitness costs and benefits. I will argue that the BA paradox did not emerge until at least the 1960s, due to the debate over the levels at which natural selection can operate (the levels of selection debate). It was only after the emergence of this paradox that BA became a major problem for evolutionary biology, a problem highlighted by W. D. Hamilton. Then, in *section 2*, I will argue that the widespread use of BA within eusociality research was ultimately due to the influence of Hamilton and his groundbreaking theory of kin selection. Firstly, I will assess why Hamilton applied *kin selection* to eusocial insects, and argue that he did so not just because of the debate over the levels of selection, as is commonly claimed, but also because he rejected previous ideas of eusocial colonies as a form of biological individuality. Importantly, I will show that Hamilton rejected the colonies-as-individuals argument *because* he already viewed the non-reproductive worker castes as examples of BA *prior* to developing kin selection. Thus, I will then assess why Hamilton applied the *concept of BA* to eusocial insects, and I will argue that he did so because of the Sturtevant-Hamilton problem of sterility. Finally, I will argue that the concept of BA became so widespread in eusociality research due, in part, to an uncritical assessment of the Sturtevant-Hamilton problem of sterility. I will do so by comparing the use of the concept of BA in pre- and post-Hamiltonian eusociality research. I argue that the widespread use of the concept of BA was problematic because it led to a lack of focus on possible alternatives, such as parental manipulation.

1.1. Altruism, psychological and biological

1.1.1. Altruism

The term altruism was coined by the French philosopher August Comte, and his colleagues, in the 1830s (Allee et al. 1949). Its meaning then was what is considered today as psychological or vernacular altruism, which is the common-sense meaning of the word. Psychological altruism, in this sense, denotes unselfish (or disinterested) behaviour or the concern for the well being of others (Sober 1988). This meaning of altruism is necessarily related with intentionality and not with the outcomes of behaviour, i.e. regardless of the outcome, if someone intended to do well for another then that is altruism (Sober 1988).

The concept of altruism was initially rarely used in biology. On the rare occasions that it was used, it was intended to mean something like cooperation, i.e. to denote behaviours that were social, as opposed to selfish or egoistic behaviours (Geddes and Thompson 1889; Headley 1900; Wheeler 1911; Patten 1920; Kellogg 1922: 57). This could be because altruism, in the original sense from Comte, was about the *intention to do good for another* and therefore was understood from a psychological perspective. But in biology, behaviours were generally considered instinctive and not discussed in psychological terms (expect in rare cases, see Darwin 1874; Geddes and Thompson 1889; Patten 1920. Or for certain human behaviour, see Headley 1900; Kellogg 1922). The concept of altruism did not, therefore, initially gain widespread usage within biology.

1.1.2. Biological altruism

When J. B. S. Haldane (1932) talked of sociality his focus was on traits that are beneficial to society but costly to the individual that bears them:

> It can be shown mathematically that in general qualities which are valuable to society but usually shorten the lives of their individual possessors tend to be extinguished by natural selection in large societies unless these possess the type of reproductive specialisation found in social insects. (Haldane 1932: 130).
>
> In the case of the social insects there is no limit to the *devotion and self-sacrifice* which may be of biological advantage in a neuter. (Haldane 1932: 207-208. Emphasis added).

Both of the above quotes highlight why Haldane (1932: 131, 207-210) used the term ‘altruism’: because he was specifically referring to an extreme form of cooperation that causes an individual to benefit its group/society at a cost to itself, i.e. *the extreme ‘self-sacrifice’ of individuals for others*. In a section entitled ‘Socially Advantageous but individually Disadvantageous Characters’, Haldane (1932: 207-210) provided an argument for how such “self-sacrificing” altruistic behaviours could evolve under natural selection. However, in focusing on this type of extreme cooperation and referring to it as altruism, Haldane inadvertently created a concept that was distinct from psychological altruism. Whereas psychological altruism is to do with the conscious intentions behind the behaviour, the biological altruism (BA) that Haldane developed is about the cost and benefits of instinctive behaviour (Sober 1988, 1994; West et al. 2007).

Additionally, what the quotes above from Haldane show is that, from its beginning, eusocial insects were the main example of BA. This is because the worker castes (i.e. non-reproductive castes) in eusocial colonies help the reproductive ones, but they do not reproduce their own offspring. Therefore, they were described by Haldane (1932: 207-210) as being completely devoted to the colony at the expense of their own reproductive fitness. However, Haldane appeared to imply that this type of “altruism”, *in eusocial insects*, is not a problem for evolution because of the reproductive division of labour:

> In a beehive the workers and young queens are samples of the same set of genotypes, so any form of behaviour in the former (however suicidal it may be) which is of advantage to the hive will promote the survival of the latter, and thus tend to spread through the species. (Haldane 1932: 208).

In other words, the workers can afford to sacrifice themselves because of the reproductives reproducing their kind for them, *due* to the reproductive division of labour in the colony. Even though Haldane used the term ‘same set of genotypes’ here, I do not think he argued that the members of the colony are genetically identical, but rather that they are closely related and all products of the same reproductives, namely, they share very similar genotypes.

It is often claimed that Darwin discussed and/or developed the concept of BA (claim 3), which if true would mean that the concept is much older than Haldane’s work. Firstly, it is often claimed that Darwin (1859: 175-180) considered eusocial insects as a serious problem to his theory of natural selection because workers do not reproduce but help the reproductive(s) to do so — i.e. BA — (Cronin 1991; Ratnieks et al. 2011). However, this claim is incorrect, Darwin actually considered eusocial insects as a serious challenge to his theory because of the *polymorphism that has evolved among the non-reproductive castes* (Richards 1981, 1983; Hunt 2007: 183-187; Ratnieks et al. 2011). In other words, Darwin initially found it difficult to explain the fact that, despite not being able to reproduce, workers in some species have evolved to be morphologically distinct to the reproductive castes. However, Darwin did not consider the fact that some workers do not reproduce to be a serious issue (Richards 1981, 1983; Prete 1990). Secondly, it is also claimed that Darwin’s (1874: 129-183) discussion of the evolution of morality in humans is analogous to the more recent discussion of the evolution of BA (Wilson and Wilson 2007). However, this is also an incorrect reading of Darwin; the concept of morality employed by Darwin is more similar to psychological altruism rather than biological altruism (chapter 2). In the next chapter I will argue in more detail that Darwin did not discuss and/or develop the concept of BA. In doing so, I will also explore how such claims about Darwin are used in order to add historical weight to current theoretical perspectives.

1.1.3. The BA paradox and the levels of selection debate

The concept of BA is, by definition, paradoxical for evolutionary theory (Cronin 1991; Sober 1994; Alonso and Schuck-Paim 2002; Wilson and Wilson 2007; Chancellor 2015); how can a trait that causes a long-term cost to its bearer evolve? The paradoxical nature of BA did not become apparent, however, until around the 1960s, as I will now explain. Initially, most non-individualistic or social behavioural traits were grouped under the broad concept of cooperation and not seen as a problem for evolutionary theory (Allee et al. 1949). It has been argued that the costs of cooperative traits were not correctly taken into account because many biologists held the now outdated good-for-the-species view (Cronin 1991: 174-183). According to this view, adaptations are for the benefit of the species as well as the individual (Allee et al. 1949: 602-605). As a result, potentially costly traits, e.g. BA, are not problematic and can still evolve so long as they benefit the species, even if they cause a cost to their bearer. Consequently, many traits that are now considered to be examples of BA, such as alarm calling in vervet monkeys (and many bird species), or food sharing in vampire bats, etc., were considered as examples of regular cooperation (Cronin 1991). As a result, initially the concept of BA was not widely used by biologists after its inception.

Furthermore, when the concept of BA was used, authors employed the theory of (old) group selection to argue for its evolution (Sturtevant 1938; Williams and Williams 1957). Original proponents of group selection argued that selection between groups can explain the evolution of potentially costly cooperative traits (Hamilton 1963; Wilson and Wilson 2007). Even though BA causes a cost to its bearer, it also causes its bearer to benefit others. If those benefits are directed to the bearer’s group, the group will then collectively benefit from the trait (BA) even though it is costly to the individual. Consequently, groups with more altruists will be more successful than groups with less altruists, due to the increased group-benefits in the former. In other words, it was argued that even though BA is costly for its individual bearer, it is good for the group.

It is interesting to note at this point that J. B. S. Haldane (1932: 207-210) argued that the evolution of his concept of BA is likely only possible in eusocial insects precisely because of their reproductive division of labour (Huxley 1942: 482). Haldane explored the possibility of BA evolving within groups where all members reproduce, i.e. groups that do not have a reproductive division of labour, but seemed to conclude that BA would be unlikely to evolve in this scenario:

> When we pass to small social groups where every individual is a potential parent, matters are complicated. (Haldane 1932: 208)

> But it is hard to see how such behaviour [BA] could become congenitally fixed in a species which did not practise reproductive specialisation [reproductive division of labour]. (Haldane 1932: 131).

Haldane, then, also used group selection to argue for the evolution of BA, but he argued that BA would only successfully evolve in specific types of groups — i.e. those with reproductive specialisation (e.g. eusocial colonies).

Thus, initially, the paradoxical nature of BA was not made apparent by authors because of 1) the good-for-the-species view, which argued traits evolved for the good of the species as well as the good of individuals, and 2) the use of group selection as an argument for the evolution of BA. However, in the 1960s these ideas began to be challenged, and a major debate emerged over the levels at which natural selection can operate, i.e. individual versus group selection — which is commonly referred to as the *levels of selection debate* (Cronin 1991; Wilson and Wilson 2007; Chancellor 2015). Compelling arguments were made against the efficacy of group selection as a cause of evolutionary change (Hamilton 1963; Maynard Smith 1964; Williams 1966; Wilson and Wilson 2007). For example, it was argued that inter-group selection, although theoretically possible, was unlikely to be evolutionary significant because intra-group selection (individual selection in the classical sense) operates at a higher tempo and would undermine inter-group selection (Hamilton 1963; Wilson and Wilson 2007). As a consequence, any form of higher-level selection was widely rejected by biologists (Cronin 1991; West et al. 2007). This meant that it was no longer possible to explain the evolution of BA by appealing to group selection. Consequently, if group selection cannot explain the evolution of BA, then this concept becomes a major issue for evolutionary biology: for a trait to evolve by natural selection if must confer a fitness benefit (or at least no cost) to the individual, so how can a trait that causes a long-term fitness cost to the individual evolve? This line of argument was not only applied to BA; cooperative behaviours in general began to be considered a problem for evolutionary biology (Cronin 1991). Any behaviour that does not directly benefit the individual itself is potentially costly, therefore seems to contradict natural selection (Hamilton 1963).

In response to the initial rejection of group selection, W. D. Hamilton (1963, 1964a, 1964b, 1972, 1975, 1996) developed his hugely influential inclusive fitness theory, which provided an answer to the evolution of cooperation and BA that was based on individual selection not group selection. The key observation by Hamilton (1963, 1964a) was that the degree of genetic relatedness between full-siblings is on average the same as it is between parent and offspring, i.e. full siblings are just as likely to share specific genes as are parent and offspring. Therefore, he argued that individuals may do just as well investing energy and resources aiding their siblings (cooperation) as they would by aiding their offspring (parental care). This principle is what Hamilton (1964a) referred to as inclusive fitness. Specifically, inclusive fitness refers to the sum of an individual's direct and indirect fitness — where *direct fitness* equals the individual's success in personal reproduction, and *indirect fitness* equals 'the component of fitness gained from aiding the reproduction of related individuals' (West et al. 2007: 416). Hence the name "kin selection" given to this theory by J. Maynard Smith (1964).

Hamilton (1964a, 1964b) argued that the evolution of BA can be explained by his inclusive fitness model. A main component of the inclusive fitness model is what is now referred to as Hamilton's rule (Birch and Okasha 2015). Hamilton's rule is defined as $rb > c$ — where r equals the coefficient of relatedness, b the benefit to the recipient, and c the cost to the focal individual (Birch and Okasha 2015). Following Hamilton's rule, BA can evolve via natural selection if the cost to the focal individual is outweighed by the benefit to close relatives; $rb > c$. In other words, even though BA causes a long-term fitness cost to the focal individual, the gene for this trait can evolve in the population if the trait is differentially expressed, the benefits are directed at closely related individuals, and furthermore, the benefits to the relatives are significantly greater than the cost to the focal individual (for more details and different conceptions of the rule see Birch and Okasha 2015). Hamilton's focus on the concept of BA led to more attention being paid to the concept by biologists, as a result, the concept of BA became much more widely used within evolutionary biology from the 1960s (Barash 1992; Hunt 2007).

The levels of selection debate did not dissipate, however, and it continues to be an important debate within evolutionary biology (West et al. 2008; Wilson 2008a; Nowak et al. 2010; Abbot et al. 2011; Wilson and Nowak 2014; Birch and Okasha 2015). This is because, around the 1980s, authors once again argued for higher level selection and new forms of group selection (Damuth and Heisler 1988; West et al. 2007; Reeve and Hölldobler 2007; Wilson and Wilson 2007; Gardner and Grafen 2009). In the new approach, the idea of group selection differed markedly from old group selection. Old group selection argued that when selection occurs at the group level, traits evolve for the good of the group, i.e. selection does not occur below the level of the group when the group becomes the unit of selection (West et al. 2007). Whereas, new group selection was based on the notion of multi-level selection (MLS), i.e. the idea that selection occurs at multiple levels simultaneously: e.g. at the levels of the gene, cell, cell aggregate, multicellular organism, group, population, etc. MLS is based on the Price equation, which divides gene frequency change within a population into within- and between-group selection dynamics (Wilson and Wilson 2007; West et al. 2008). This idea was used to argue that high degrees of cooperation within groups would lead to a higher degree of between-group selection compared to within-group selection.

But multi-level selection theory is not only used to argue for group selection, instead MLS, in its basic form, is the claim that selection takes place at multiple levels simultaneously. Indeed, Hamilton (1975) incorporated MLS into kin selection theory when addressing group effects on individual fitness across the entire population, with the use of the Price equation (Wilson and Wilson 2007; Wilson 2008a).[1] As a result, MLS is generally divided into two forms. MLS1 is used to track the effects of group-living on individual fitness, whereas MLS2

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[1] Hamilton also worked closely with G. Price when the latter developed the Price equation (Hamilton 1996).

is used to argue for group selection by assessing the degree of between-group selection compared to within-group selection (Damuth and Heisler 1988). But even though MLS is now a mainstream part of evolutionary theory — the Price equation is often used to formalise kin selection models — group selection (MLS2) is still a contested idea (West et al. 2008; Wilson 2008a; Birch and Okasha 2015). Group selection is particularly popular within eusociality research, however, due to B. Hölldobler, E. O. Wilson, and colleagues, and their work on colony selection within different species (Reeve and Hölldobler 2007; Wilson and Hölldobler 2009; Hamilton and Fewell 2013; Wilson and Nowak 2014).

In sum, kin selection and group selection are seen by authors as the only theories capable of explaining the evolution of BA (Hamilton 1964a, 1964b; Sober 1988; Okasha 2013). Authors initially considered that the only way to explain its evolution was by using old group selection, or good-for-the-species, arguments, due to the cost of BA to the individual that bears the trait. When old group selection was rejected, Hamilton (1964a, 1964b) provided a groundbreaking solution based on individual selection (i.e. kin selection). However, with the emergence of MLS and new group selection, a debate has continued between authors over the best explanation for the evolution of BA (Nowak et al. 2010; Abbot et al. 2011; Okasha 2013). Thus, the levels of selection debate — i.e. kin selection versus group selection (MLS2) — continues on in evolutionary theory.

Importantly, it was not until the emergence of the levels of selection debate in the 1960s that the paradoxical nature of BA became apparent. Since then, the main focus has been on explaining how such a paradoxical trait could evolve under natural selection, with much less focus paid to the concept itself and its application to specific cases; i.e. is it a correct description of the behaviour of the non-reproductive castes in eusocial insect colonies? Indeed, because the concept of BA is so widely applied to the non-reproductive castes of eusocial insect colonies, authors have had to solve the BA paradox in order to explain the evolution of eusociality. As a consequence, kin selection and group selection are the current mainstream evolutionary theories of eusociality (Alonso and Schuck-Paim 2002; Hölldobler and Wilson 2009; Ratnieks et al. 2011; Wilson and Nowak 2014). In the next section I will explore in more detail the history behind the widespread use of the concept of BA within eusociality research.

1.2. Hamilton, eusociality and the concept of BA

Today, Hamilton's kin selection theory is a fundamental element of evolutionary theory (Bourke and Franks 1995; West et al. 2008). It is considered as one of the most important developments in evolutionary biology since Darwin's theory of natural selection (Queller 2001; Alonso and Schuck-Paim 2002). Kin selection theory profoundly changed the study of cooperative and social evolution. Indeed, within eusociality research kin selection is the mainstream evolutionary theory, and in this respect, Hamilton has left a huge legacy. But, as above, group selection is becoming increasingly popular among authors, and the debate between kin selection and group selection is ongoing. As a result, any recent, or major, historiography of eusociality research focuses on the levels of selection debate (see for example: Wilson and Sober 1989; Cronin 1991; Hölldobler and Wilson 2009). Additionally, as I will show below, due to the influence of Hamilton's theory of kin selection, the concept of BA has been widely used in eusociality research since around the 1960/70s. This is because Hamilton applied the concept of BA to the behaviour of the non-reproductive castes in eusocial insects, and used kin selection to explain their evolution. Due to the huge success of kin selection, many subsequent authors conceptualised the evolution of eusociality as the evolution of BA, following Hamilton.

It is often claimed that Hamilton applied the theory of kin selection and the concept of BA to eusociality due to the levels of selection debate (Cronin 1991; Price et al. 2011). In other words, because Hamilton developed kin selection due to the rejection of group selection, it is assumed that he applied the theory, and the concept of BA, *to eusocial insects* for the same reason; i.e. non-reproductive workers are biologically altruistic, and they evolved because their inclusive fitness is better increased by helping the reproductive(s) rather than attempting to be solitary reproductives themselves. However, I argue that (i) the reason why Hamilton applied *kin selection* to eusociality and (ii) the reason why he applied the *concept of BA* to eusociality should be investigated independently. This is because conceptualising the evolution of eusociality as the evolution of BA is not a necessary consequence of applying kin selection to evolutionary studies of eusociality. For instance, coercion and parental manipulation are also compatible with kin selection and are viable alternatives that could be applied to the reproductive division of labour in eusocial insect colonies; i.e. the non-reproductive castes could have evolved due to parental coercion rather than BA. Thus, it cannot be assumed that Hamilton applied the concept of BA to eusocial insects because of his principle of inclusive fitness. In this section I will assess both (i) and (ii).

1.2.1. Why did Hamilton apply kin selection to eusociality?

W. D. Hamilton (1963, 1964a, 1964b) developed his theory of kin selection as a general theory for the evolution of cooperation (including BA) and sociality because of his initial rejection of group selection. However, I will now argue that Hamilton applied kin selection to eusociality for more specific reasons. Firstly, Hamilton rejected the theories that colonies are like individuals, that were so prevalent before the 1960s (as I will show below); secondly, he already considered the non-reproductive worker castes of eusocial insects as examples of BA prior to developing kin selection.

> In what sense can the self-sacrificing sterile ant be considered to "struggle for existence" or to endeavor to maximize the numbers of its descendants? Since the founding of the theory of evolution by natural selection, most biologists have evaded this question by focusing attention exclusively on the colony as *the reproducing unit*. (Hamilton 1972: 193. Emphasis added).

This quote points to the fact that, for the specific case of eusociality, Hamilton argued for kin selection because he doubted a previous argument that eusocial insect *colonies* are biological individuals (or at least evolutionary individuals, see Pradeu 2016). The last sentence in the quote from Hamilton, above, points to this. By using the term "the reproducing unit" Hamilton is referring to the argument, proposed by A. Weismann (1909: 32-36), R. A. Fisher (1930: 180-187), and others, that I will refer to as the "germ-soma" argument. The claim, using the "germ-soma" argument, is that in the special case of eusocial insects, the colony is the individual under selection due to the reproductive division of labour. In other words, it was argued that eusocial colonies are evolutionary individuals because they are units of selection. When authors presently make the argument that eusocial colonies are evolutionary individuals, they are typically making the claim that colonies are *groups that are units of selection* using group selection (for example see Hölldobler and Wilson 2009). However, unlike these present arguments, the "germ-soma" argument was simply the claim that individual selection in the classical sense can be applied to the colony (or at least to the reproductives only) because of the reproductive division of labour. Thus, I refer to this earlier argument using the term "germ-soma" in order to distinguish it from the more recent evolutionary approaches to the notion that colonies are like individuals, which are based on group selection and MLS (Hölldobler and Wilson 2009; Haber 2013. See also chapters 4 and 5).

Weismann (1909: 35-36) likened the reproductive division of labour to the germ-soma division in multicellular organisms. He argued that worker polymorphism, and other factors of eusocial colonies, could evolve because selection affects the "germ-cells" (genomes) of the reproductives via the success of the colony. In other words, the non-reproductive castes evolve by selection affecting the reproductives in the colony, just as somatic cells evolve via selection affecting the germ cells in multicellular organisms (Fisher 1930: 180-187). My claim that the "germ-soma" argument is not a form of group selection and is separate from the levels of selection debate is further supported by the fact that in R. A. Fisher's (1958: 49-50, 199-205) second edition of *The Genetical Theory of Natural Selection*, in which he argued against any form of group selection or good-for-the-species arguments, he still made the similar argument as Weismann that eusocial colonies are a form of biological individual (or at least analogous to one) due to the reproductive division of labour:

> The selection in this case must act exclusively upon the reproductive insects *via* the prosperity of the society from which they arise; and although the effect of such selection may be to modify only the sterile workers, this presents no more difficulty than that a selection acting exclusively upon the gametes of a sheep, *via* the observable characteristics of the animal which bears them, should modify the nature of its wool. (Fisher 1958: 201).

Indeed, the idea of classifying eusocial insect colonies as some form of biological individuality has a long history (see Wheeler 1911, 1928; Emerson 1939: 181), and the argument based on the reproductive division of labour by Weismann and Fisher, above, can be traced back to Darwin (1859:175-180).[2] It is this line of reasoning that Hamilton challenged when he applied his theory of kin selection to eusocial insects:

> There is powerful precedent for this [arguing for the colony as a reproducing individual]. Darwin himself took this course. He saw only a "minor" difficulty in the evolution of sterility, and he passed over it in a few lines as he proceeded to discuss the "great" difficulty of how the special aptitudes of the workers could be passed on in latent form by their fertile sisters […]. A difficulty over sterility exists, nevertheless […]. Soon Mendelian genetics resolved Darwin's difficulty of latency […]. But the disappearance of this problem does not seem to have given greater prominence to the other, and *the question of how worker sterility comes to be selected continued to receive only occasional comment for a long time*. (Hamilton 1972: 193. Emphasis added).

Certainly, Hamilton (1972: 193-195) admitted that eusociality represents a major problem for evolution by natural selection. But unlike Darwin (1859: 175-180), Hamilton argued that this major problem was not how the non-reproductive castes could evolve to be different to the reproductive castes when they do not directly reproduce; in fact, he argued that this problem is solved by Mendelian genetics, that were not available to Darwin. For Hamilton (1972), the major evolutionary problem of eusociality was the evolution of sterility (i.e. the non-reproductive castes). However, for Hamilton, the prominence of the "germ-soma" argument led to the issue of sterility to be obscured.

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[2] I will address the colonies-as-individuals arguments in later chapters (4 and 5) of my thesis. I will address Darwin's argument in chapter 2.

Hamilton was well versed in the biology of eusocial insects (Emlen 2001). He argued that aspects such as polygyny (multiple queens), polyandry (multiply-mated queens), and worker reproduction, within colonies highlight the problem of the "germ-soma" argument:

> If [polygyny, polyandry or worker reproduction] is true of any, we have a difficulty for the common view (supported, as we have seen, by Darwin) that selection in social insects is entirely an intercolony matter. (Hamilton 1972: 194. Emphasis added).

It is clear from this quote that Hamilton argued that evidence of polyandry, polygyny, or worker reproduction in any species of eusocial insects undermines the strength of the "germ-soma" argument in general. This is because, as above, the "germ-soma" argument claimed that colonies are evolutionary individuals — i.e. individual selection can be applied to eusocial insect colonies just as it can be applied to individual organisms. But, for Hamilton, genetic homogeneity was important for individuality; i.e. genetic homogeneity would decrease the potential for internal competition. Hamilton (1964b: 25) only allowed for a form of colony-individuality when colonies are made up of clones (or at least a high degree of genetic relatedness), because in this case they would be genetically homogenous and the potential for conflict is very low, which is highlighted in his argument for multicellular organisms as "colonies" formed of clones:[3] 'This is borne out well enough by the behaviour of the clones which make up the bodies of multicellular organisms'. But, even though relatedness is high within typical eusocial insect colonies they are not genetically homogeneous, rather, the genetic relationships are more like that within families; for example, in typical monogynous colonies

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[3] Indeed, elsewhere, Hamilton (1972: 198-199) even spoke of the concept of the superorganism — albeit in brief and without a proper explanation — when he discussed the case of inbreeding within long-lived termite colonies, which potentially increases the degree of relatedness almost up to the level of multicellular organisms, which could lead to very low conflict among the parts. However, he did not expand on the point and did not appear to argue for the superorganism theory.

the queen is the mother to all of the colony members and the workers are all full-siblings. Furthermore, factors such as polyandry, polygyny, and worker reproduction further reduce genetic relatedness within colonies. Therefore, the fact that there are eusocial insect species that have evolved, and are maintained, despite features that reduce genetic relatedness, convinced Hamilton that something other than colony selection is occurring. In other words, because colonies with polyandry, polygyny, or worker reproduction have reduced relatedness, they cannot be considered as evolutionary individuals, according to Hamilton (1964b, 1972), and therefore, the "germ-soma" argument does not apply to them. Moreover, Hamilton (1972) argued that the fact that some species have evolved despite the lack of colony selection (i.e. those with reduced genetic relatedness due to polyandry, for example) undermines the "germ-soma" account for the evolution of eusociality more generally. Specifically, if those species with polyandry, etc., can be explained without the need to appeal to colony selection, then Hamilton argued that there is no need to appeal to colony selection to explain the evolution of any species of eusocial insects.

Consequently, Hamilton (1964b, 1972) argued that a better solution is to apply kin selection theory to the evolutionary studies of eusociality. He argued that kin selection can explain the evolution of eusociality better than the "germ-soma" argument can. Broadly, Hamilton argued that relatedness was a key factor for the evolution of eusociality, but not the only one, the other key factor was the altruistic workers. For instance, Hamilton (1972: 206) argued that even though individuals in some species of aphid colonies are clones (and so genetically identical), they have not evolved eusociality due to certain aspects of their biology (i.e. because they are 'sedentary sap-feeders', they have no need for more complex behaviour/cooperation). Whereas in eusocial insects, the need for more complex cooperation was present from the beginning. For instance, many species require extended parental care, build complex nests, or defend the colony collectively. In termites, there is a high need for cooperation because individuals require symbiotic gut-microbiota to digest the cellulose in their diets, but every time they moult (undergo ecdysis) they lose their gut microbiota and, therefore, rely on other members of their colony to regain them, via trophallaxis (Nalepa 2015). There are many more examples like this in all eusocial insect species, thus Hamilton argued that because of these factors workers would achieve a higher inclusive fitness by staying in the colony and helping rather than not doing so — despite the fact that this will decrease their direct fitness. So, for Hamilton (1972), kin selection could explain the existence of cooperation and cohesiveness within eusocial colonies in spite of the possible factors that could undermine them (polygyny, worker reproduction, etc.), whereas the "germ-soma" explanation could not.

It is important to note at this point that polyandry and polygyny are now known to only be present in evolutionary advanced species that are obligately eusocial, thus they are likely to be derived traits that evolved after eusociality evolved within the species (Oldroyd and Fewell 2007; Crozier 2008; Hughes et al. 2008; Boomsma 2009). Therefore, although these factors reduce genetic relatedness within colonies, they are likely not to be factors that cause selection against eusociality. Moreover, in certain contexts these factors can actually be beneficial to colony cohesion and maintenance; e.g. improved disease resistance (Cremer et al. 2007; Wilson 2008b). I will address this further in chapter 3.

In sum, Hamilton (1972) argued that the use of the "germ-soma" argument led to the problem of sterility to be missed, or at least not fully appreciated, because its focus on inter-colony selection and reliance on the analogy between colonies and organisms. This is important for Hamilton because he considered the evolution of non-reproductive castes as the most serious evolutionary problem posed by eusocial insects. This is because he believed that the non-reproductive worker castes are examples of BA. Therefore, I argue, that the main reason Hamilton rejected the "germ-soma" argument was because he *already viewed the non-reproductive workers of eusocial insect colonies as examples of BA*. But why did Hamilton apply the concept of BA to eusocial insects? I will explore this in more detail next.

1.2.2. Why did Hamilton apply BA to eusociality?

> In the early days I was continually being told that there was no such thing as altruism […]. I badly needed examples, therefore, where both self-sacrifice and the limits to it were indisputable. [Eusocial] insects became one of my main examples. (Hamilton 1996: 20).

Hamilton first became interested in BA during his undergraduate studies and he began his PhD with the aim of providing an explanation, within the framework of the Modern Synthesis, for the evolution of BA (Hamilton 1996: 11-30; Segerstrale 2013: 45-77). During his undergraduate studies Hamilton (1996: 22-23) was heavily influenced by J. B. S. Haldane's (1932) original argument for the concept of BA, as well as work by R. A. Fisher. Indeed, the early part of Hamilton's career was devoted to providing a mathematical explanation for BA (Hamilton 1996). The quote above highlights that from an early stage Hamilton considered the non-reproductive worker castes of eusocial insects as one of the main examples of BA. In this regard, however, Hamilton was mainly inspired by A. H. Sturtevant (1938), as I will argued presently.

Sturtevant (1938), like Hamilton, challenged the "germ-soma" explanation for the evolutionary origins of eusociality. He argued that the "germ-soma" argument is unable to explain the origin of the non-reproductive castes:

> The sterile castes of [eusocial insects] have, therefore, developed a character that is [unfavourable] by definition. It is sometimes argued that in this special case the rule still holds, since here *the colony, rather than the individual insect, is the unit in terms of natural selection*, and it may be supposed that the colony produces more offspring as a result of the division of [labour] associated with the sterile castes. It is clear, however, that all the social insects have arisen from solitary forms in which the sterile caste was absent […]. *It follows that evolution must have resulted in an increase of sterile individuals*. At some point in the history of the race there must have been a change from the individual to the colony basis of selection. Unless this change be supposed to have been a sharp one and to have been associated from the first with the necessary genetic adjustment, there must have been an intermediate stage in which some element other than the strict operation of reproductive selection was effective. (Sturtevant 1938: 74. Emphasis added).

Thus, as the quote above alludes to, Sturtevant argued that the "germ-soma" theory could not explain the origin of eusociality because it cannot explain the evolution of BA in the worker castes.

To see this, it will be useful to analyse Sturtevant's (1938) argument in more detail. Sturtevant premised his argument, which I refer to as the sterility problem, in the following way:

(i) Biologically altruistic (i.e. sterile) individuals can be maintained by natural selection in eusocial insects because the colony is the unit of selection, but;

(ii) Eusocial insects evolved from solitary ancestors, so there must have been a switch from individual selection to colony selection, however;

(iii)The switch to colony selection must have been gradual, if Darwinian selection is true;

Therefore;

(iv) There must have been an intermediary stage in which there was an increase in sterile individuals prior to colony selection.

Thus, according to this argument, the evolution of non-reproductive individuals must have occurred *in the absence of* between-colony selection. Consequently, not only is this an argument against the "germ-soma" theory, since the "germ-soma" theory relies on colony selection to explain the evolution of the non-reproductive castes; more importantly, it also entailed, for Sturtevant, that BA must have existed before the evolution of eusociality. Or, the evolution of eusociality required the evolution of BA. This is because Sturtevant (1938) argued that the non-reproductive castes of eusocial insects are biologically altruistic because they are working for the colony but do not reproduce — i.e. they "give-up" reproduction for the benefit of the colony. Sturtevant also claimed that this was not considered to be problematic, because the colony is the unit of selection due to the reproductive division of labour; as was argued by Haldane (1932: 207-210).[4] However, according to the sterility problem, since eusocial insects

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[4] Authors who argued for the "germ-soma" theory did not explicitly describe the non-reproductive castes as altruistic. This is because they viewed the worker castes as parts of a larger whole (the colony) and were thus not under direct selection.

evolved from solitary ancestors, colony selection must have occurred *after* the non-reproductive worker castes evolved. But this posed a problem; namely, how can these individuals evolve if they do not reproduce? Under natural selection, traits typically evolve if they confer a positive fitness benefit on their bearer, but in this case the workers are not reproducing and thus have a trait that causes a negative fitness consequence. And because the workers are also helping their parent, they must be biologically altruistic. Accordingly, for Sturtevant, this implied that the evolution of eusociality required the evolution of BA.

As I highlighted above, like Sturtevant, Hamilton considered the major evolutionary problem of eusociality to be the evolution of the non-reproductive castes, which he referred to as the sterility problem. Indeed, Hamilton (1973: 193) appeared to be heavily influenced by Sturtevant's (1938) sterility argument: 'Sturtevant […] outlined [the problem of sterility] with admirable clarity'. Like Sturtevant, Hamilton argued that the evolution of eusociality required the evolution of "sterile" individuals, which he considered a major problem for evolutionary theory, because the problem of sterility implies that the evolution of eusociality requires the evolution of BA. Thus, both Sturtevant (1938) and Hamilton (1972) conceptualised the evolution of eusociality as the evolution of BA, due to the problem of sterility. Sturtevant's (1938) solution to the BA paradox in eusocial insect evolution was that selection operates at multiple levels in eusocial insects; at the individual, colony, and at the population level. In other words, according to Sturtevant, selection between individual *insects*, between *colonies* (within a geographical area), and between *populations* of colonies, led to the evolution of eusocial insects. Whereas Hamilton's (1964b, 1972) solution was inclusive fitness and kin selection:

> *The sacrifice* of reproductive function *by a worker* social insect is a case of altruism to which [inclusive fitness] can be applied. (Hamilton 1972: 197. Emphasis added).

However, the Sturtevant-Hamilton problem of sterility does not necessarily entail that BA had to be involved in the evolution of eusocial insects. Specifically, BA is not necessarily required for the non-reproductive castes to evolve prior to colony level selection (conclusion (iv)). For example, the non-reproductive castes could have evolved due to coercion from the parent(s) (i.e. parental manipulation; see below and chapter 3), whereby a female coerces some of her brood into becoming workers whilst also inhibiting them from reproducing. And in fact, in the more evolutionary basal eusocial insect species, that have small colonies (only tens of individuals or less), worker reproduction is typically inhibited by the queen via aggression (Ronai et al. 2016: 281-282). For example, the queen can physically inhibit the reproductive potential of workers by eating worker laid eggs or evicting reproductively active workers. Moreover, in the more derived species, worker reproductive potential is inhibited by coercion by the colony, via pheromones or policing (Hölldobler and Wilson 2009; Shimoji et al. 2018; see also chapter 5).

Despite this, Hamilton (1964b, 1972) still argued that the worker castes do not reproduce (i.e. are “sterile”) because they are altruistic. Later, Hamilton (1996: 361) did admit that his enthusiasm for BA led him to under-appreciate the role of parental manipulation, and other forms of coercion (e.g. worker policing), in the reproductive division of labour. Nevertheless, he still argued that the evolution of non-reproductive worker castes must have involved some BA on the part of the workers: ‘Yet I am certain that an “altruistic” willingness to be manipulated is also a factor’ (Hamilton 1996: 361). And in fact, Hamilton spent a significant period of his life pursuing and developing an explanation for the evolution of BA

(Queller 2001; Segerstrale 2013). Consequently, this could have influenced his continued enthusiasm for describing eusocial insect workers as altruistic in the twilight of his career, despite the increasing evidence for coercion (I will address this recent evidence in chapter 3).

In post-Hamiltonian eusociality research, however, the main focus has been on the levels of selection debate; i.e. the explanatory models of kin selection and MLS (see Cronin 1991; West et al. 2008; Wilson 2008a; Hölldobler and Wilson 2009; Birch and Okasha 2015). In comparison, there was relatively little focus on the concept of BA and its use within eusociality research. In particular, the Sturtevant-Hamilton problem of sterility, which inspired Hamilton to apply the concept of BA to eusocial insects, has received almost no attention by subsequent authors. For example, in their recent monograph, B. Hölldobler and E. O. Wilson (2009: 17-18) referenced Sturtevant's (1938) paper, but instead of discussing how he formulated the evolution of sterility/BA in eusocial insects, they focused on his MLS solution to the problem. Consequently, the fact that the evolution of the non-reproductive castes, and by extension eusociality, does not necessarily require BA, even according to the Sturtevant-Hamilton problem of sterility, went relatively unnoticed. As a result, alongside the success of kin selection, the use of the concept of BA flourished and became widespread in eusociality research. To highlight this, I will review the use and role of BA, as well as alternatives to it, in pre- and post-Hamiltonian eusociality research.

1.2.3. BA in pre-Hamiltonian eusociality research

Prior to the introduction of kin selection by Hamilton in the 1960s, the concept of BA was rarely applied to eusocial insects. As above, when Haldane (1932) developed the concept, he argued that eusocial insects are likely to be the only possible example of BA. Sturtevant (1938) used the concept (without specifically using the term “altruism”) to describe eusocial workers. The concept of BA was also used to describe eusocial workers (as well as many other examples, e.g. cells within multicellular organisms) by W. C. Allee and colleagues (1949: 599, 683-695). However, they also supported the good-for-the-species view, i.e. old group selection, and so did not consider BA paradoxical. G. C. Williams and D. C. Williams (1957) applied the concept — also without using the term “altruism”, but instead, that of “social donor” — to eusocial workers in their argument for group selection. However, G. C. Williams (1966) was one of the main protagonists of the levels of selection debate, and he later rejected most forms of MLS (West et al. 2008). But, apart from these authors, the majority of researchers did not apply the concept of BA to eusocial insects.

I will now review some alternative concepts that were used to explain the non-reproductive castes in eusocial insects pre-1960s. However, this is not an exhaustive review since the field of eusociality research is extremely large.

Colonies-as-individuals: Many authors argued that eusocial insect colonies are a form of biological individual (Weismann 1909; Wheeler 1911, 1928; Fisher 1930; Bodenheimer 1937; Sturtevant 1938; Richards 1953; for more information, see Emerson 1939). The colonies-as-individuals perspective included the “germ-soma” argument (*see 1.2.1.*), which did not employ the concept of BA. Another interesting variant of the conception of colonies-as-individuals was the notion of the *superorganism*. This was first applied to eusocial insects by W. M. Wheeler (1926; 1928). Unlike the “germ-soma” approach, which argued that colonies are individuals from an evolutionary perspective (i.e. classical selection operates on colonies rather than the individual insects due to the reproductive division of labour), early versions of the superorganism approached the colonies-as-individuals view from a physiological perspective (Wheeler 1928; Emerson 1939, 1952). By focusing on the actual organization of colonies, the superorganism approach argued that colonies were higher-order individuals with analogous properties to prototypical organisms (Wheeler 1928; Emerson 1939, 1952).[5] The superorganism approach did not describe the behaviour of the non-reproductive castes as BA because the non-reproductives were considered parts of the colony superorganism. Wheeler (1911: 325), who was the prominent figure in the early superorganism approach, did on occasion use the term "altruism", but he did so to refer to cooperation rather than BA, as it is currently understood. Elsewhere, Wheeler (1928: 309-312) also discussed traits that could be seen as similar in definition to BA (i.e. socially beneficial traits) but he did not define them as individually costly in terms of fitness. Instead, Wheeler (1928: 309-312) argued that eusocial insects exhibit "trophic" or "regressive" traits, such as sterility, polymorphism, reduced size, and many more, because the colony is an emergent whole, i.e. a *superorganism*. Thus, in the superorganism perspective during this period, the concept of BA was not applied to the non-reproductive workers because they were considered to be lower-level parts in a higher-level biological individual.

Dominance: Another alternative to the concept of BA was that of dominance. J. B. Free (1955), and colleagues (Free et al. 1969), argued that dominance hierarchies exist in eusocial insect colonies, with the reproductives at the top, and that this led to the evolution of the reproductive division of labour and thus to eusociality. They argued that in smaller, more simple, eusocial colonies dominance based on aggression creates and maintains the division of labour. For example, the workers are prevented from reproducing by physical aggression from the queen, or even more dominant workers (worker policing). If the queen is removed, or when

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[5] However, today the superorganism argument is typically approached from an evolutionary perspective using MLS (Wilson and Sober 1989; Haber 2013). In chapter 4, I will explore in more detail historical and present notions of the superorganism.

the queen starts to lose her ability to dominate, due to old age for example, the more dominant workers will start to oviposit (Free et al. 1969). Hamilton (1964b; 1972) referenced the work by Free and colleagues, appealing to it as evidence against the "germ-soma" argument; he argued that their work highlighted the type of internal conflict within colonies that would undermine the individuality at the colony level.

But Hamilton did not address the fact that these authors claimed that the workers are coerced by the queen rather than giving up reproduction due to BA. For example, in some species of bumblebees, during the late stage of the colony life cycle when the queen starts to senescence and lose control over workers, the queen and some reproductively active workers physically fight over egg production, with both parties eating each other's eggs or guarding comb cells from each other (Free et al. 1969). This shows that workers are not biologically altruistic, and given the chance, they will try to oviposit. In other words, the fact that the workers do not reproduce could be because of external inhibition by the reproductive rather than because of BA. This is not to say that Hamilton is wrong to claim that kin selection can explain this queen-worker aggression, but rather that Hamilton could be wrong in applying the concept of BA to the workers in this case. But I will expand more on this point in chapter 3.

Free (1955) argued that physical dominance is only likely to be possible in small colonies, whereas in larger colonies with thousands to millions of insects physical dominance would be almost impossible, in these latter species dominance is likely to be maintained by pheromonal signals. Physical dominance hierarchies, for Free, might be the basis for the evolution of eusociality but as organizational complexity (e.g. polymorphic castes) evolved within species, such as in honey bees (*Apis mellifera*), dominance via pheromonal signals would also evolve. Dominance appears to be a forerunner of the "parental manipulation" theory proposed by Alexander (1974), below.

Food sharing: Others argued that eusociality evolved due to the increasing complexity of food sharing, or trophallaxis (Nixon and Ribbands 1952; Ribbands 1953). Ribbands (1953) argued that trophallaxis creates a social medium — which was first argued for by Wheeler (1928) — that is the basis of colony organization. Ribbands (1953) argued that the first worker castes, in the evolution of eusociality, could have emerged due to the queen underfeeding a subset of her brood. The targeted brood, which were underfed, would develop into smaller/less fecund adults, for example, and therefore be inclined to remain in the nest as workers rather than disperse and attempt to become solitary reproductives. As eusociality evolved, workers themselves could become involved in the control of brood nutrition, i.e. workers could take over from the queen in feeding brood differentially according to whether workers or queens were required by the colony. Finally, further organizational complexity could have evolved in some species via adult-adult worker trophallaxis (for example, Ribbands argued that worker-worker trophallaxis within colonies allows for an added layer of organizational complexity because it enables information about food supplies, among other things, to be shared between colony members). Elsewhere, Ribbands (1953: 205) did use the term "altruism", but he did so in order to denote psychological altruism, rather than biological altruism, when he discussed the evolution of ethics; he did not apply the concept of BA to eusocial insects.

1.2.4. BA in post-Hamiltonian eusociality research

Thus, the concept of BA was rarely used in eusociality research prior to Hamilton, as I highlighted above. But ever since Hamilton (1964a, 1964b, 1972) conceptualised the evolution of eusocial insects as the evolution of BA, and used kin selection to explain their evolution, the concept became the mainstream description of the behaviour of non-reproductive castes. Consequently, many authors subsequently conceptualised the evolution of eusociality as the evolution of BA, as the selected quotes below allude to:

> Social insects […] provide the most extreme forms of *altruism*. (Gadagkar 1990: 113. Emphasis added).

> The eusocial insects […] exhibit *biological altruism*. (Bourke and Franks 1995: 37. Emphasis added).

> Kin-selection has thrived in the explanation of a wide variety of biological phenomena, chiefly the evolution of *biological altruism as that found in sterile castes of eusocial insects*. (Alonso and Schuck-Paim 2002: 6843. Emphasis added).

> The major features of insect societies that fascinate biologists are the *self-sacrificing altruism* expressed by colony members, the complex division of [labour], and the tremendous plasticity demonstrated in the face of changing environments. (Page Jr. and Erber 2002: 91. Emphasis added).

> Indeed most of the *extreme cases of altruism* are found within families such as in social insects. (Lehmann and Keller 2006: 1370. Emphasis added).

> Thus, while only 2% of known insect species are eusocial, these species compose most of the insect biomass'… 'Why, then, has eusociality been so rare? The answer is that it

> requires collateral *altruism*, which is [behaviour] benefiting others at the cost of the lifetime production of offspring by the altruist. (Wilson 2008b: 17. Emphasis added).

> Discussions about caste evolution in termites have been mostly focused on the evolution of *altruistic* help. (Roisin and Korb 2011: 156. Emphasis added).

It has even led to somewhat contradictory statements, such as the following:

> [Recent] results show that workers are frequently *coerced* into acting altruistically. Hence, the altruism seen in many modern-day insect societies is not voluntary but *enforced*. (Ratnieks and Wenseelers 2008: 45. Emphasis added).

> Recent studies suggest that this reproductive altruism in workers is, to a large extent, a trait *enforced* by worker policing. (Shimoji et al. 2018: 2. Emphasis added).

Kin selection was a groundbreaking theory and came to be widely regarded as a fundamental aspect of evolutionary theory (Queller 2001; Alonso and Schuck-Paim 2002; West et al. 2008). Consequently, the majority of research focused on working out the theoretical details of kin selection, as well as finding empirical support for the theory in the form of sex-ratio conflicts, policing, etc. (Queller and Strassmann 1998; Queller 2001 — see also Chapter 5). In comparison, relatively little focus was paid to the theoretical and empirical groundings for the application of the concept of BA to eusocial insects. In particular, little attention has been paid to the reason why Hamilton applied the concept, namely the Sturtevant-Hamilton problem of sterility. This is problematic, I argue, because it led to the widespread use of the concept of BA within post-Hamiltonian eusociality research.

As I argued above, the Sturtevant-Hamilton problem of sterility does not necessarily entail that BA is required for eusociality to evolve, it only entails that the non-reproductive castes evolve. This could happen due to the workers being altruistic but, importantly, it could also happen due to another cause, such as coercion for example. However, this point has gone relatively unnoticed due to the lack of focus on the problem of sterility, as argued for by Sturtevant (1938). Moreover, the renewed focus on the problem of sterility by Hamilton (1964b, 1972) led to a predominate focus by later researchers on explaining the evolution of eusociality from the perspective of the workers. In other words, attempting to explain how some individuals evolved to become non-reproductive workers became the key to explaining the evolution of eusociality, as the quotes above highlight. Thus, the majority of authors, following Hamilton, described the non-reproductives as biologically altruistic and conceptualised the evolution of eusociality as the evolution of BA:

> The altruism of worker insects is often referred to as a Darwinian puzzle or paradox. How can natural selection, which normally favours the evolution of traits that increase an organism's reproduction, favour the reverse — *foregoing reproduction*. (Ratnieks and Helanterä 2009: 3170. Emphasis added).

It could be argued that despite Hamilton and the problem of sterility, the concept of BA would still have become prevalent due to the emergence of the Modern Synthesis and the consequent gene-centred approach to evolutionary theory. In other words, individualistic approaches, like kin selection, became prevalent due to the rejection of old group selection and the resultant levels of selection debate. Thus, more emphasis was placed on explaining the evolution of eusociality from the perspective of the individuals within the colony. Colonies-as-individuals arguments, such as the superorganism, began to wane around the 1960s, as I highlighted above (for more details, see chapter 4). Additionally, the Modern Synthesis led to a gene-centred view of evolution around the same period (Cronin 1991; West et al. 2008). Consequently, individual traits were typically explained from a genetic perspective, e.g. an individual has trait *X* because of gene *x*, and this gene evolved because *X* causes a fitness benefit to its bearer. Thus, it could be argued that the worker trait — not reproducing and working for the colony — is due to a gene possessed by the workers, namely a gene for BA. Indeed, eusociality researchers typically explained the evolution of non-reproductive castes as the evolution of a 'gene for altruism', i.e. a gene that causes a personal cost to its bearer but also causes it bearer to benefit close relatives — who are likely to share the gene — (Hölldobler and Wilson 2009: 21-24; Ronai et al. 2016: 255-256).

Whilst the levels of selection debate, and the gene-centred approaches, undoubtedly influenced the popularity of the concept of BA in post-Hamiltonian eusociality research, they cannot be the only causes. This should be made clear by the fact that coercion is also compatible with such gene-centred approaches. For example, the reproductive division of labour could have evolved due to a gene that encodes a trait which enables an individual to coerce some of her offspring into becoming non-reproductive workers. However, alternatives such as this were not given the same amount of attention that the concept of BA received, I argue, because a lack of analysis on the Sturtevant-Hamilton problem of sterility. Which is evidenced by the almost universal conceptualisation of the evolution of eusociality as the evolution of BA in post-Hamiltonian eusociality research.

Indeed, the use of the concept of BA to describe the non-reproductive castes has rarely been questioned since Hamilton's introduction of kin selection. The exception to this being the theory of parental manipulation (Alexander 1974; Michener and Brothers 1974; Charnov 1978; Alonso and Schuck-Paim 2002; Hunt 2007; Kapheim et al. 2015). Parental manipulation was first introduced by R. D. Alexander (1974), then again shortly after by C. D. Michener and D. J. Brothers (1974). Parental manipulation, according to these authors, argued that eusociality could evolve if a reproductive was capable of coercing some of her offspring into becoming non-reproductive workers. If the resultant colony was more successful than the non-eusocial solitary alternative, then eusociality would be selected for. However, these early approaches still employed the concept of BA to describe the trait of the non-reproductive castes.

Michener and Brothers (1974) argued that it was likely that a mix of parental coercion and worker BA led to the evolution of eusocial insects, a view which Hamilton later shared, as I highlighted above. A few years later, E. L. Charnov (1978) argued for a version of parental manipulation that did not involve BA. Charnov argued parental coercion, but not worker BA, would be enough for the evolution of eusociality. He argued that if reproductives developed the ability to coerce some of their offspring into becoming non-reproductive workers this would be selected for (for more details of Charnov's argument see chapter 3 — 3.2.1.). And more recently some authors have begun to explore the parental manipulation approach again (e.g. Alonso and Schuck-Paim 2002; Hunt 2007). In these lines, one study found evidence for parental coercion but no evidence for worker BA in a facultative eusocial bee — *Megalopta genalis* — (Kapheim et al. 2015).

However, apart from the above, authors rarely critically addressed the theoretical and empirical grounding for the use of BA in eusociality research. Instead, particularly within the debate over the evolution of eusociality, the focus was mainly on the explanatory models and the levels of selection debate, i.e. kin selection versus group selection (Cronin 1991; Wilson and Wilson 2007; Hölldobler and Wilson 2009; Okasha 2014). As a result, not only did the use of the concept of BA become widespread within the field, but multiple conceptual issues emerged that remain unresolved. These issues, which I will address in greater detail in chapter 3, include problems with defining the costs and benefits (i.e. short vs. long term, and relative vs. absolute), and a problem with the current definition that could render the concept vacuous. As a consequence, different explanatory models employed and/or defined the concept differently. For example, within MLS models the cost and benefits of BA are defined relatively, with respect to the group; i.e. BA causes its bearer to have a lower fitness within its group, but groups with more BA individuals would do better than predominately selfish groups (Sober 1988; Wilson and Dugatkin 1992; Kerr et al. 2004; Wilson 2008a). Whereas in kin selection accounts the fitness consequences of BA are defined in terms of absolute fitness, i.e. with respect to the whole breeding population (West et al. 2007). Additionally, many authors, particularly within kin selection models, conceive of BA in terms of fitness consequences alone, and apply it to any cooperative traits that cause negative selection on the focal individual and positive selection on recipient individual(s) (Ratnieks and Wenseleers 2008; Foster 2009). This is due to the definition of BA from Hamilton’s (1964a) seminal papers on kin selection. However, this definition is problematic as it could describe multiple traits, such as worker BA and parental coercion; both traits would cause negative selection on the workers and positive selection on reproductives. Thus, the fitness consequences definition potentially renders the concept of BA vacuous.

In sum, the conceptual issues of BA that I just briefly described, are also factors in the continued widespread use of BA in eusociality research. Hamilton applied the concept of BA to eusocial insects because of the Sturtevant-Hamilton problem of sterility, and due to the success of kin selection and lack of assessment on the sterility problem, the concept of BA became widespread in post-Hamiltonian eusociality research. As a result, the evolution of eusociality is almost universally conceptualised as the evolution of BA. Thus, the concept of BA became synonymous with the behaviour of the non-reproductive castes of eusocial insects. Similarly, the definition of BA was altered by different authors in order to fit their specific explanation of eusocial insects, rather than actually questioning the use of the concept of BA itself.

I have argued that the widespread use of the concept of BA to describe the non-reproductive castes has negatively affected eusociality research. Moreover, I have argued that it may not be the correct description of the behaviour of the worker castes. These points will be the main focus of the rest of this thesis. For example, in chapter 2, I will argue that the uncritical use of the concept of BA also led to poor historiographies of eusociality research; many authors (post-Hamilton) have claimed that the BA of eusocial insects has been a problem for evolutionary biologists since Darwin, which I will show to be false. In chapter 3, I will explore current theories for the evolution of eusociality and the role of BA within them, i.e. whether BA is necessarily required by the theory and/or if there is empirical evidence for it. In chapter 4, I will show that one of the main alternatives to BA, the superorganism account, which was once so prevalent, radically declined in post-Hamiltonian eusociality research. Although it saw a revival, due to the emergence of new group selection, it is currently only employed from an evolutionary perspective of biological individuality, i.e. colonies as units of selection. Finally, in chapter 5, I will propose an organizational approach to the superorganism in order to argue that colonies of some species of eusocial insects can be considered as superorganisms in a physiological-like sense, as well as an evolutionary sense. I do so in order to provide a stronger argument against the current widespread use of BA within eusociality research; i.e. if a colony is a physiological-like superorganism then, consequently, the non-reproductive castes cannot be biologically altruistic because they are lower-level parts of a higher-order system.

Conclusion

In this chapter I have argued that the concept of biological altruism, contrary to claim (2), is a relatively recent problem for eusociality research (and for evolutionary biology more generally). In section 1, I highlighted how the psychological notion of altruism, developed by A. Comte in the 1830s, differs from BA; with the former necessarily to do with intentionality and the latter with the cost and benefits of behaviour on individual fitness. Even though the concept of BA was developed in 1932 by J. B. S. Haldane, it did not emerge as a major problem for biology until at least the 1960s. This was primarily due to the levels of selection debate. With the initial rejection of any form group selection, BA could no longer be explained by the claim that it is beneficial to the group even though it is costly to its bearer. As a response to this, W. D. Hamilton developed his hugely influential theory of kin selection and inclusive fitness. Kin selection successfully explained how costly cooperation, such as BA, could evolve within the framework of the Modern Synthesis. Kin selection fundamentally changed how cooperation was studied. However, with the introduction of MLS, group selection ideas re-emerged around the 1970/80s, and with this a major debate over kin selection versus group selection emerged (i.e. the levels of selection debate), which still continues to this day, even within eusociality research.

In section 2, I traced the history of the concept of BA within eusociality research. I have argued that the concept of BA did not become widely used until the 1960s, due to Hamilton and the groundbreaking theory of kin selection. It is commonly argued that Hamilton applied the theory of kin selection and the concept of BA to eusociality due to the levels of selection debate. However, I argued that the reasons why Hamilton applied the theory of kin selection and why he applied the concept of BA to eusociality should be assessed independently. I argued that Hamilton applied kin selection to eusocial insects because he rejected the colonies-as-individuals argument *and* because he already considered eusocial insects as an example of BA. I then assessed why Hamilton applied the concept of BA to eusocial insects. I highlighted that he did so because of the Sturtevant-Hamilton problem of sterility. Following Sturtevant, Hamilton conceptualised the evolution of eusociality as the evolution of BA. However, I argued that the Sturtevant-Hamilton problem of sterility does not necessarily entail that BA is required in order for eusociality to evolve. But due to a focus on the explanatory models, and a lack of re-assessment of the Sturtevant-Hamilton problem of sterility, this point went relatively unnoticed in post-Hamiltonian eusociality research, leading to the widespread use of the concept of BA. Finally, I argued that prior to Hamilton, the concept of BA was rarely applied to eusocial insects, instead alternatives such as the superorganism, dominance, food-sharing, and more, were in use. Whereas in post-Hamiltonian eusociality research, the evolution of eusociality is widely conceptualised as the evolution of BA.

The widespread use of the concept of BA in post-Hamiltonian eusociality research was problematic as it led to a lack of focus on alternatives such as parental manipulation. This is problematic because, as I will show in chapter 3, recent evidence supports the fact that eusociality evolved due to parental coercion. In addition, I will argue in chapter 3 that a prominent focus on the explanatory models, rather than on the concept of BA itself, led to multiple definitions of the concept in use.

In the next chapter, I will argue that the widespread use of the concept of BA was also problematic because it led to inaccurate historiographies of eusocial research (claims (2) and (3)). Not only is this problematic because it is historically inaccurate, but also, because it leads to a feedback effect that reinforces the uncritical use of the concept. This is because the claim, that BA has been a fundamental problem for eusociality research since Darwin, has the effect of adding considerable historical weight to current prominence of the concept. In other words, by claiming that one of the founding fathers of modern biology also found the concept of BA problematic, specifically with respect to the non-reproductive castes of eusocial insects, adds considerable historical weight to the current use of the concept.

Chapter 2 — Biological altruism: history justified by theory justified by history

Introduction

In the previous chapter I highlighted three common claims that are made about the concept of BA within eusociality research, namely:

(1) That BA *is* a fundamental issue in eusociality research
(2) That BA *has been* a fundamental issue in eusociality research since Darwin
(3) That Darwin discussed and/or developed the concept of BA and its associated paradox

I argued, in the previous chapter, that claim (2) is inaccurate. I highlighted the history of the concept of BA and argued that BA was only considered as a fundamental issue for eusociality research from at least the 1960s due to Hamilton and the theory of kin selection. Hamilton applied the concept of BA to eusocial insects due to the Sturtevant-Hamilton problem of sterility, and explained their evolution using kin selection. Due to the success of kin selection, and a lack of re-assessment of the Sturtevant-Hamilton problem of sterility, subsequent authors typically conceptualised the evolution of eusociality as the evolution of BA, following Hamilton. As a consequence, the use of the concept of BA became widespread in post-Hamiltonian eusociality research.

In this chapter I will focus on claim (3) and argue that it is also inaccurate. Moreover, I will argue that, within post-Hamiltonian eusociality research, current theoretical perspectives have affected historical claims on the concept of BA and, in turn, these historical claims have been used by researchers in order to justify their current theoretical perspectives. Or in other words, historiographies of BA have been affected by the present, but in turn, the present is justified, in part, by such historiographies.

I will begin, in section 2.1., by reviewing claims in the literature that Darwin discussed and/or developed the concept of BA and its associated paradox (claim (3)). When authors invoke claim (3), they typically do so in reference to Darwin's argument for the evolution of morality in *The Descent of Man* and his treatment of the evolution of eusocial insects in *On the Origin of Species*. In section 2.1.1., I will assess Darwin's argument from *The Descent of Man* and argue that his notion of morality is not equivalent to the concept of BA. In 2.1.2., I will then show that Darwin did initially consider eusocial insects to be an almost fatal problem for his theory of natural selection, but this was not because he considered them to be an example of BA, but instead because of the fact that the non-reproductive castes have evolved to be different to the reproductives, despite not directly producing their own kind — which he referred to as his "special difficulty" (Darwin 1859: 175). In 2.1.3. I will explore the cause of the inaccurate historical claims (2) and (3), arguing that these claims likely emerged due to the current widespread use of the concept of BA. Consequently, I will show that current theoretical perspectives have affected the historiography of eusociality research, and how in turn, this inaccurate historiography is used to justify current theoretical perspectives. Specifically, I will argue that the current widespread use of the concept of BA within eusociality research is supported, in part, by claims that Darwin also applied the concept to eusocial insects.

Finally, in section 2.2., I will argue that Darwin is not only invoked in order to justify the current use of the concept of BA, but also by opposing camps in the debate over the evolution of eusociality. Specifically, within eusociality research, some authors have claimed that Darwin's solution to his "special difficulty" was group selection, whereas others have claimed that Darwin's solution was an early form of kin selection (and BA). Both camps within this debate reference Darwin and interpret his solution through the eyes of the present in order to give historical weight to their theoretical perspective. However, I will argue that both interpretations are inaccurate; Darwin's solution was neither group selection or BA via kin selection. Instead, Darwin applied classical selection to the reproductives and argued that eusocial insects could have evolved due to the ability of reproductives to produce non-reproductive worker offspring.

2.1. Did Darwin discuss and/or develop the concept of BA?

> Although for Darwin the anomaly was not the sterile workers' altruism, commentators today commonly take for granted that it was. (Cronin 1991: 299).

As I have argued in Chapter 1, one of W. D. Hamilton's major legacies on eusociality research was the concept of BA. In pre-Hamiltonian eusociality research the concept of BA was rarely used to describe the non-reproductive castes, instead the reproductive division of labour was conceptualised and explained in alternative ways — such as the idea of colonies as individuals, or dominance, or food sharing. In post-Hamiltonian eusociality research the concept of BA became widely used; the evolution of eusociality is almost universally conceptualised as the evolution of BA. This is due, in part, to a lack of attention towards the philosophical and historical groundings for the application of BA to eusocial insects. For example, a lack of attention has been paid to the reasons why Hamilton applied the concept of BA to eusocial insects, namely the Sturtevant-Hamilton problem of sterility, which has contributed to the current mainstream view that the evolution of eusociality must require the evolution of BA. Additionally, a lack of historical investigation into the origin and emergence of BA within eusociality research has led to the claims that BA has been a fundamental problem since Darwin (claim (2)). Moreover, the mainstream conceptualisation of the evolution of eusociality as the evolution of BA, in post-Hamiltonian research, is further entrenched by claims that Darwin developed and/or discussed the concept of BA and its associated paradox — claim (3) — (Hunt 2007; Ratnieks et al. 2011). For example:

> Darwin […] had already applied group selection arguments to explain the evolution of *altruism* in social insects. (Korb and Heinze 2004: 295. Emphasis added).

> Darwin did not use the term [altruism], although it was clear that he was talking about behaviours that cause individuals to 'sacrifice themselves for the common good', as he put it in [*The Descent of Man*]. (Wilson 2008a: 370. Emphasis added).

Moreover, many authors have claimed that eusocial insects posed a major problem to Darwin when he was developing his theory of natural selection due to the proposed BA of the non-reproductive castes:

> The *altruism* of some members of an insect colony raises the question of how it is possible for traits to be retained and passed on which decrease the probability that their bearers will leave progeny. […] Darwin was aware of this apparent contradiction and recognized its importance. […] This question [the evolution of BA], the principal subject

> of this chapter, can then be said to be as old as the theory of evolution by natural selection. (Starr 1979: 36. Emphasis added).

> A major goal of sociobiology is to explain the evolution of […] altruistic behaviour within the framework of the theory of natural selection. Social insects which provide the most extreme forms of altruism and were *recognized by Darwin himself* […] as posing a serious challenge to his theory have quite naturally been the focus of most attention in this regard. (Gadagkar 1990: 113. Emphasis added).

> How can genetically prescribed selfless behaviour arise by natural selection, which is seemingly its antithesis? *This problem has vexed biologists since Darwin*, who in *The Origin of Species* declared the paradox — in particular displayed by ants — to be the most important challenge to his theory. (Nowak et al. 2010: 1057. Emphasis added).

There are many more claims such as these within the literature (see Hunt 2007; Ratnieks et al. 2011). The majority of which, as like the ones above, are presented more as statements than as detailed arguments for what Darwin actually argued, and what he really found problematic with eusocial insects. But authors typically make such claims about Darwin in order to add historical weight to their application of the concept of BA to eusocial insects (Ratnieks et al. 2011). In other words, these authors are trying to add legitimacy to the present with appeal to the past (Ruse 1980). However, I will argue that the claims that Darwin discussed and/or developed the concept of BA are incorrect. I will do so, firstly, by assessing Darwin's (1874) argument for the evolution of morality in *The Descent of Man*. Secondly, I will address Darwin's (1859) treatment of eusocial insects, and his "special difficulty" with them, from the

Origin of Species. Both of these elements of Darwin's work are often cited by authors when making claim (3).

2.1.1. Did Darwin discuss BA in the Descent of Man?

Darwin (1874: 129-133), in the *Descent of Man*, appeared to discuss the concept of BA in his discussion on the evolution of morality and sociality (Cronin 1991; Rosenberg 1992; Wilson and Wilson 2007; Wilson 2008a; Sober 2011). Or at least, he discussed traits that appeared to match Haldane's definition of BA, namely; individually costly but socially beneficial:

> It must not be forgotten that although a high standard of morality *gives but a slight or no advantage to each individual* man and his children over the other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly *give an immense advantage to one tribe* over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to *sacrifice themselves for the common good*, would be victorious over most other tribes; and this would be natural selection. (Darwin 1874: 132. Emphasis added).

What Darwin argued for here is that "morality" (namely, behaviours directed at helping others), in early humans, does not result in a direct benefit to the individuals that bear them, but will be beneficial to the group. Therefore, at first glance, this appears to fit the definition of BA from Haldane; indeed, some authors have made this claim (e.g. Wilson and Wilson 2007). So, it could be argued that Darwin was the first to develop the concept of BA, albeit under a different name and for the special case of "higher" moral faculties of humans. However, I will show that the concept of morality that Darwin argued for is not the same as BA, instead it is more similar to psychological altruism.

To begin with, although Darwin did speak of the possible costs and benefits of moral behaviour, as the above quote alludes to, for him, these are the *results* of morality, not its defining features. For Darwin (1874: 110-112), there is no clear distinction between instinctive and moral behaviours. He argued that there is no way to objectively assess the "motives" (*intentionality*) behind any seemingly moralistic behaviour. In other words, Darwin objected a previous distinction between instinctive and moral behaviours, namely: behaviours that are performed on impulsive reflex (i.e. immediate) are instinctive, whereas behaviours performed after deliberation (and that are for the benefit of others) are intentional, and thus moralistic. This distinction was based on the idea that moral behaviours are only possible by animals with rationality *because* moral behaviours are not instinctive, but require forethought and intention (deliberation). Darwin argued against this view, he claimed that there are cases of behaviours in animals — all of which are for the benefit of others and would be classed as moral if performed by humans — that appear to be performed after deliberation. Moreover, conversely he argued that there are cases of moral behaviours in humans that seem to be performed instinctively. Darwin argued, consequently, that instead of a distinction between instinctive and moral behaviours there should be a distinction between moral and non-moral animals (i.e. capable or not of morality):

> As we cannot distinguish between motives, we rank all actions of a certain class as moral, *if performed by a moral being*. A moral being is one who is capable of comparing his past and future actions or motives, and of approving or disapproving of them. We have no reason to suppose that any of the lower animals have this capacity; therefore, when a

> Newfoundland dog drags a child out of the water, or a monkey faces danger to rescue its comrade, or takes charge of an orphan monkey, we do not call its conduct moral. But in the case of man, who alone can with certainty be ranked as a moral being, actions of a certain class are called moral, whether performed deliberately, after a struggle with opposing motives, or impulsively through instinct, or from the effects of slowly-gained habit. (Darwin 1874: 111-112. Emphasis added).

This move allowed Darwin to discuss the concept of morality from an evolutionary perspective. This is because instead of needing to explain moral behaviours from a purely psychological perspective, which is entailed by the distinction he argued against, Darwin could explain how humans evolved to be animals capable of morality. His solution was that the social instincts were key, but also the emergence of intelligence:

> The following proposition seems to me in a high degree probable — namely, that any animal whatever, endowed with well-marked social instincts, the parental and filial affections being here included, would inevitably acquire a *moral sense* or conscience, *as soon as its intellectual powers had become as well, or nearly as well developed, as in man*. (Darwin 1874: 98. Emphasis added).

I argue then that for Darwin, even though he rejected a previous definition of morality based on instinctive and deliberative behaviours, morality is a concept that is necessarily to do with intentionality, as shown by the above quotes. This is because, to be a moral animal, an animal must be capable of intentionality in order to reflect and assess upon previous and future behaviour. Therefore, it is clear that if Darwin's concept of morality is at all similar to our current understanding of altruism then, by this, we must mean *psychological* altruism rather than biological altruism. Moreover, that Darwin's concept of morality is closer to psychological altruism rather than BA further highlights why the concept of altruism was not widely used in biology prior to Haldane. The concept of altruism, as originally developed by Comte, was a psychological one necessarily to do with intentionality. As I highlighted in the previous chapter (section 1.1.1.), within biology behaviours were not studied from a psychological perspective, they were considered instinctive, therefore the concept of (psychological) altruism was not required. It was not until Haldane — with his biological notion of altruism defined by costs and benefits of behaviour rather than intentionality — that the concept of altruism could be applicable to biological research.

However, it could be claimed, contrary to my argument, that even though Darwin's concept of morality is closer to psychological altruism than BA, he still discussed traits that are socially beneficial but individually costly, i.e. Haldane's BA, because he argued that there are behavioural examples in animals that if performed by humans would be considered moral. In other words, if there are examples of behaviours in animals that are for the benefit of others and would be considered moral in humans, and if a high degree of morality in humans can be costly to individuals (but beneficial to the group, as the above quote above — Darwin 1874: 132 — shows), then it can be argued that Darwin also implied, possibly indirectly, that there are individually costly but socially beneficial traits in animals; i.e. Darwin discussed the concept BA too. Although this argument is plausible, it does not stand up after a closer inspection of Darwin's argument. What this counter argument does not take into account is that, unlike Haldane, Darwin did not argue for a specific trait that is beneficial to the group but costly to the individual. Rather, Darwin discusses the possible costs, or more accurately, the possible *lack of advantage* that are the *results of certain instincts*. It must be remembered that for Darwin (1874: 97-100) the "social instincts" are essential for morality, not only intentionality; he argued that social instincts are the basis from which morality evolved. By social instincts Darwin meant cooperative traits that cause individuals to live in social groups:

> [But] it is a more probable view that these sensations [of unease/anxiety in individuals when separated from their groups] were first developed, in order that those animals which would profit by living in society, should be induced to live together, in the same manner as the sense of hunger and the pleasure of eating were, no doubt, first acquired in order to induce animals to eat. (Darwin 1874: 105).

Social instincts are necessary for the evolution of morality because, as the above quote alludes to, these instincts cause individuals to cooperate and live in social groups. Therefore, Darwin (1874, chapters 1-5) argued that as early humans evolved greater capacities of intelligence, they were able to reflect on these feelings induced by the social instincts and consequently, psychological concepts of right and wrong emerged. In other words, humans could reflect on these feelings of unease when they do not act for the good of their group, for example, and adjust their future behaviour accordingly.

The important point I am trying to emphasize here is that Darwin did not define social instincts according to fitness costs and benefits, but rather he defined them as traits that cause their bearers to cooperate for the benefit of their group, or to at least associate together (live socially). Any cost or benefit to the *individual* is just the possible byproduct of these traits. For instance, Darwin (1874: 105) argued that these social instincts could have evolved because they cause their bearers to cooperate in groups, which *if beneficial* would lead to those social groups outcompeting selfish/solitary individuals. This argument is similar to Darwin's argument for the evolution of morality in humans, which has been interpreted as a group selection argument (Ruse 1980; Rosenberg 1992; Wilson and Wilson 2007; Chancellor 2015). However, that Darwin spoke of group selection does not imply that he also discussed BA.

2.1.2. Darwin's "special difficulty" with eusociality

> I will not here enter on these several cases, but will confine myself to one *special difficulty*, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect-communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind. (Darwin 1859: 175. Emphasis added).

The above remarks from Darwin are often quoted by such authors, as above, who claim that eusocial insects posed a serious problem for Darwin because of the "altruistic" worker castes. However, these remarks from Darwin are often quoted out of context. Darwin did indeed find eusocial insects a major stumbling block when developing his theory of natural selection. It has even been argued that they played a part in the fact that Darwin did not publish the *Origin* until 1859 even though he started developing his theory in 1838 (Richards 1983; Prete 1990; van Wyhe 2007: 193).[6] Eusocial insects, particularly honey bees and ants, were studied for their colonial organization and their unique traits prior to Darwin. Aspects such as the ecological success of eusocial insects, the reproductive division of labour within colonies, the ability of honey bees to create almost uniform hexagonal honeycomb cells, the ability of some ant species to use workers of other species as their own (the so-called "slave-making" ants),

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[6] It has been argued that the principle reason Darwin took so long to publish his theory was because he wanted to be thorough in his application of it, as well as wanting to finish other, pre-planned, works beforehand (van Wyhe 2007).

and many more, were well-known phenomena.[7] Therefore, any new theory of evolution would need to address these well-known and fascinating aspects of eusocial insects. However, at first Darwin struggled to explain many aspects of eusocial insects using his theory of natural selection (Prete 1990). But by the time he began writing the *Origin*, Darwin had overcome all but one problem that eusocial insects posed to his theory, one that he referred to as the "special difficulty", as in the quote above (Richards 1981: 229, 1983; Prete 1990).

What most authors refer to when they claim that Darwin discussed BA in the *Origin* is the "special difficulty". But for Darwin, this "special difficulty" was not BA, nor was it that most members of the colony do not reproduce — and that even in some species the worker castes evolved to be physically sterile. Instead, the special difficulty for Darwin posed by eusocial insects was the fact that, in some species, the *non-reproductive castes have evolved to be behaviourally and/or morphologically different to the reproductive castes*, *despite not directly reproducing their own kind* (Cronin 1991; Ratnieks et al. 2011). Specifically, Darwin (1859: 175-180) found the fact that the non-reproductive castes have evolved to be different to the reproductives, and that in some cases further physical subcastes have evolved such that some colonies have two or more non-reproductive physical subcastes (i.e. soldiers, minor or major workers, etc.), to be a major problem for his theory of natural selection. To illustrate this, it will be useful to take a more detailed look at Darwin's discussion of this problem in the *Origin*.

Sterility in eusocial insects was not overly problematic in Darwin's opinion. Darwin (1859: 175-176) argued that because sterility occasionally occurs in other species then it could

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[7] The scientific study of eusocial insects dates back to at least the nineteenth century, a prime example being the classical work of Kirby and Spence (1818); see also: Richards (1981); Prete (1990).

also occur in eusocial insects, and, that it is not problematic that this occurred in the worker castes. Darwin argued that it would not be a disadvantage if some eusocial insect colonies occasionally produced workers that were sterile but still able to work. In fact, he argued that it could even be advantageous:

> How the workers have been rendered sterile is a difficulty; but not much greater than that of any other striking modification of structure; for it can be shown that some insects and other articulate animals in a state of nature occasionally become sterile; and if such insects had been social, and had it been profitable to the community that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection. (Darwin 1859: 175-176).

Darwin passed over the issue of worker sterility relatively quickly, hence highlighting the fact that this was not the "special difficulty". For Darwin, the main difficulty was to explain how the non-reproductive castes could evolve different traits and instincts to the reproductives, when they do not reproduce their own kind:

> But I must pass over this preliminary difficulty [sterility]. The great difficulty lies in the working ants differing widely from both the males and the fertile females in structure […] and in instinct. (Darwin 1859: 176).

> But with the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how is it possible to reconcile this case with the theory of natural selection? (Darwin 1859: 176).

In other words, how could the non-reproductive castes evolve to be different from the reproductives and to each other (for example soldiers and workers, or different types of worker within the same colonies) when they do not produce their own offspring? Darwin struggled with this question for a long time. He first came across the problem in the 1840s and only managed to come up with his solution — after multiple attempts — once he had already started writing the *Origin* in the mid-1850s (Richards 1981, 1983; Prete 1990). Darwin's solution was that natural selection affects the workers via the reproductives that produce them. I will assess in more detail Darwin's solution to his special difficulty in *section 2.2.*, but the important point I want to emphasize here is that Darwin's (1859: 175-180) "special difficulty" was to do with the issue of how polymorphism, and other unique traits, of the non-reproductives castes could have evolved despite the fact that they do not reproduce. Hence, the "special difficulty" for Darwin was not that the worker castes of eusocial insects do not reproduce, or that they are biologically altruistic. Therefore, to claim then, that Darwin discussed and/or developed the concept of BA (albeit without using the term altruism), as many authors have done (Cronin 1991; Rosenberg 1992; Wilson and Wilson 2007; Sober 2011), would be historically inaccurate. Indeed, such a claim could be said to be guilty of viewing history through the eyes of contemporary ideas, or so-called Whiggish historiography. In other words, these authors are imposing a modern concept, which did not exist in Darwin's time, onto Darwin's arguments, and then subsequently judging his argument based on this. Whilst Whiggish historiography is not necessarily an issue in itself, particularly in the history of science (Griffiths 1995), in this particular case I have argued that it is problematic. When authors claim that Darwin discussed and/or developed BA, they do so in order to add legitimacy to the concept, i.e. if one of the founding figures of modern biology discussed BA, then this lends support to the view that the concept is of fundamental importance to biology. However, I have already shown in the previous chapter that BA was not considered a fundamental issue for eusociality research until around the 1960s.

2.1.3. Why did claims (2) and (3) emerge?

Why then have later authors claimed that Darwin's "special difficulty" was with the concept of BA? Some have argued that this misinterpretation of Darwin traces back to E. O. Wilson (1971, 1975b) and two of his seminal books of the 1970s, *The Insect Societies* and *Sociobiology*, respectively (Hunt 2007; Ratnieks et al. 2011). In his discussion on caste determination, Wilson (1971: 146-147) seemed to interpret Darwin's "special difficulty" to be about how the non-reproductive castes could evolve to be different from the reproductives. However, later, in his discussion on the evolution of eusociality and social behaviour, Wilson (1971: 320, 1975b: 117-118) was less clear about Darwin's "special difficulty". For instance, Wilson began by quoting Darwin's claim that eusocial insects presented him with a special difficulty — the first sentence from Darwin's quote at the begging of 2.1.2., above — then subsequently framed the problem with the following question:

> How, [Darwin] asked, could the worker caste of insect societies have evolved if they are sterile and leave no offspring? (Wilson 1971: 320).

Which, incidentally, is very similar to how many authors have framed the BA paradox, as I argued in chapter 1 (Gadagkar 1990; Cronin 1991; Nowak et al. 2010). Indeed, Wilson (1971: 320) actually used the term "paradox" immediately after the quote above. In asking this question immediately after quoting Darwin's "special difficulty" sentence, Wilson is in danger of causing the reader to conflate Darwin's lesser issue of sterility with his greater issue of polymorphism amongst the non-reproductive castes. Moreover, a few sentences later Wilson used the concept of BA as if this concept was the problem Darwin referred to as the "special difficulty":

> To save his own theory, Darwin introduced the idea of natural selection operating at the level of the family […]. With the entire family serving as the unit of selection, it is the capacity to generate sterile but *altruistic* relatives that becomes subject to genetic evolution. (Wilson 1971: 320. Emphasis added).

In fact, the claim that Wilson (1971) was the first to make the reference to Darwin's special difficulty (Ratnieks et al. 2011: 482), that prior to 1971 this section of the *Origin* was rarely quoted or referenced (Hunt 2007: 184) is not completely true. Actually, Darwin's special difficulty was referenced a number of times prior to 1971 (Weismann 1893: 313-314, 1909: 35; Wheeler 1923: 255; Emerson 1939: 196-197, 1960: 309, 328; Allee et al. 1949: 31; Richards 1953: 159-160). However, these authors focus more on Darwin's solution to his great difficulty, with some using Darwin to justify their own theory (which I will discuss further, in section 2.2. below). M. T. Ghiselin (1969) discussed Darwin's argument for the evolution of eusociality, and sociality in general, within the context of BA. However, Ghiselin (1969: 58) used a broad definition of BA that appears to be synonymous with cooperation. Wilson used the definition of BA from Hamilton (1964a) with reference to Darwin's special difficulty. Therefore, Wilson appears to be the first to (indirectly) suggest that the concept of BA and its associated paradox has been problematic for biology since at least Darwin. It is useful to point out here that most authors prior to Wilson, that had argued for the existence of BA in nature, did not make reference to Darwin's "special difficulty" (Haldane 1932; Sturtevant 1938; Williams and Williams 1957).

E. O. Wilson has had a huge influence on eusociality research with both his *The Insect Societies* and *Sociobiology* books being widely referenced (Dugatkin 2006). Wilson (1975b) even made the claim that BA is the central problem that sociobiology must solve (Dugatkin 2002). And in fact, after Wilson (1971) discussed, and quoted, Darwin and his discussion of the "special difficulty" of eusocial insects from the *Origin*, subsequent authors began to make the claim (3), above, that Darwin discussed and/or developed the concept of BA (Hunt 2007; Ratnieks et al. 2011). But it is unlikely that a few pages from these two books of E. O. Wilson could be the only reason why so many authors have subsequently claimed that Darwin discussed BA, or, that BA has been a fundamental problem since Darwin.

The emergence of the claims (2) and (3) is mainly a result of the widespread use of the concept of BA after the introduction of kin selection. As I argued in the previous chapter, Hamilton applied the concept of BA to eusocial insects due to the Sturtevant-Hamilton problem of sterility. This led Hamilton to reject the colonies-as-individuals argument, that was previously popular, and apply the theory of kin selection to the evolution of eusociality. The groundbreaking success of inclusive fitness and kin selection led to the widespread use of BA within eusociality research. Subsequent authors followed Hamilton in conceptualising the evolution of eusociality as the evolution of BA. But because the majority of research predominately focused on the explanatory models, there was little attention paid to why Hamilton applied the concept of BA to eusocial insects; namely the Sturtevant-Hamilton problem of sterility. Consequently, the fact that the Sturtevant-Hamilton problem of sterility does not entail that the evolution of BA is necessarily required for the evolution of eusociality went unnoticed by the majority of authors. In other words the majority of authors in post-Hamiltonian eusociality research, simply applied the concept of BA to the worker castes following Hamilton. But BA cannot be assumed, it must be argued both theoretically and empirically. This is because parental manipulation can also lead to the emergence of non-reproductive worker castes (Kapheim et al. 2015). But due to the lack of critical attention towards the use of the concept of BA, this point was rarely emphasised. For these reasons, the use of the concept of BA emerged and remained widespread within post-Hamiltonian eusociality research.

As a result of this mainstream view, many authors in the recent decades have made the inaccurate historical claims (2) and (3), above. Specifically, because many authors today conceptualise the evolution of eusociality as the evolution of BA, following Hamilton, they often view the history of eusociality research as being centred around the problem of BA too (Ratnieks et al. 2011). Thus, it is often claimed that BA has been a fundamental issue for eusociality research since Darwin (claim (2)), and that Darwin discussed and/or developed the concept (claim (3)). But, as I showed in chapter 1, claim (2) is incorrect; BA has only been considered a fundamental problem for eusociality research since around the 1960s, due to Hamilton and the theory of kin selection. Many authors interpreted Darwin's "special difficulty" with eusocial insects as one to do with BA. Even in cases like that of J. M. Herbers (2009), who recognised that Darwin's "special difficulty" was not with BA, but then went on to discuss the "special difficulty" as if it were about the BA paradox since, she argued, eusociality researchers have equated the "special difficulty" with the BA paradox. This general interpretation of Darwin's "special difficulty" as if it were to do with the problem of BA is likely due, in part, to E. O. Wilson, who seemed to originally argue for claims (2) and (3) (Hunt 2007: 183). But, more importantly, it is a result of the current widespread use of BA within eusociality research.

However, this is not only an important issue for historical accuracy, but also because claims (2) and (3) are used to add historical justification for the continued use of BA to describe the non-reproductive castes of eusocial insects (Ratnieks et al. 2011). The current theoretical perspective has affected recent historiographies on the concept of BA, which in turn, act to justify current theoretical explanatory approaches. More specifically, I argue that, due primarily to the Sturtevant-Hamilton sterility problem, authors typically only conceptualise the evolution of eusociality as the evolution of BA. And subsequently, they view the history of evolutionary studies on eusocial insects to be centred around BA. Additionally, they then apply these historical claims in their theoretical work as motivation, and historical precedence, of conceptualising the evolution of eusociality as the evolution of BA. Here we see an example:

> Those on the forefront of evolutionary biology, from Charles Darwin through E. O. Wilson and W. D. Hamilton, have found the questions surrounding cooperation and altruism in animals to be both fascinating and frustrating. Darwin (1859) found the cooperative and *altruistic* [behaviours] that are typically displayed by sterile caste members in the social insects ‘‘one special difficulty, which at first appeared to me to be insuperable, and actually fatal to my whole theory,’’ while Wilson described such actions as ‘‘the central theoretical problem of sociobiology’’. (Dugatkin 2002: 459. Emphasis added).

Thus, claims (2) and (3) act to justify claim (1) — that BA *is* a fundamental problem for eusociality research currently. This is not only the case for the concept of BA. Some authors also interpret Darwin’s solution to his “special difficulty” in order to justify their explanatory models for the evolution of eusociality. For example, some argue that Darwin’s solution was the first form of kin selection (Ghiselin 1974: 216-218; Wilson 1975b: 86; Queller and

Strassmann 1998: 166; Cronin 1991; Herbers 2009: 216), whilst others argue that Darwin was arguing for group selection (Hölldobler and Wilson 2009: 16-18; Nowak et al. 2010: 1057; Chancellor 2015). As with the concept of BA, these historical claims are used to justify current theoretical positions with respect to the evolution of eusocial insects. For these reasons, I think it is useful to take a brief look into what Darwin actually argued for as his solution to his special difficulty of eusocial insects, which I will do in the next section.

2.2. Darwin and eusociality: group selection, kin selection, or something else?

> [Participants] on both sides of today's debate about the levels of selection […] have invoked the past in defence of their own positions and criticism of their opponents'. (Ruse 1980: 629)

As I have argued throughout this chapter, in post-Hamiltonian eusociality research many authors have used Whiggish historiographies to justify their current theoretical/conceptual perspectives. This also applies to the debate over the two main explanatory models that are used to explain the evolution of eusociality, namely kin selection and group selection (i.e. MLS). For instance, B. Hölldobler and E. O. Wilson (2009: 16-48) began their history of theoretical explanations for the evolution of eusociality with Darwin and they interpret his explanation as group selection, which is the explanatory model that they also favour (see also, Wilson and Hölldobler 2005; Reeve and Hölldobler 2007; Wilson 2008b). On the other hand, R. H. Crozier (2008) interprets Darwin as the first to argue for kin selection as an explanation for the evolution of eusociality, a position Crozier favours. It is therefore important to assess what Darwin argued for with respect to the evolution of eusociality.

I will assess Darwin's solution to the "special difficulty" whilst bearing in mind the effect that the widespread use of the concept of BA had on eusociality researchers in the post-Hamiltonian era. I will argue that Darwin's solution was neither kin selection nor group selection.[8] That in fact, Darwin's explanation was not from the perspective of the non-reproductive castes but, rather, from the perspective of the reproductives. Thus, I will further support the claim that Darwin did not develop or discuss the concept of BA.

As I have pointed out above, Darwin only found a solution to the "special difficulty" — the problem of how the non-reproductive castes could evolve to be different to the reproductives, and each other, when they do not reproduce their own kind — after he began to write the *Origin* (Richards 1983; Prete 1990). Darwin began the argument for his solution in the following way:

> This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that *selection may be applied to the family*, as well as the individual, and may thus gain the desired end. (Darwin 1859: 177. Emphasis added).

Since Darwin (1859: 177) began his argument by claiming that selection can be 'applied to the family, as well as the individual', it has been argued (Chancellor 2015) that Darwin's solution to his "special difficulty" is a form of MLS, specifically group selection. G. Chancellor (2015: 145) considered the quote above to be clear evidence that Darwin argued for group selection

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[8] I am not here providing an argument of whether Darwin did or did not discuss MLS in general. The aim here is to assess what Darwin argued for as the solution to his *special difficulty*. For a more detailed debate on Darwin and the issue of levels of selection see: Cronin 1991; Borrello 2010; Chancellor 2015, and references therein. However, I think it is clear that Darwin did argue for group selection at least once when he discussed the evolution of morality in humans.

to explain eusocial insect evolution. Whereas others (Herbers 2009: 216) have used the above quote from Darwin to argue that his solution was kin selection, i.e. that non-reproducing individuals can evolve to be different to their reproductive relatives via the success of the latter. In other words, even though the worker castes do not reproduce, if they benefit the reproductives (and the colony), then the reproductives will be more successful at producing offspring that can also produce similar workers.

However, it is important to note that Darwin did not discuss the "special difficulty" with eusocial insects in reference to the debate over the levels of selection, instead he discussed this issue whilst trying to argue for his theory of natural selection in general. Moreover, he specifically used this "special difficulty" in order to argue against Lamarckism (Hamilton 1972: 194; Richards 1981) — a point I will return to shortly. Therefore, it is within this context that Darwin should be interpreted. Darwin's treatment of eusocial insects in the *Origin* can be split into two parts; a solution to the "special difficulty" and an explanation for the evolutionary origins of eusocial insects.

It should be noticed that, as opposed to the earlier quote above (Darwin 1859: 177), for the solution to the "special difficulty", Darwin specifically discussed natural selection affecting the reproductives rather than the more vague notion of selection being applicable to the family. This is because in the former case Darwin just made a general claim that selection can operate at multiple levels — which is clear by his later arguments such as in *The Descent of Man*, see footnote 2 above. Indeed, after Darwin (1859: 177) stated that selection can be applied to the family he discussed cases of vegetable and cattle breeding. Whereas in the case of eusocial insects, for which he provided a detailed explanation, Darwin argued that natural selection could produce non-reproductives that are morphologically different to the reproductive caste by affecting the latter only, as is seen in the following quote:

> With these facts before me, I believe that natural selection, *by acting on the fertile parents*, could form a species which should regularly produce neuters, either all of large size with one form of jaw, or all of small size with jaws having a widely different structure; or lastly, and this is our climax of difficulty, one set of workers of one size and structure, and simultaneously another set of workers of a different size and structure; — a graduated series having been first formed, as in the case of the driver ant, and then the extreme forms, from being the most useful to the community, having been produced in greater and greater numbers *through the natural selection of the parents which generated them*; until none with an intermediate structure were produced. (Darwin 1859: 179. Emphasis added).

But for the evolutionary origins of eusociality in insects, Darwin's argument was slightly different:

> Thus I believe it has been with social insects: a slight modification of structure, or instinct, correlated with the sterile condition of certain members of the community, has been advantageous to the community: consequently the fertile males and females of the same community flourished, and transmitted to their fertile offspring a tendency to produce sterile members having the same modification. And I believe that this process has been repeated, until that prodigious amount of difference between the fertile and sterile females of the same species has been produced. (Darwin 1859: 177).

This argument could, and has been, interpreted as group selection. In other words, Darwin argued for inter-colony (inter-community) selection (Borrello 2010: 7-12; Chancellor 2015). But, I argue, these interpretations are misplaced. What Darwin argued for here was simply individual selection amongst the reproductives of the population. Specifically, if some reproductives could cause a portion of their offspring to be sterile — or more appropriately, to be non-reproductive workers — and, therefore an incipient eusocial colony with a reproductive division of labour. If this was beneficial to the reproductives in producing more fertile offspring, then the reproductives that can produce such incipient colonies, by coercing some of her offspring into becoming non-reproductive offspring, would be more fit than solitary reproductives that cannot. Natural selection would then lead to an increase in such incipient colonies with reproductive division of labour in these species. To interpret Darwin from the perspective of the levels of selection debate misses the subtlety of this argument for the evolution of eusociality. This is important because Darwin's argument could directly affect current theoretical perspectives on the evolution of eusociality, which I will argue for below.

As mentioned above, Darwin used the example of the eusocial insects, specifically his "special difficulty" with them, in order to argue against Lamarckism.[9] For Darwin, the evolution of sterility (i.e. the non-reproductive caste) was an essential element for such complex cooperation in eusocial insects if natural selection is true:

> As ants work by inherited instincts and by inherited tools or weapons, and not by acquired knowledge and manufactured instruments, a perfect division of labour could be effected

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[9] Although it is unclear exactly what Darwin meant by Lamarckism; R. W. Burkhardt Jr. (2013) argued that Darwin also allowed for the inheritance of acquired characters/traits in the theory of natural selection. However, the point here is not to debate over Darwin's interpretation of Lamarck but, instead, to emphasize that Darwin did not discuss the "special difficulty" in the context of the levels of selection debate.

> with them only by the workers being sterile; for had they been fertile, they would have intercrossed, and their instincts and structure would have become blended. (Darwin 1859: 180).

> For no amount of exercise, or habit, or volition, in the utterly sterile members of a community could possibly affect the structure or instincts of the fertile members, *which alone leave descendants*. I am surprised that no one has advanced this demonstrative case of neuter insects, against the well-known doctrine of Lamarck. (Darwin 1859: 180. Emphasis added).

What Darwin argued for in the quotes above is that, unlike humans or other higher animals, behavioural and physiological specialisation of the workers in eusocial insects could only occur under natural selection if the workers do not reproduce. This is because their specialisation is dependent primarily on inheritance rather than being acquired via learning or culture.[10] Therefore, I argue, Darwin did not consider the workers to be "visible" to natural selection, i.e. the non-reproductive castes are not under direct individual selection and therefore do not have unique personal fitness values — they depend on the colony for their survival. Darwin turned his "special difficulty" with the eusocial insects, which he initially thought of as fatal to his theory of natural selection, to his advantage as he considered it strong evidence against alternative theories of evolution, specifically Lamarckism.

It is important to note that Darwin's explanation for the evolution of eusocial insects is similar to the "germ-soma" theory by Weismann, Fisher, et al., that was so prevalent in pre-

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[10] Darwin (1873: 417) did not discount that individual workers could adapt their behaviour or that some could have more "sagacity" than others, however he argued that this sagacity, as well as their behavioural repertoire, is also ultimately dependent on selection of the reproductives.

Hamiltonian eusociality research, as shown in chapter 1. Indeed, Weismann (1893: 313-314) summarised Darwin's explanation as selection favouring reproductives that produce "sterile" workers, and that those colonies with sterile workers would do better than those without. Similarly, O. W. Richards (1953: 159-160), argued that the non-reproduction (or sterility) of worker castes was not a problem for Darwin because natural selection affects colonies via the reproductives. In other words, the special traits of the non-reproductive castes can evolve by natural selection affecting the reproductive castes. For example, if a reproductive can produce a colony formed of two types of non-reproductive caste (e.g. workers and soldiers), and if these colonies do better than ones with only one type of non-reproductive caste, then selection will favour those reproductive that can produce colonies with two types of non-reproductive caste.

Whether or not Darwin's explanation is supported by current empirical data is unimportant for the current point under consideration. What is important is that it is a mistake to view Darwin's explanation through the perspective of the levels of selection debate, or the BA paradox, because these issues were not the focus of Darwin's argument. Darwin's explanation for the evolution of eusociality was in two parts. The first aspect of his explanation was that, in the evolutionary origins of eusociality, reproductives that produced non-reproductive workers, and thus colonies, were more fit than those that did not. The second aspect, which dealt specifically with the "special difficulty", was that the non-reproductive castes can evolve special traits by selection affecting the reproductives that produce them. But Darwin's explanation was neither group selection nor kin selection via worker BA, as many authors have argued (see above). Instead, Darwin was simply applying classical selection to the reproductives producing a colony. Natural selection affects colonies (and therefore the non-reproductive castes) via the reproductives, and this is what I argue Darwin meant by natural selection being applied to communities in eusocial insects.

More importantly, this shows that 1) Darwin took the perspective of the reproductives rather than the perspective of the workers, and 2) he did not consider workers as biologically altruistic.

As shown in Chapter 1, Hamilton appeared to be aware that Darwin's "special difficulty" was not BA. However, Hamilton (1972) argued that because Darwin was not aware of Mendelian genetics, he was also unaware that colonies are not genetically homogeneous and unaware therefore, of possible genetic conflict within colonies. Hamilton argued that this is why Darwin did not consider the evolution of the non-reproductive castes as problematic. Like Hamilton, Hölldobler and E. O. Wilson (2009: 17) also argued that, had Darwin been aware of Mendelian genetics, he would have considered the evolution of non-reproductives as the major problem because, if the members of the colony are not genetically homogeneous, then the fact that individuals "give up" reproduction in favour of helping others becomes problematic (i.e. the BA paradox). As I highlighted in the previous chapter, Hölldobler, E. O. Wilson, as well as most current eusociality researchers, formulate their views from the perspective of the worker castes due to the Sturtevant-Hamilton problem of sterility. Darwin, on the other hand, took the perspective of the reproductives. According to Darwin, throughout the evolutionary history of eusociality the worker castes were never evolutionary individuals in their own right. As above, from the evolutionary origins of eusociality the worker castes were not directly affected by natural selection, instead the reproductives that produced them were. And more importantly, instead of being a problem for Darwin, the fact that some members of the colony are "sterile" proved to be essential evidence for his theory over Lamarckism; the reproductive division of labour was what enabled Darwin to explain away the "special difficulty".

There is another set of examples from eusocial insects that are often taken as clear cases of BA. But these are not instances of sterility or non-reproduction but, instead, examples of workers sacrificing their lives. For example, because the stings of honey bee workers are barbed they typically die if they sting intruders in defence of the colony, whereas the queen's sting is not barbed and not used to defend the colony (Queller and Strassmann 1998: 317). Darwin (1859: 151-152) also discussed the case of self-sacrifice by worker honey bees when stinging in defence of the colony. Some authors (Gardner and Foster 2008: 1-2; Chancellor 2015: 147) have used this to claim that Darwin did discuss BA, as his explanation for the barbed sting of honey bee workers was that they evolved because they were beneficial to the community (colony). In other words, it is argued that Darwin's explanation fits the definition of BA because he claimed that the barbed sting benefits others at the cost of the life to the worker. But to interpret Darwin's discussion of self-sacrificing traits in eusocial insects in terms of BA has implications for the understanding of Darwin's broader argument for the evolution of eusociality. This is because, if an individual is biologically altruistic, then this implies that this individual is under natural selection and therefore has a personal fitness value; otherwise it would not make sense to describe the individual as benefitting others at a *cost to its own fitness*. But, as I have just argued, from the evolutionary origins of eusociality, Darwin did not consider the non-reproductive castes as evolutionary individuals; i.e. the workers do not directly partake in natural selection. Therefore, to suggest that Darwin considered the self-sacrificing defence of the colony by workers as a case of BA is to imply that Darwin considered every member of the colony to be under individual selection, which I have shown to be incorrect.

Finally, to interpret Darwin's explanation in terms of kin selection (via worker BA) or group selection is not only historically inaccurate, but also risks affecting the current debate on the evolution of eusociality. This is because kin selection (via worker BA) and group selection are not the only possible theories for the evolution of eusociality (Hunt 2007), as I will explore in more detail in chapter 3. Thus, to restrict an interpretation of Darwin to one or another theory is dangerous because Darwin is still often invoked in order to justify current theoretical perspectives (Ruse 1980; Ratnieks et al. 2011). Not only was Darwin not aware of Mendelian genetics but, more importantly, he was not aware of the modern debate over the levels of selection and the theories of kin and group selection as we understand them currently (Borrello 2010: 7-14). Moreover, Darwin's argument for the evolution of eusociality, and consequently his solution to the "special difficulty", is, if at all, more similar to the theory of parental manipulation (which I explore in more detail in chapter 3) and colonies-as-individuals arguments (which I explore in chapters 4 and 5).

Conclusion

In this chapter I have argued that, within eusociality research, history is often appealed to in order to justify the present. In particular, many authors have claimed that Darwin discussed and/or developed the concept of BA. These claims are inaccurate however, as the concept of BA, and its associated paradox, did not become widely studied until around the 1960/70s due to the influential work of Hamilton, as I have shown in chapter 1.

I have highlighted that within post-Hamiltonian eusociality research, claims started to emerge arguing that BA has been a fundamental problem in biology since at least Darwin (claim (2)). Additionally, many authors have claimed that the reason why Darwin considered eusocial insects as the greatest difficulty to his theory of natural selection, which he referred to as the "special difficulty", was because of the BA exhibited by the non-reproductive castes (claim (3)). Such claims have the effect of justifying the current theoretical perspective, for example the widespread use of the concept of BA to describe the non-reproductive castes of eusocial insects. If an author argues that Darwin discussed a problem using the same concept or theory as themselves then this has the consequence of adding historical weight to their own argument (Ruse 1980), whether this is the intention of the author consciously or not.

However, I have shown that Darwin did not discuss or develop the concept of BA. In section 2.1.1., I argued that Darwin did not discuss the concept of BA in his argument for the evolution of morality in *The Descent of Man*. Many authors have argued that Darwin's concept of morality is the same as the modern concept of BA. However, this interpretation is inaccurate. Although Darwin did discuss the possible costs of moral behaviour, he argued that these were only possible consequences of the trait, not its defining feature. The key aspect of Darwin's argument was that moral behaviours were only possible in *moral animals*, because moral behaviours require intentionality. Thus, if Darwin's concept of morality can be said to be similar to the concept of altruism, we must mean by this that it is similar to *psychological altruism* rather than BA. In section 2.1.2., I demonstrated that, contrary to many claims, Darwin's "special difficulty" with eusocial insects in the *Origin* was not to do with the concept of BA. Rather, the "special difficulty" was the fact that the non-reproductive castes have evolved to be different to the reproductive castes (and in some cases amongst themselves, e.g. workers and soldiers) despite not reproducing their own kind. Consequently, claim (3) — that Darwin discussed and/or developed the concept of BA — is inaccurate. I argued, in section 2.1.3., that claim (3) mainly emerged due to the widespread use of the concept of BA within post-Hamiltonian eusociality research. I already highlighted in the previous chapter that claim (2) is also inaccurate, the concept of BA was not considered as a fundamental issue for eusociality research until at least the 1960s. Due to the success of kin selection, many authors conceptualised the evolution of eusociality as the evolution of BA, following Hamilton. Thus, the concept of BA came to be seen as a fundamental problem for eusociality research. Consequently, many authors viewed the history of eusociality research to be centred around the concept of BA and made the inaccurate claims (2) and (3).

In section 2.2., I argued that history is not only used to justify the continued widespread application of the concept of BA to eusocial insects, it is also used by opposing camps in the debate over the evolution of eusociality. Many authors use their interpretations of Darwin's solution to the "special difficulty" to either argue for kin selection and BA or to argue for group selection. For example, Hölldobler and E. O. Wilson (2009) began their overview of the history of evolutionary theories of eusociality with Darwin, and interpreted his explanation as group selection, which is the theory that they hold for the evolution of eusociality. Crozier (2008), in turn, claimed that Darwin was the first to argue for a form of kin selection via BA, which is the theory that he prefers. However, I argued that these claims are guilty of Whiggish historiography, they are attempts at judging the past from the perspective of the present.

Darwin's treatment of eusocial insects was constituted of two parts, the solution to the "special difficulty" and an explanation for the evolution of eusociality. For the solution to the "special difficulty", Darwin argued that the non-reproductive castes can evolve their special traits (e.g. polymorphism) by selection affecting the reproductives that produced them. This, in turn, led Darwin to an explanation for the evolutionary origins of eusociality. He argued that if some reproductives could cause a portion of their offspring to be non-reproductive workers, and if this was beneficial to the reproductives in producing more fertile offspring, then the reproductives that can produce colonies (via non-reproductive workers) would be more fit than reproductives that cannot. Those reproductives that can produce eusocial colonies would be selected for, and over evolutionary time, these colonies could evolve ever more complex division of labour due to selection affecting the reproductives.

I have argued that Darwin's solution to the "special difficulty", and by extension his argument for the evolutionary origins of eusociality, was not group selection. Darwin simply applied classical selection to reproductives that can produce eusocial colonies. Not only was Darwin not aware of the levels of selection debate, his main purpose when tackling the "special difficulty" was to overcome a potentially fatal problem to his theory. In actual fact, he even considered his solution to the "special difficulty" as strong evidence for his theory of evolution by natural selection against alternatives such as Lamarckism. Moreover, neither is kin selection via BA an accurate interpretation of Darwin's solution to the "special difficulty". Darwin did not consider the non-reproductive castes as biologically altruistic. Instead, unlike modern kin selection theorists, Darwin took the perspective of the reproductives, and argued that the non-reproductive castes could evolve if they benefit the reproductives that produced them. It could be argued that this is a general form of kin selection, albeit without the notion of inclusive fitness — Darwin was unaware of Mendelian genetics. But, as I highlighted in the previous chapter, current kin selection theorists typically conceptualise the evolution of eusociality as the evolution of BA. Consequently, authors who interpret Darwin's solution as kin selection, such as Crozier (2008), are implying that Darwin argued that eusocial insects evolved due to the altruistic workers and kin selection.

Thus, again, this is not simply an issue over historical accuracy. The Whiggish interpretations of Darwin's treatment of eusocial insect evolution in the *Origin* risk affecting the current debate over the evolution of eusociality. Interpreting Darwin's solution to the "special difficulty" as either group selection or kin selection (via worker BA) adds historical weight to current arguments for each perspective, to the detriment of possible alternatives. I have argued that both interpretations are inaccurate; Darwin did not apply group selection to the evolution of eusociality and, even though his argument could be interpreted as a general form of kin selection, Darwin did not consider the non-reproductive castes as biologically altruistic. Consequently, *if* Darwin's solution to the "special difficulty" is similar to any current theory, it is more similar to parental manipulation (which is compatible to kin selection — see chapter 3) as his explanation was from the perspective of the reproductive; he argued that eusocial insects evolved due to the ability of reproductives to produce non-reproductive workers. This could have implications for the current debate over the evolution of eusociality; not only did Darwin not consider the non-reproductive castes as biologically altruistic, but he did not consider them to be evolutionary individuals in their own right. In other words, Darwin argued that, since the evolutionary origins of eusociality, the non-reproductive worker castes did not directly partake in natural selection; such a position could be worth reconsidering once again by current eusociality researchers.

Chapter 3 — Evolutionary theories of eusociality: is BA fundamental?

Introduction

Recently, J. H. Hunt (2007: 183-187) has challenged the claim that the concept of BA is a fundamental problem for eusociality research (claim (1)). He argued that, in fact, the widespread use of BA has impeded eusociality research because it has led to important biological factors to be ignored, e.g. phenotypic plasticity. Moreover, Hunt argued that BA is just one of multiple ways to conceptualise the non-reproductive castes, as is supported by the fact that the concept did not become widespread until after Hamilton introduced his theory of kin selection. On the other hand, F. L. W. Ratnieks and colleagues (2011), have argued that the concept of BA *is* a fundamental problem for eusociality research, but this went relatively unnoticed until the important work of J. B. S. Haldane (1932), Hamilton (1964a, 1964b, 1972), J. Maynard Smith (1964), and more.

In this chapter I will assess the claim, above, that the concept of BA is a fundamental problem for eusociality research (claim (1)). I will do so by assessing the role of the concept of BA within evolutionary studies of eusocial insects. In the previous chapter I argued that the current widespread use of the concept of BA led to the incorrect historical claim that the concept has been a fundamental problem for eusociality research since Darwin. Instead, as I highlighted in chapter 1, the concept only became widely used in the 1960s due to the influence of Hamilton and kin selection theory. Prior to this time BA was rarely employed by eusociality researchers, with alternatives such as the superorganism, coercion, the "germ-soma" argument, and others, in use instead. The concept of the superorganism has seen a resurgence in the 1980s, due to the introduction of new group selection. Since then, the presence of colony selection has been demonstrated in many species, typically the most evolutionary derived species with large, complexly-organized colonies. In such species, the colony is the unit of selection; i.e. a superorganism. This has consequences for the use of the concept of BA; if the colony is the unit of selection, then the concept of BA is not applicable to the workers. This is because the concept is only applicable to evolutionary individuals since its definition is based on fitness consequences to its bearer; BA is a trait that causes its bearer to benefit others at a cost to itself. But in superorganisms, the non-reproductive castes are not evolutionary individuals in their own right, they are parts of a higher-level system. Therefore, the concept of BA is only theoretically applicable to eusocial insect species in which colony selection does not occur. This is typically the case in the simplest species, which are the target of evolutionary theories for the origin of eusociality.

Firstly, in section 3.1., I address some current definitional issues with the concept of BA. I will argue that there are currently multiple definitions of the concept of BA in use due to the current mainstream evolutionary theories of eusociality — kin selection and MLS. In section 3.1.1., I will assess the notion of weak BA, which is the preferred definition of the concept by MLS. I argue that weak BA is not true BA because the fitness consequences of the trait are defined relatively. Kin selection theorists define the fitness consequences of BA in terms of absolute fitness — with respect to the whole breeding population — but, in section 3.1.2., I will argue that the current mainstream definition (of BA) is potentially vacuous. This is because kin selection theorists typically define BA in terms of fitness consequences alone — a trait that causes negative selection to the focal individual and positive selection to those that it interacts with. But I will argue, that other cooperative traits could also fit this definition, such as coercion. Thus, in section 3.1.3., I will propose a new definition of BA with an added clause that stipulates that the trait that causes the fitness consequences must be possessed by the focal individual.

Secondly, in section 3.2., I will review the mainstream theories for the evolution of eusociality — kin selection and group selection — and the role of the concept of BA within them. Specifically, I will examine whether the concept of BA, that I argued for above, is used and/or required by either of the theories. Additionally, I will assess if there is any evidence to support the application of BA to eusociality. I will argue that only kin selection is applicable with the concept of BA, whereas group selection is only compatible with weak BA, which I argued is not true BA. But I will highlight that there is a lack of empirical evidence to support the application of BA to the non-reproductive castes, in fact, recent evidence supports the alternative claim that offspring are coerced into the non-reproductive castes. Thus, I will argue, similarly to Hunt, that the concept of BA *is not* a fundamental problem for eusociality research, contrary to claim (1). Moreover, there is no evidence to support the claim that it is the correct description of the behaviour of the non-reproductive castes.

3.1. Biological altruism: definitional issues

There have been definitional issues with the concept of BA since its origin, and debate continues over the correct way to define the concept (Okasha 2013). J. B. S. Haldane (1932: 207) simply defined BA as a trait that is ‘socially valuable but individually disadvantageous’. This definition is quite vague and does not specify, for example, whether the cost must be short- or long-term. However, Haldane (1932: 130-131, 210) did argue that the altruism in eusocial insects is ‘congenital’, and therefore is an inherited lifetime trait, as opposed to forms of altruism in other species (such as humans) that he argued is actually beneficial to the individual and is therefore more like cooperation. In other words, what may seem like BA in other animals is actually mutualism (behaviour that benefits both the individual and others — West et al. 2007), or in the case of humans, possibly psychological altruism. Moreover, as I have shown in chapter 1 (1.1.2.), Haldane (1932: 207-210) also emphasized the self-sacrificing aspect of BA, whether that be sacrificing one's life or foregoing reproduction. Thus, congenital altruism — or biological altruism as it is now known — denotes long-term costs to the focal individual. Haldane, therefore, argued that the evolution of his concept of BA is likely to only be possible in eusocial insect species precisely because of their reproductive division of labour (Huxley 1942: 482).

Subsequent authors overlooked the fact that Haldane limited his concept of BA to eusocial insects only — or more specifically to any species that exhibits a reproductive division of labour. This is mainly because of the influence of Hamilton and his theory of kin selection. As I have shown in chapter 1, it was only after Hamilton argued for inclusive fitness as a model for kin selection theory in the 1960s that the concept of BA became widely used, particularly in eusociality research. With the introduction of inclusive fitness, Hamilton had provided the first mathematical model to explain the evolution of cooperative traits, including BA, and consequently redefined the concept of BA in terms of this explanatory model. This was the first significant alteration to the definition of BA since Haldane. Hamilton defined BA as negative selection on the focal individual but positive selection for the recipients of the focal individual's behaviour, according to absolute fitness values in the whole population (West et al. 2007). Added to this, the levels of selection debate, and the rejection of good-for-the-species (or old group selection) arguments, led to authors applying the concept of BA to more species, including those that do not exhibit a reproductive division of labour, unlike Haldane. In other words, authors applied the concept to any example of negative selection for the focal individual and positive selection for the recipients of the focal individual's behaviour. But this led to further definitional issues with the concept of BA.

For example, the notion of reciprocal altruism emerged. Reciprocal altruism was introduced by R. L. Trivers (1971) in order to account for the evolution of BA without kin selection. In other words, reciprocal altruism was intended to explain how BA can evolve among non-relatives or even between different species. Trivers (1971) argued that BA can evolve among non-relatives if altruistic individuals preferentially benefit other altruistic individuals that have helped them in the past, a form of evolutionary game theory (Wilson and Wilson 2007). But reciprocal altruism is not true BA because the cost of this type of cooperative act is short term and is ultimately beneficial to the focal individual, i.e. if the focal individual preferentially benefits another individual in order to gain a future benefit in return then this is a form of mutualism because both individuals benefit (Hamilton 1996: 263; West et al. 2007). For this reason it is has been argued that reciprocal altruism should be referred to simply as mutualism, or reciprocal cooperation (West et al. 2007: 420). But the case of reciprocal altruism highlights the issue of whether the cost and benefits involved in BA should be defined as short- or long-term fitness effects. I prefer to follow S. A. West, and colleagues (2007) in defining the fitness effects of BA as long-term costs and benefits, measured over the lifetime fitness of the focal individual. This is because if an individual benefits another at a cost to itself in the short-term, that individual could offset that cost in the future by reproducing, for example. Moreover, a trait or behaviour that causes the focal individual to benefit others at a short-term cost to itself could be beneficial in the long-term if this ensures that it obtains future benefits that offset the initial short-term costs, such as reciprocal cooperation. Thus, defining the costs and benefits in the short-term is in danger of rendering the concept too general; i.e.

this notion of BA would not differentiate between forms of mutualism and genuine cases of BA whereby an individual reduces its own fitness when benefitting another.

Issues to do with the definition of BA still persist however, which I will discuss in more detail next. In section 3.1.1., I will address the issue over defining the costs and benefits of BA relative to the focal individual's group or in terms of the absolute fitness of the focal individual across the whole population. In section 3.1.2., I address an issue with the definition that I feel has been missed within the literature. Namely, I will argue that current definitions of BA lack a cause that specifies that the costs and benefits of BA must derive from the focal individual. Finally, based on the issues discussed in this section, I will argue for a definition of BA, in section 3.1.3., that not only captures the original "self-sacrificing" element of the concept from Haldane but can also still fit with the current usage of the concept.

3.1.1. Absolute and relative (or weak and strong) definitions

As I have shown in Chapter 1, group selection was widely rejected for around a decade or so from the 1960s due to the emergence of the debate over the levels at which natural selection operates. But with the subsequent renewed interest in group selection a major conceptual issue arose for the concept of BA. This conceptual issue is to do with whether the fitness consequences (i.e. the cost and benefits) of BA should be defined relative to the focal individual's group only, or whether they should be defined with reference to the whole breeding population, i.e. defined in absolute terms (West et al. 2007; Wilson 2008a).

As I explained in chapter 1, old group selection focused on between group (*inter-group*) selection rather than within group (*intra-group*) selection. Old group selection argued that inter-group selection drives individuals within groups to behave primarily for the benefit of the group rather than behaving with unrestrained selfishness (West et al. 2007; Wilson 2008a) — which is similar to the good-for-the-species perspective that was also popular prior to the 1960s (see Cronin 1991). Whereas, using MLS theory, new group selection theorists argued that selection can occur at multiple levels simultaneously and brought attention to how group-level factors affect individual fitness within groups; i.e. both inter- and intra-group selection dynamics are important (West et al. 2008). Consequently, the attention of group effects on individual fitness led some authors to once again claim that it is possible for BA to evolve via group selection (Wilson 1975a, 2008a; Sober 1988).

To do this, D. S. Wilson (1975a) argued that the fitness consequences of BA should be defined relatively. Wilson argued that if an individual benefits others in its group, at a cost to itself, resulting in the focal individual have a lower fitness than other members of its group, then that is BA. Furthermore, because such altruistic individuals increase the fitness of non-altruist individuals in their group, then their group will be more successful than other groups with no (or fewer) altruists. Thus, inter-group selection could drive the evolution of BA, according to this approach. However, even though these individuals have a lower fitness in their group, they have a higher fitness value compared to members in less successful groups, due to inter-group selection. In other words, according to this view, altruistic individuals have a low relative fitness (i.e. fitness relative to other members of their group) but a *high absolute fitness* (i.e. defined in comparison to the whole breeding population). Consequently, this type of BA is often referred to as ‘weak’ BA (West et al. 2007: 420-421; Okasha 2013).

It has been argued that weak BA should not be classed as a form of BA (West et al. 2007, 2008). This is because even though an individual with weak BA will have a lower fitness in their group, that individual will actually have a high absolute fitness value because of the beneficial effects of being in a successful group. In other words, weak BA is actually beneficial to the focal individual rather than costly, when absolute fitness is taken into account. Therefore, weak BA is more akin to mutualism rather than true BA, because both the focal individual and members of its group benefit from the weakly altruistic behaviour/trait — the non-altruistic members of the group benefit directly from the weakly altruistic members of the group, and the weakly altruistic members benefit from being in successful groups — (West et al. 2007, 2008).

Wilson (2008a) further pointed out, however, that even though weak BA increases the focal individual's absolute fitness, it cannot evolve without group selection:

> Traits for which $\Delta p < 0$ within groups are precisely those that require the ingredients of group selection to evolve. (Wilson 2008a: 370. Emphasis their own).

What Wilson means by this is that weak BA cannot evolve without inter-group selection. This is because if there is a single group, i.e. the whole breeding population, weak altruists will be less fit than non-altruists (just as weak altruists are less fit within groups), therefore non-altruists will outcompete weak altruists (Okasha 2013).

However, if the population is not structured into groups, then weak BA will equate to strong BA. This is because if there are no discreet groups in the population then the whole breeding population equals one group. Consequently, in this case, relative fitness will equal absolute fitness because, as I have shown above, relative fitness means the fitness of an individual related to its group but here the group = the breeding population. Therefore, in this case, relative fitness = absolute fitness. Or more simply, when a population is not structured into groups, there is no group-relative fitness. Thus, the focal individual's group equals the breeding population, and weak BA equals strong BA; altruistic individuals will have a lower fitness with respect to the whole breeding population and consequently, BA will decline in the population. But, as I have shown in Chapter 1, Hamilton (1964a, 1964b) already provided an explanation for the evolution of (strong) BA, even in cases of non-group structured populations. Consequently, Wilson's (2008a) argument that weak BA cannot evolve without group selection appears to be incorrect. Without a group-structured population weak BA collapses into strong BA, and strong BA does not require group selection in order to evolve.

Defining the costs and benefits of BA relatively, with respect to the members of the group, is not theoretically sound. Weak BA decreases the *relative* fitness of the focal individual but *actually increases its absolute fitness* due to between-group selection; i.e. weak altruists are less fit in their groups but are more fit because groups with weak altruists in them are more successful than groups with less or no weak altruists. But in non-group structured populations there is no relative fitness as there are no discreet groups, thus the costs and benefits of fitness must be defined in absolute fitness terms. Thus, in group structured populations, weak BA is a form of mutualism as it increases the focal individual's absolute fitness, and in non-group structured populations, weak BA = strong BA. Consequently, defining BA using relative fitness is not only unhelpful but may cause more confusion in the debate (West et al. 2007, 2008). 'Weak BA' and BA are two distinct traits that likely require two independent explanations, consequently labelling the former as BA could obscure this point. A trait that increases the absolute fitness of its bearer, via between-group selection, is interesting in its own right, but it is not a case of BA. Therefore, the costs and benefits of BA are best defined with respect to absolute fitness.

3.1.2. A case for an additional clause

As I have shown in chapter 1, the concept of BA was introduced and defined in 1932 by J. B. S. Haldane. He defined BA as a trait that causes an individual to benefit others at a cost to themselves and emphasized the self-sacrificing aspect of the concept. This definition of the concept received relatively little attention until the famous papers on kin selection by Hamilton (1964a, 1964b). Hamilton argued for a more precise definition that was more suitable for his mathematical model (inclusive fitness) than Haldane's original definition was. Hamilton (1964a) focused on the selective outcomes of BA, namely, that BA results in *selection against* the focal individual but *selection for* the individuals that benefit from the focal individual. Specifically, he defined BA as negative selection on the focal individual but positive selection for the recipients of the beneficial behaviour (−/+ selection dynamics), measured in long-term absolute fitness values — relative to the whole breeding population — (West et al. 2007). Whilst Hamilton's notion of BA was a more precise definition than Haldane's, in terms of mathematical modelling, it lost the "self-sacrificing" element of the original. In other words, Hamilton's new definition is about fitness consequences and simply points to a situation where there is negative selection for the focal individual and positive selection for individuals that it interacts with. Typically, biologists currently conceive of the concept in the same way due to the huge influence of Hamilton and kin selection. Many biologists understand BA in terms of fitness consequences and use the concept to describe cooperative traits that cause negative selection on the focal individual and positive selection on recipient individual(s) (Foster et al. 2006; Lehmann and Keller 2006; Ratnieks and Wenseleers 2008; Foster 2009).

However, defining BA based solely on fitness consequences is problematic. This is because defining the concept in this way is in danger of rendering the concept vacuous. Specifically, this definition cannot, without further assumptions or context, pick out the cause of these selection dynamics. To illustrate this it will be useful to briefly describe a hypothetical, but biologically possible, example.

Take, for example, a solitary female (Q) that produces 3 daughters in her first brood. When the daughters emerge, they remain in the nest to form a cooperative group with Q. But these 3 younger females (W) do not partake in direct reproduction but instead help Q to reproduce more (reproductive) offspring. Consequently, W are under negative selection because they do not reproduce and Q is under positive selection due to the cooperation of W. Without any further information, the concept of BA (if defined by fitness consequences) can be applied to this example, specifically to W, but crucially, so can the concept of coercion (if also defined by fitness consequences). In other words, without any further information, it is equally possible that either 1) W are biologically altruistic and increase their inclusive fitness by not reproducing but helping Q, or 2) that Q coerces W into becoming non-reproductive helpers. Both 1 and 2 result in negative (direct) fitness for W and positive fitness for Q (i.e. −/+ selection dynamics).

Most authors would agree, however, that the concepts of BA and coercion describe different social/cooperative traits. Yet here there is a situation in which both concepts are equally applicable if the concepts are defined solely in terms of fitness consequences, and if we have no additional information about the cause of the W phenotype. Of course it could be argued that biologists will apply either of the concepts based on further information, i.e. they are context-based concepts. However, this reply misses the point that if both of these concepts are defined only by their fitness consequences then they both share exactly the same definition. Defined by *fitness consequences* their respective definitions would be:

BA_f = a trait that causes negative fitness to the focal individual and positive fitness on the recipient individual(s)

$\mathit{Coercion}_f$ = a trait that causes negative fitness to the focal individual and positive fitness on the recipient individual(s)

In the hypothetical example, above, the focal individual is any member of W since our research focus is to explain why the young females became non-reproductive cooperatives for Q. But whether the young females develop into the W phenotype via BA, in an attempt to increase their inclusive fitness, or via coercion from Q, the fitness consequences will be the same; namely a trait (BA or coercion) causes negative fitness on W and positive selection on Q. Consequently, both BA_f and $\mathit{coercion}_f$ will be equally applicable regardless of the actual cause for the young females developing into the W phenotype.

Therefore, defining the concept of BA on fitness consequences alone is not adequate. The definition also requires an additional clause stipulating that the trait that causes the −/+ selection dynamics must be possessed by the focal individual. For instance, for BA to be applicable to the hypothetical example above, it must be shown that the trait that causes W to not reproduce but help Q to do so is internal to W. In other words, if the young females develop into the W phenotype due to an internal factor, i.e. in order to increase their own inclusive fitness, this would be a case of BA, because the young females became non-reproductive helpers ‘of their own accord’. Whereas if young females became non-reproductive helpers due to a trait that Q possesses, e.g. the ability to physical dominate her offspring, then this would be a case of coercion but not BA.

3.1.3. Biological altruism: a proposed definition

I have shown above, that there are currently multiple definitions of the concept of BA in use, weak BA and (strong) BA. The former defines the fitness consequences of BA with respect to the group, whereas the latter defines fitness consequences in absolute terms, with respect to the whole breeding population. Weak BA is the favoured version of the BA concept used by group selection theorists (Wilson 1975a; Sober 1988; Hölldobler and Wilson 2009). It is argued that even though weak BA causes the focal individual to be less fit within its group, its absolute fitness is raised because its group is more successful than groups with less or no weak altruists (less cooperative groups). Thus, weak BA is not truly costly to the focal individual, it is a form of mutualism because the focal individual benefits from weak BA (West et al. 2007). Consequently, using the concept BA to refer to a trait that is costly to an individual in its group (costly to its relative fitness) but actually beneficial to its absolute fitness is likely to add confusion to the debate, this is because such a trait is different to true BA (which is costly to an individual's absolute fitness) and potentially requires a different explanation (i.e. group selection).

Additionally, I have shown that since Hamilton (1964a) the concept of BA has been defined in terms of fitness consequences only. However, I argue that this is also problematic as it potentially renders the concept vacuous. As above, although Hamilton's definition was more precise than Haldane's (1932) original, it lost the self-sacrificing element of the original. Following Hamilton, the concept of BA is currently defined (BA_f) as a trait that causes negative fitness on the focal individual and positive fitness on the recipient(s) (West et al. 2007, 2008). But if the concept of coercion is also defined solely in terms of fitness consequences then it would share the same definition (*coercion*$_f$). As I have shown above, if defined solely by fitness consequences then both BA (*BA*$_f$) and coercion (*coercion*$_f$) could equally describe the phenotype W in the hypothetical example above, regardless of the actual cause of W. Consequently, the concept of BA requires an extra clause in the definition stipulating that the trait that causes the −/+ selection dynamics must be possessed by the focal individual.

Therefore, I propose the following definition for the concept of biological altruism:

> BA = a trait *possessed by the focal individual*, that causes it to benefit others at a long-term cost to itself, resulting in negative selection on the focal individual and positive selection on the recipient(s)

Whereby the fitness consequences are measured in absolute terms, with reference to the whole breeding population.

3.2. The evolution of eusociality

In this section, I will review the mainstream theories for the evolution of eusociality — kin selection and group selection — and the role of the concept of BA within them. Specifically, I will examine whether the concept of BA, that I argued for above, is used and/or required by either of the theories. Additionally, I will assess if there is any evidence to support the application of BA to eusociality.

3.2.1. Kin selection: BA and parental manipulation (coercion)

Since Hamilton's (1964a, 1964b) famous papers, kin selection has been the mainstream theory for the evolution of eusociality. Against the backdrop of the Modern Synthesis and the resultant gene-centred view of evolution, kin selection was very appealing to eusociality research. This is because it provided an explanation for the evolution of the apparent BA of eusocial insect workers in genetic terms, within the framework of the Modern Synthesis (Hunt 2007: 194-195).

As I have shown in chapter 1, Hamilton (1963, 1964a, 1964b) developed kin selection in order to explain the evolution of cooperation, in particular BA, in terms of individual selection. Kin selection theory is based on the notion of inclusive fitness, which is the sum of an individual's *direct fitness*, i.e. their personal success, and *indirect fitness*, i.e. their contribution to the success of their close relatives (West et al. 2007). The key innovation of kin selection was the idea that cooperative traits need not only increase direct fitness to evolve, but, in special cases, they can also evolve by increasing indirect fitness. Thus, kin selection is based on the principle of inclusive fitness maximisation (Foster et al. 2006; West et al. 2007; Birch and Okasha 2015). Put simply, natural selection is the process of individuals attempting to increase their inclusive fitness. Typically, this occurs through the increase of direct fitness, but in the case of BA, for example, inclusive fitness is maximised by increasing indirect fitness instead of direct fitness.

Inclusive fitness maximisation occurs via Hamilton's rule. As I have shown in Chapter 1, Hamilton's rule is defined as $rb > c$ — where r equals the coefficient of relatedness, b the benefit to the recipient, and c the cost to the focal individual (Birch and Okasha 2015).

Following Hamilton's rule, BA can evolve via natural selection if the cost to the focal individual is outweighed by the benefit to close relatives; rb > c. The key feature of eusociality is the reproductive division of labour, i.e. that colonies have reproductive and non-reproductive castes — typically a queen (and king in termites) and worker castes, respectively. Thus, in the case of eusocial insects, it is argued that even though the workers do not reproduce, whilst cooperating for the colony, the cost of not reproducing is outweighed by the benefits this behaviour provides to the colony. Furthermore, so long as the trait is not expressed in the queen (and king in termites) but only in the worker castes, then this trait can evolve via the reproductives.

Hamilton (1964b, 1972) argued that the evolution of the non-reproductive castes is most troubling and important aspect of eusocial insects that must be explained by evolutionary theories. This is because he conceived of the evolution of eusociality as the evolution of BA due to the Sturtevant-Hamilton problem of sterility, as I argued in chapter 1. According to the Sturtevant-Hamilton problem of sterility, the evolution of the non-reproductive castes occurred in the absence of colony selection (because eusocial insects evolved from solitary ancestors), thus, it follows that some individuals in the species evolved despite not directly reproducing. Hamilton concluded that the worker castes evolved because they are biologically altruistic and he applied kin selection in order to explain this. He argued that some individuals in the species increased their inclusive fitness by becoming non-reproductive workers rather than attempting personal reproduction.

It is important to point out, again, that the concept of BA is not entailed by kin selection theory. It is equally theoretically possible that some individuals evolved to be non-reproductive workers due to coercion from the queen (Kapheim et al. 2015). In this case, the non-reproductives evolve because of a trait possessed by the queen that enables her to coerce some of her offspring into becoming workers, rather than a trait (BA) possessed by the offspring that causes them to increase their inclusive fitness by developing into workers.

But due to the success of kin selection, Hamilton had a huge impact on eusociality research. As a consequence, since Hamilton, subsequent authors have also argued that the presence of the reproductive division of labour, specifically the non-reproductive castes, is the most troubling feature that theories of the evolution of eusociality must explain. It is often questioned how the non-reproductive castes can evolve via natural selection if they do not reproduce (Gadagkar 1996; Queller and Strassmann 1998; Dugatkin 2002; Ratnieks and Wenseleers 2008; Wilson 2008b). Thus, authors typically conceptualise the evolution of eusociality as the evolution of BA, following Hamilton; alternatives such as parental manipulation received less attention.

Under the kin selection framework, it is argued that in certain environmental and/or developmental conditions, some offspring would have a higher inclusive fitness if they remained at their maternal nest to become non-reproductive workers rather than attempting to establish their own nests. For instance, if there is high competition for suitable nesting sites, in terms of location to the primary food sources for example, then some offspring might have a higher inclusive fitness by foregoing personal reproduction and increasing their indirect fitness by remaining at the nest to help produce siblings, rather than dispersing and attempting to establish their own nest. Moreover, the size of an individual may affect their ability to disperse and successfully establish their own nest in many species. For example, if an individual is too small, due to poor nutrition levels during development, they may not have enough fat stores in order to provide sufficient energy whilst they establish their nest (as foraging is often not possible until after nest establishment), thus, becoming workers in their parental nest would be more beneficial to their inclusive fitness (Harris and Beggs 1995; Smith et al. 2007). Thus, typically, kin selection theorists argue that the reproductive division of labour (and consequently eusociality) evolved due to BA; some offspring remained at the nest to become non-reproductive workers because they exhibited BA and attempted to increase their inclusive fitness.

Is BA compatible with kin selection?

But is the concept of BA, as defined above in *3.1.3.*, compatible with kin selection theory? Yes it is because, firstly, the definition of BA already employed by kin selection is similar to the definition I argued for above, albeit without the added clause to do with the possession of the trait that causes the specific fitness consequences. Hamilton (1964a, 1996) developed kin selection in order to explain the evolution of BA (and other cooperative traits) and, whilst doing so, he provided the basis for the definition of BA that is used today by most kin selection theorists; namely BA_f (West et al. 2007, 2008). Kin selection theorists already define the fitness consequences in terms of absolute fitness, with reference to the whole breeding population. Moreover, the cost to the focal individual is defined as a long-term cost. Secondly, the added clause from the definition of BA in *3.1.3.* is compatible with kin selection. Importantly, the concept of inclusive fitness is a causal one (Birch and Okasha 2015). As above, inclusive fitness is the sum of direct and indirect fitness, and the latter refers to the focal individual's *causal impact* on the direct fitness of others (West et al. 2007):

> An organism's inclusive fitness is defined as a weighted sum, over all individuals in the population (including itself), of those portions of each individual's reproductive output

> for which the organism is *causally responsible*, with the weights given by relatedness coefficients. (Birch and Okasha 2015: 25. Emphasis added).

Thus, kin selection is already compatible with the definition of BA I argue for in *3.1.3.* due to inclusive fitness. Specifically, inclusive fitness can be used to determine whether the trait that causes the −/+ fitness consequences is possessed by the focal individual or by another (i.e. the queen). For instance, if the focal individual's inclusive fitness is raised by it becoming a non-reproductive worker, this is possible evidence that they possess a trait that causes them to benefit others at a cost to their direct fitness (i.e. BA). Whereas, if the focal individual's inclusive fitness is not increased by them becoming a non-reproductive worker, then this is strong evidence that they are not altruistic, i.e. that the cost to the focal individual is due to a trait possessed by another individual (the queen in this case) that causes the focal individual to benefit her at a cost to itself (Kapheim et al. 2015). In other words, in the latter case, the focal individual becomes a non-reproductive worker not because they are attempting to increase their inclusive fitness (BA) but due to coercion from the queen (i.e. parental manipulation).

Does the evidence point to BA or to coercion and parental manipulation?

In the decades since the introduction of kin selection, there has been a lot of theoretical and empirical work done in order to support the theory as an explanation of eusociality; with a particular focus on sex-ratio conflicts within colonies (see Queller and Strassmann 1998; Abbot et al. 2011). However, there is relatively little empirical support for the role of BA in the evolution of eusociality (Alonso and Shuck-Paim 2002; Abbot et al. 2011). This is partly because the factors that led to the *evolution of eusociality* within a species may be different to the factors that lead to the *maintenance of eusociality* (Gadagkar 1996; Alonso and Schuck-

Paim 2002). It is now widely accepted that eusociality evolved directly from solitary ancestors, the *'subsocial'* route, as opposed to evolving from a more simple form of cooperative group living without a reproductive division of labour, the *'semi-social' or 'parasocial'* route to eusociality (Boomsma 2009; Howard and Thorne 2011).[11] Thus, the factors for the emergence of a reproductive division of labour and colonial living in a previously solitary species are likely to be different to the maintenance, and evolution of further organizational complexity, within species that have already evolved eusociality. Consequently, the simple eusocial insect species that exhibit facultative eusociality, such as the sweat bee *Megalopta genalis* (see chapter 5), have become good candidate species for studying the factors involved in the evolution of eusociality (Kapheim et al. 2015). In such species, every generation typically exhibits both solitary and eusocial nests within the population, thus biologists can directly observe the factors that lead to a nest becoming eusocial rather than remaining solitary. Despite this, the majority of empirical support for kin selection as an explanation for the evolution of eusociality is provided indirectly from the studies on sex-ratio conflicts and other phenomena in already established eusocial species (Alonso and Schuck-Paim 2002; Foster et al. 2006; Abbot et al. 2011); even though this provides support for the theory of kin selection, *it does not provide direct support for BA*. In other words, whilst there is ample support for kin selection as a general theory of social and eusocial evolution, there is currently no empirical support for the role of BA in the evolution of eusociality. Which I will argue for presently.

Recent evidence supports the alternate view that the reproductive division of labour is a result of coercion (parental manipulation) rather than BA. However, because many biologists defined the concept of BA based solely on the fitness consequences (BA_f), as above, the

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[11] Although, for termites (*Isoptera*), there is less evidence for the subsocial argument, but importantly, there is no current evidence for the parasocial argument for termite evolution (Howard and Thorne 2011; Nalepa 2015).

evidence for coercion was interpreted as evidence for BA (Foster et al. 2006; Shimoji et al. 2018). For instance, F. L. W. Ratnieks, T. Wenseleers (2008), and colleagues (Foster et al. 2006), have argued for the contradictory concept of enforced or coerced BA. However, this is problematic because both coercion and BA are separate concepts that imply different forms of cooperation, as I argued above. Ratnieks and Wenseleers (2008) argued that parental manipulation (i.e. coercion) was not likely to have been the cause for the evolution of the reproductive division of labour (and thus eusociality). They argued that i) coercion requires acquiescence,[12] thus the reproductive division of labour must have evolved first, via BA, in order for coercion to act on it and reinforce the helping behaviour of the workers. And ii) because parental manipulation theory does not require that workers evolve the costly concept of BA, eusociality should be much more prevalent than it is if parental manipulation is true. However, both points i) and ii) are problematic.

Ratnieks and Wenseleers (2008: Box 1) use a theoretical model in order to argue for point i). They argued that BA alone would not account for the extreme degree of reproductive division of labour that is typically found in eusocial insect colonies. According to their model, without coercion acting on the reproductive division of labour (i.e. if the reproductive division of labour was due to BA alone) a percentage of the workers would be selected to reproduce (around 13% for workers of singly mated queens and around 54% for workers of multiply mated queens) because workers are more closely related to their sons then brothers, in haplodiploid *Hymenoptera*. Thus, they argued that only through coercion can eusocial insect colonies achieve the extreme degree of reproductive division of labour that is typical (i.e. only 1-2 reproductives and tens to millions of non-reproductives). Using Hamilton's rule they

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[12] Hamilton (1996: 361) also argued that parental manipulation would require acquiescence of the workers otherwise they would evolve mechanisms to evade coercion.

provide an elegant model to support their claim and applied it to honey bees (*Apis mellifera*) and a selection of wasp species (including *Vespula vulgaris*). They demonstrated that, in the absence of policing in queenless colonies, a percentage — close to that predicted by their model — of workers had activated ovaries and could thus potentially reproduce (Wenseleers and Ratnieks 2006; Ratnieks and Wenseleers 2008). Whilst their data supports their claim that the extreme reproductive division of labour is only possible through different forms of coercion (i.e. queen and/or worker policing of worker-laid eggs, ovary suppression via pheromones, polymorphic castes etc.), it does not support their claim that the remaining non-reproductive workers are altruistic. In other words, it does not support point i). In fact, it provides evidence against the previously mainstream view that workers are altruistic; i.e. this shows that worker reproductive potential is externally inhibited. Moreover, since they did not study the development of the colonies, but only what happens if you disturb mature colonies by removing the queen, then all that can reasonably be inferred from their empirical data is that the ontogenetic emergence of the reproductive division of labour in these species is multifaceted and complex. Moreover, genetic models such as theirs ignore the multiple biological factors that may also inhibit worker reproduction in the species that they studied, e.g. developmental plasticity, polyethism, pheromone signals, competition for ovipositing space, dominance, etc. For example, in the common wasp (*Vespula vulgaris*) many workers do have activated ovaries in queenless colonies but fail to successfully raise their offspring because multiple eggs are often oviposited in the same comb cells (Potter 1964). As I will show in chapter 5, in *V. vulgaris*, colony organization rapidly declines after queen death (foraging and other tasks almost cease) and cannibalism of the brood by workers occurs (Potter 1964). Thus, the fact that a large percentage of workers still do not reproduce in the absence of coercion, in *V. vulgaris*, is better explained by these biological and organizational factors rather than by the concept of BA or enforced BA. Furthermore, in their study, Wenseleers and Ratnieks (2006) used colonies from evolutionary advanced eusocial insect species, in which eusociality is obligate; i.e. species whereby selection likely takes place at the colony level. Therefore, their use of the concept of BA to such cases is misplaced. If the colony is the unit of selection then the members of that colony do not directly partake in selection, and thus, the non-reproductive castes are not evolutionary individuals, i.e. they do not have direct fitness values. Since BA is a concept that refers to a trait that causes direct fitness consequences for its bearer (and those individuals that it interacts with) then the concept is not applicable to the non-reproductive castes of colonies that are evolutionary superorganisms. Therefore, even if their data supports their model for coercion, it does not support their use of BA. However, point ii) of their argument may still be correct.

Following E. L. Charnov (1978), Ratnieks and Wenseleers (2008) argued that, *in the evolutionary origins of eusociality*, if a female is singly mated then parental manipulation benefits the parents and reproductive siblings of workers and, crucially, this is not costly to the non-reproductive workers. This is so because, as Hamilton (1964a) pointed out, full siblings of singly mated females have the same average degree of relatedness as parent-offspring (i.e. 1/2).[13] Therefore, from the worker's perspective, there is little difference between helping to rear full siblings or producing one's own offspring. Thus, they argued that if BA was not required then eusociality should have evolved many more times than it has (point ii):

> In fact, given that both parents and siblings benefit from coercing offspring to help their parents […] and that offspring are indifferent to being coerced if they are rearing full

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[13] This is the case for both diploid and haplodiploid species. But in the latter, the argument applies to daughter offspring of the queen and full sister relationships.

> siblings […] we suggest that eusociality should be more common if it had originated as a result of coercion. (Ratnieks and Wenseleers 2008: 50).

However, whilst Charnov (1978: 456-457) did argue that the offspring of a singly mated parent would be indifferent to raising full siblings or their own offspring, he did not use this to argue for BA and against the role of coercion, or parental manipulation, in the evolutionary origins of eusociality. Indeed, Charnov (1978) actually argued that parental manipulation, *but not BA*, is likely to have been the key to the evolution of eusociality. He argued that this is because, although offspring would attempt to oppose the coercion of their parent if they were not biologically altruistic, the offspring would not evolve mechanisms to evade coercion because there is no selection for this:

> It seems likely that the first attempts at parent→offspring parasitism would result in actions by the offspring to prevent it […]. However, mother has a large advantage here. She is selected to pursue the parasitism even if she kills some of her daughters — while her daughters are not selected to continue stopping her. A daughter loses fitness by being killed by its mother; it does not gain by killing its mother. (Charnov 1978: 457).

But Charnov (1978: 460) argued that the conditions for successful parental manipulation, and thus the evolution of eusociality, would be rare — singly-mated female and daughters remaining at the nest — thus, providing an argument why eusociality rarely evolved. Thus, point ii) of Ratnieks and Wenseleers' (2008) argument may not be correct either.

Ratnieks and Wenseleers' (2008) argument for enforced BA relies on points i) and ii) above. However, I argue that the fact that some workers still do not attempt to reproduce in the absence of coercion does not, in itself, support their claim that BA is also involved (point i)). They must provide evidence for this. I argue that the reason that they did not was because Ratnieks and Wenseleers (2008) employed the fitness consequences (*BA$_f$*) definition of BA, thus they consider any worker in the colony that does not reproduce as altruistic. In other words, according to their use of the concept, any worker that does not reproduce automatically qualifies as altruistic because it has a negative fitness but confers positive fitness on the reproductive individuals in the colony, i.e. satisfying the −/+ selection dynamics (i.e. *BA$_f$*). But this use of the concept of BA is problematic, as I argued in *3.1.2.* Therefore, to claim that BA is involved, Ratnieks and Wenseleers must provide evidence that any worker that still does not reproduce, in the absence of coercion, does so because of a trait that they possess which causes them to maximize their inclusive fitness by not reproducing. Point ii) of Ratnieks and Wenseleers' argument — that eusociality would be more prevalent if it evolved due to parental manipulation alone — was based on the statement from Charnov (1978); i.e. that offspring (workers) would be indifferent to parental manipulation. However, Charnov (1978) argued that the conditions for this would be rare, and unlike Ratnieks and Wenseleers, he argued that parental manipulation was key for the evolution of eusociality. Indeed, other authors have argued that the ecological and biological conditions — e.g. lack of suitable nesting sites, monogamy, and extended parental care — are likely to be the key factors for the rarity of eusociality (Queller 1996; Boomsma 2009). Too much focus on genetic models, and the concept of BA, has the danger of authors potentially missing key biological and ecological factors in the evolution of eusociality (Hunt 2007). Consequently, Ratnieks and Wenseleers must provide more evidence in order to justify their argument for BA (or enforced BA).

Recently, some eusociality researchers have specifically assessed whether BA does play a role in the reproductive division of labour and the evolution of eusociality. K. M.

Kapheim, and colleagues (2015), assessed whether daughters of the facultative sweat bee *Megalopta genalis* become workers because they are altruistic or due to parental manipulation. In every generation, *M. genalis* (reproductive) females can either become solitary reproductives or produce a eusocial colony. Kapheim and colleagues (2015) found that offspring do not increase their inclusive fitness by remaining in the nest as non-reproductive workers, instead, they found that they do so because of coercion from the queen. The queen produces workers, firstly, by providing a restricted diet to daughter offspring (those that she wants to become workers) resulting in daughters that are smaller than the queen, secondly, this enables the queen to coerce her smaller daughters into becoming non-reproducing workers (Kapheim et al. 2013, 2015, 2016). Thus, in *M. genalis*, whether a female remains a solitary reproductive or produces a eusocial colony is not decided by the presence of altruistic workers, instead it is decided by the ability of the female to coerce some of her offspring into becoming workers.

In sum, there is a lack of direct evidence for the role of BA in the evolution of eusociality using kin selection models. Most arguments for BA are justified by theoretical models, for example the kin selection model by Ratnieks and Wenseleers (2008) above. There is, however, a lack of direct empirical evidence for BA. The majority of empirical evidence used to support arguments for BA is actually only evidence for the general theory of kin selection (Queller and Strassmann 1998; Alonso and Schuck-Paim 2002). This lack of direct evidence for BA has not been made apparent due to most eusociality researchers employing the fitness consequences definition (BA_f); i.e. according to this definition of the concept, workers are "altruistic" simply by the fact that they do not reproduce. But this definition of the concept is problematic because coercive traits would also qualify as BA, as I argued in *3.1.2.* For BA to be applicable to workers it must be demonstrated that offspring develop into non-reproducing workers due to internal causes; e.g. to maximize their inclusive fitness. Indeed, Kapheim and colleagues (2015) found, in *M. genalis*, daughters do not increase their inclusive fitness by becoming workers but instead become workers because of coercion from the queen. Parental manipulation is a form of kin selection because the coercion occurs between related individuals (Bourke and Franks 1995). Therefore, given the lack of direct empirical evidence for BA and the increasing evidence for coercion in the reproductive division of labour within colonies (Ratnieks and Wenseleers 2008; Kapheim et al. 2015; Shimoji et al. 2018), the role of parental manipulation in the evolution of eusociality should be investigated further.

3.2.2. Group selection: MLS1 and MLS2

As I have shown in Chapter 1, the levels of selection debate in the 1960s led to the widespread rejection of group selection in evolutionary biology (Cronin 1991; Chancellor 2015). Even though new forms of group selection emerged in the subsequent decades, kin selection remained the mainstream model for studying the evolution of cooperation and sociality (West et al. 2007, 2008). However, due to the influential work of B. Hölldobler, E. O. Wilson and colleagues, group selection is once again at the forefront of eusociality research (Wilson and Wilson 2007; Hölldobler and Wilson 2009; Nowak et al. 2010; Wilson and Nowak 2014). As I highlighted in chapter 1, new group selection is based on MLS, which emphasises the fact that selection can occur at multiple levels simultaneously (Wilson and Wilson 2007; West et al. 2008; Birch and Okasha 2015). MLS is differentiated into two versions, namely *MLS1*: the effects of group living on individuals, and *MLS2*: groups that are units of selection, or groups that are more than simply the sum of their parts (Damuth and Heisler 1988; Hamilton and Fewell 2013). More simply, MLS1 is applicable to cases where groups are not units of selection but individual fitness is affected by being part of a group, and MLS2 is only applicable to cases in which groups have properties or traits at the collective level that result in group selection — whereby between-group selection is high and within-group selection is low or zero — (Okasha 2014). Thus, MLS2 is group selection.

For eusociality research, MLS1 is more appropriate to the evolution of eusociality, and the more evolutionary basal species. This is because colony selection is unlikely to have occurred in the evolutionary origins of eusociality as it does not occur in the extant basal species that are facultatively eusocial; e.g. *M. genalis*. Thus, the main focus of this approach would be to assess whether MLS1 drove the evolution of eusociality. Whereas MLS2 is only applicable to the more evolutionary derived species in which colonies are potentially the units of selection (i.e. between-colony selection is stronger than within-colony selection); e.g. honey bees (*A. mellifera*), etc. (Hölldobler and Wilson 2009; Johnson and Linksvayer 2010). In this context MLS2 is, therefore, appropriate for studying the evolution of the superorganism but not the evolutionary origins of eusociality (Maynard Smith and Szathmáry 1995; Hou et al. 2010; Hamilton and Fewell 2013).

Is BA compatible with MLS?

True BA, as I have defined it in *3.1.3.*, is not compatible with MLS. This is because, according to this approach, individual selection is defined as within-group selection and consequently, individual traits that affect fitness, like BA, are defined in terms of relative fitness (Okasha 2013). MLS theorists redefined BA in terms of relative fitness (West et al. 2007; Wilson 2008a). According to MLS, even though BA causes individuals to be less fit within their groups, it can evolve in the population because groups with more altruists out compete groups with less altruists. However, in this case the “altruists” also benefit, in terms of absolute fitness, due to the fact that they are in more successful groups. Thus, only weak BA is compatible with group selection, but as I have argued above in *3.1.1.*, weak BA is not true BA (West et al. 2007). However, even though BA is not compatible with MLS, this theory could still be applicable to the study of the evolutionary dynamics in eusociality: MLS1 could possibly explain the evolution of eusociality, and MLS2 could possibly explain the evolution of the superorganism.

MLS or kin selection?

It is widely argued that MLS and kin selection are formally equivalent as they both correctly describe population gene frequency for a given trait (West et al. 2008; Birch and Okasha 2014). However, S. Okasha (2014) argued that this does not entail that they provide the same causal explanation; kin selection argues that traits evolve due to Hamilton’s rule and inclusive fitness maximization, whereas MLS argues that traits evolve due to within- and between-group selection dynamics. Consequently, Okasha (2014) argued that biologists should choose between the two different approaches based on causal aptness, i.e. choose the approach that better describes the causal structure of selection for a specific case. In group structured populations, kin selection may be more appropriate if group fitness is simply the sum of the fitness of each member in the group. In this case, individual selection is primary (even if group membership affects individual fitness) as groups are not units of selection (MLS1). Kin selection can also deal with group effects on individual fitness and, thus, in cases where groups are not units of selection (MLS1) both kin selection and MLS1 are two different ways to describe the same situation (West et al. 2008; Birch and Okasha 2015). Moreover, kin selection is generally considered to be easier to apply than MLS1 (West et al. 2008). However, when group are units of selection then biologists should apply MLS2, since in this situation kin selection does not correctly describe the causal structure of selection (for more details on the mathematical aspects of each model, and their issues, see Okasha 2014). In other words, certain traits evolve within the population because of the selection between groups, which causes group level adaptations to evolve (e.g. polymorphism in the non-reproductive worker castes).

As A. H. Sturtevant (1938) argued long ago, selection at the colony level is unlikely to occur in the evolutionary origins of eusociality since eusociality evolved from solitary ancestors. Moreover, colony selection does not occur in the most basal extant eusocial insect species (Johnson and Linksvayer 2010). In many of the facultative eusocial species there is little physical difference between the queen and workers and, consequently, workers are fully totipotent, even in species with slight body size differences between the queen and workers such as *M. genalis* (Bourke 1999; Anderson and McShea 2001; Smith et al. 2009). In such species, even though workers typically do not reproduce, workers can replace the queen in the event of her death, for example. Thus, in these species, selection is typically operating at the individual level, specifically on those individuals that reproduce (i.e. queens, queen/king in termites). It could be argued that the queen benefits from being in the colony and therefore MLS1 is more causally apt than kin selection. However, if coercion is the main factor in the reproductive division of labour (as current evidence alludes to, see above) then the workers do not benefit from being in the group. Instead, if the reproductive division of labour emerges due to coercion then kin selection is more causally apt. Since the non-reproductive workers evolve due to parental manipulation (via kin selection) rather than the indirect benefits of being in a group. Specifically, those individuals that can successfully produce non-reproductive workers are selected for, thus the worker phenotype is indirectly selected for via the reproductive parents. An argument very similar to Darwin's (see chapter 2).

However, once colony selection emerges in a species, then MLS2 is more appropriate than kin selection. As the organizational complexity within colonies increases, for example larger colony size, increased polymorphism, pheromone signalling, polyethism, etc., then obligate eusociality emerges whereby members of the colony cannot develop or survive as solitary individuals (i.e. decrease of worker totipotency), consequently the colony itself becomes the evolutionary individual (Bourke 1999; Johnson and Linksvayer 2010; Okasha 2014). Colony selection feeds back onto the organization of the colony and drives the evolution of further organizational complexity. Consequently, between-group selection becomes the primary cause of the evolution of traits in these species. Thus, MLS2 is more causally apt for the maintenance and further evolution of eusociality compared to kin selection (Anderson and McShea 2001; Hölldobler and Wilson 2009; Okasha 2014).

3.2.3. Evolution of eusociality: a summary

Both kin selection and group selection (MLS) are the mainstream evolutionary approaches to eusociality today, but a strong debate continues between theorists and biologists as to which is more appropriate (West et al. 2008; Nowak et al. 2010; Abbot et al. 2011; Wilson and Nowak 2014; Birch and Okasha 2015). It has been shown that both models are formally equivalent, consequently some have argued that kin selection should be preferred as it is a more general theory (West et al. 2007, 2008). However, even though they are formally equivalent, both models provide different causal explanations for the evolution of a given trait; in the former inclusive fitness and Hamilton’s rule and in the latter within- and between-group selection dynamics. Recently, Okasha (2014) has provided an appealing argument for how researchers can choose between the two approaches for a given species or trait, namely causal aptness. Broadly, this approach argues that kin selection is more appropriate in situations where groups are not the unit of selection and, alternatively, when groups are the unit of selection then group selection (MLS2) is more appropriate.

Okasha's (2014) causal aptness approach is welcome since the evolution of eusociality is likely to involve two distinct stages, whereby kin selection occurs and then MLS2 occurs. *Firstly*, in the evolutionary origins of eusociality colony selection did not likely occur. This is because eusociality evolved from solitary ancestors, thus selection was likely to have taken place between solitary reproductives and reproductives that produce (small) colonies that consist of non-reproductive workers (Sturtevant 1938; Boomsma 2009; Johnson and Linksvayer 2010). The evidence from the extant basal eusocial insect species supports this. Colony selection does not occur in facultatively eusocial species such at the sweat bee *M. genalis* (Kapheim et al. 2015). Therefore, eusociality is likely to have evolved from a process of kin selection. *Secondly*, as colonies evolved more organizational complexity and obligate eusociality emerged, so did colony selection. In other words, as colonies became larger and individuals became more specialized (i.e. worker polymorphism) the division of labour became more complex (Bourke 1999). Consequently, individuals became totally dependent on the colony for their development and survival (obligate eusociality), and between-group selection emerged. Colony selection likely drove the evolution of further organizational complexity, which resulted in the emergence of hierarchically-organized superorganisms (i.e. evolutionary and physiological individuality at the colony level) such as in *A. mellifera* (see chapter 5). Thus, obligate eusociality is likely to have evolved via MLS2. *Consequently*, kin selection is more appropriate for studying the evolutionary origins of eusociality and MLS2 more appropriate for studying the maintenance of eusociality and the evolution of superorganisms.

However, eusociality researchers should take caution not to focus solely on the genetic level when using either kin selection or group selection. This is because important biological factors, such as developmental plasticity, may also have played a key role in the evolution of eusociality (Hunt 2007: 194-201; Nalepa 2015; Ronai et al. 2016). M. J. West-Eberhard (1996; 2003) proposed the groundplan theory, which argued that division of labour could evolve due to developmental life phases (i.e. reproduction, foraging, etc.), that developed in solitary ancestors, being differentially expressed among the members of eusocial colonies, resulting in reproductive and non-reproductive castes (Hunt 2007; Johnson and Linksvayer 2010). Other authors have argued that, due to developmental plasticity, individuals have differences in their response thresholds to different tasks, resulting in division of labour within groups (Robinson 1992; Page Jr. and Erber 2002; Schulz et al. 2002). In other words, differences in response thresholds among members of a group would result in some individuals more responsive to cues for foraging and other more responsive to cues for nest construction, for example. This argument has been supported experimentally; solitary bees were forced to nest together and a division of labour naturally emerged, with one becoming a dominant reproductive and the other(s) doing "worker" tasks (Page Jr. and Erber 2002). Such developmental plasticity could enable parents to manipulate the development of their offspring such that they are more prone to undertake "worker" tasks, and coercion from the parent could enforce this and inhibit their reproduction. In other words, forms of division of labour within groups may emerge more naturally than was previously assumed under the more genetic-focused approaches of the Modern Synthesis. As well as other factors, such as monogamy and extended parental care, developmental plasticity may promote the evolution of parental manipulation.

Since eusociality has evolved multiple times within insects, therefore the evolutionary origins may differ in certain species (Hunt 2007; Hölldobler and Wilson 2009). However, most evidence points to eusociality evolving from solitary ancestors (subsocial route), rather than from other forms of sociality (semi-social route) (Boomsma 2009). Consequently, theories that are compatible with kin selection, i.e. worker BA, parental manipulation, the groundplan theory, are good candidates to explain the evolutionary origins of eusociality. But the maintenance and evolution of organizational complexity in extant eusocial insect species is more likely to be a case of colony selection. Thus, in this case MLS2 approaches are more appropriate (Okasha 2014). Importantly, due to the lack of direct evidence of BA, researchers should not only focus on the concept of BA in evolutionary studies of eusociality, but should also address the alternatives such as parental manipulation, the groundplan theory, etc. (Hunt 2007; Kapheim et al. 2015).

Conclusion

In this chapter I have assessed the role of BA in evolutionary studies of eusociality. In part 1 I highlighted some definitional issues with the concept of BA. Firstly, I argued that weak BA, which is the version of BA employed by MLS models, is not true BA because it defines the fitness consequences in terms of relative fitness. Weak BA is defined as a trait that causes its bearer to benefit other members of its group at a cost to itself, resulting in the focal individual having a lower fitness within its group. However, because groups with more weak altruists do better than groups with less or none, then weak BA results in an increase in the focal individual's absolute fitness, via between-group selection. In other words, weak BA reduces the focal individual's relative fitness within its group but increases its absolute fitness within the whole breeding population. Weak BA involves no cost in terms of absolute fitness and is not, therefore, true BA (West et al. 2007). Secondly, I highlighted an issue with the definition of BA that is employed in kin selection models, one that is rarely touched upon within the literature. Specifically, since Hamilton (1964a) many authors define the concept of BA based on fitness consequences alone (BA_f), but this is problematic because it potentially renders the concept vacuous. This is because BA is not the only trait that can cause the −/+ selection dynamics. For instance, whilst BA would cause the negative selection for the focal individual and positive selection on individuals it interacts with, so too could traits such as coercion, for example. Defining BA by fitness consequences alone cannot pick out the cause of the fitness consequences without further context. Thus, I argued that the concept of BA requires an additional clause stipulating that the focal individual possesses the trait that is the cause of the fitness consequences. Consequently, I proposed the following definition of BA: a trait *possessed by the focal individual*, that causes it to benefit others at a long-term cost to itself, resulting in negative selection on the focal individual and positive selection on the recipient(s).

In part 2 I reviewed the role of BA in the two mainstream evolutionary theories of eusociality, namely kin selection and group selection. I argued that, despite the widespread use of BA within eusociality research, only kin selection is compatible with the concept of BA that I proposed; group selection is only compatible with weak BA but, as I argued in part 1, weak BA is not true BA. However, there is a lack of empirical evidence for BA in eusocial insects. On the other hand, there is empirical evidence for coercion and parental manipulation (Ratnieks and Wenseleers 2008; Kapheim et al. 2015; Shimoji et al. 2018). Further, I argued that both kin selection and MLS are likely to be involved in the evolutionary dynamics of eusociality, this is because there is likely to be at least two phases in the evolution of eusocial insects; the origin of eusociality (first phase) and the emergence of the superorganism (second phase). Eusociality likely evolved from solitary ancestors in insects (the subsocial route), and therefore in the evolutionary origins of eusociality colony selection is unlikely to occur. Specifically, selection is likely to have taken place between females that are solitary and females that can coerce some of their offspring into being non-reproductive workers (eusociality). Therefore, in the first phase, eusociality likely evolved due to parental manipulation (kin selection). In some species, organizational complexity within colonies increased over generations and the members of the colony become more specialised (a decrease in individual totipotency). Consequently, obligate eusociality emerged and colony selection arose in these species. In other words, selection began to primarily take place between colonies in the more complex eusocial species. Additionally, colony level selection fed back on colony organization leading to the evolution of the superorganism, such as in honey bees (which I will explain in more detail in chapters 4 and 5). Thus, in the second phase, superorganisms evolved via group selection (MLS2). Importantly, there is no evidence that BA occurred in either phase of eusociality evolution; in the first phase, even though kin selection occurs, it is not altruistic workers but parental manipulation that drove eusociality to evolve, in the second phase, colonies are the units of selection and thus BA is not applicable to individual members of the colony — weak BA could be applicable but, again, this is not true BA.

It is theoretically possible that BA occurred in eusocial insects; i.e. it is possible that the non-reproductive workers evolved because they are biologically altruistic. However, there has been little empirical research done in order to directly test this, even though there has been a lot of empirical research carried out that supports the theory of kin selection more generally. When this question has been empirically assessed, the evidence points to coercion rather than BA (Kapheim et al. 2015). In other words, in the evolutionary origins of eusocial insects, parents coerced some of their offspring into becoming non-reproductive workers (i.e. parental manipulation theory). Moreover, there is plenty of evidence from many species of eusocial insects, especially in the more derived species, that coercion (from the queen and other workers) is crucial for the development and maintenance of the reproductive division of labour once eusociality has evolved. Furthermore, in those species where colony selection occurs, the colony is the unit of selection not the individual insects, which entails that the worker castes cannot be biologically altruistic, since BA is by definition a trait that concerns evolutionary individuals (i.e. those individuals under direct selection). Therefore, even though BA is theoretically possible in the evolutionary origins and the more basal species without colony selection, there is currently no evidence for it. Moreover, this undermines the claim that the concept of BA is a fundamental problem for eusociality research (claim (1)). Researchers should look at the alternatives to BA, such as coercion or developmental plasticity, when researching the evolutionary origins of eusociality under kin selection. In general, more empirical research, from a greater number of evolutionary basal eusocial insect species without colony selection, needs to be carried out in order to assess whether BA does occur in any species, or whether factors such as coercion are more widespread than was recently known.

In the next chapters I will explore the concept of the superorganism in more detail, but from a functional/organizational perspective rather than solely from an evolutionary perspective, as above. In chapter 4, I will review the history and current status of the concept, showing that it is currently typically understood from an evolutionary perspective (using group selection), even though originally it was primarily used from an organizational/physiological perspective. In chapter 5, I develop an organizational approach to the superorganism, one that focuses on the ontogenetic and actual organizations within colonies. I apply this approach to three case studies in order to assess the types of individuality at the colony level — i.e. evolutionary (unit of selection) and/or physiological-like (hierarchical-organization) — across different representative species of eusocial insects, with the aim of further showing that BA is not likely to be a correct description of the worker castes. I will show that colonies of some species qualify as evolutionary units of selection, whereas those in the most evolutionary derived species also qualify as physiological-like superorganisms because of their hierarchical-organization. In other words, colonies of some species can be considered, in many aspects, to be analogous to physiological individuals because of their integrated organization. Thus, in such cases the individuals in those colonies do not develop into workers because of BA but rather they do so because they act as functional parts of an integrated hierarchically-organized unit; i.e. they are responding to regulatory signals from the collective colony level.

Chapter 4 — The superorganism: from the past to the present

Introduction

Due to their unique organizational properties — such as the reproductive division of labour, high cooperation, polymorphism, etc. — eusocial insect *colonies* have long been viewed as biological individuals in their own right (Emerson 1939; Hamilton 1972). Indeed, this led Wheeler (1928) to apply the concept of the superorganism to eusocial insects; he argued that colonies are higher-order biological organisms. In chapter 1, I argued that one of the reasons that the widespread use of the concept of BA was problematic for eusociality research was the decline of alternative perspectives, particularly the superorganism argument. This was due to Hamilton's kin selection theory and the conceptualisation of the evolution of eusociality as the evolution of BA. Because kin selection was such a groundbreaking theory for eusociality research (and evolutionary biology in general) it led to the widespread use of the concept of BA. This, in turn, led to a prominent view, in post-Hamiltonian eusociality research, that eusocial insect colonies are *groups* formed of altruistic and non-altruistic individuals. However, as I argued in the previous chapter, if colonies exhibit a form of individuality at the colony level (either evolutionary and, possibly, physiological-like) then the concept of BA is not applicable to the members of the colony as they are not evolutionary individuals in their own right, instead they are lower-level parts in a higher-order system.

In this chapter, I will review the history and current state-of-the-art of the superorganism concept. I will begin, in section 4.1., by reviewing the history of the colonies-as-individuals argument. I will highlight how the concept of the superorganism was originally approached from and evolutionary and a physiological perspective. In other words, it was used to argue that eusocial insect colonies are higher-level biological individuals in the fullest sense of the term. I will then assess the decline of the concept, highlighting the prominent role of kin selection and the concept of BA in its decline. I will then introduce the notion on eusociality complexity spectrum. This is the notion that there is qualitative differences in colony organization across eusocial insects; whereby in the large colonies of the most complex species (typically the evolutionary derived species), colony organization and cohesiveness are the result of a network of interactions among the members. I then argue that research into complex eusocial insects, as well as the emergence of new group selection, led to the revival of the idea of the superorganism in post-Hamiltonian eusociality research. However, the concept is currently understood using an evolutionary perspective of biological individuality. Consequently, today the concept is used to denote colonies that are units of selection; i.e. evolutionary superorganisms.

In section 4.2., I assess why the superorganism is currently only approached from an evolutionary perspective. I will argue that this is the result of the problem of hierarchy. It is often presupposed that colony cohesiveness is the result of self-organization in complex species, and that, even the large colonies of the most complex eusocial insect species can be explained without referring to a top-down hierarchical control. As a result, current explanatory approaches that focus on the physiological and proximate causes for colony cohesiveness (i.e. the actual organization) are centred around the concept of self-organization — which I will refer to as the self-organization (SO) approach. According to this view, even the most complex eusocial systems can be explained by appealing to a set of local interactions between parts of an initially disordered system, without the need of any hierarchical control. Consequently, colonies in complex eusocial insects are typically conceived of as self-organized groups that can be units of selection, and thus evolutionary superorganisms. Finally, I will conclude that whilst the evolutionary notion of the superorganism is useful, particularly for an etiological perspective, it cannot assess the organizational differences across colonies of different species.

4.1. The superorganism: from a physiological to an evolutionary perspective

4.1.1. The superorganism of old

In pre-Hamiltonian eusociality research the colonies-as-individuals argument was widespread, as I highlighted in chapter 1. One of the first to develop the idea of colonies-as-individuals into theory was W. M. Wheeler (1911; 1920; 1926; 1928). Wheeler was a leading biologist of his time and had a great impact on eusociality research, publishing numerous works on ants and other eusocial insects (Melander and Carpenter 1937). Not only was Wheeler well-read in biology but also in philosophy (Melander and Carpenter 1937). Consequently, Wheeler (1911; 1926) approached the problem of individuality in eusociality from a philosophical, as well as biological, perspective.

Eusocial insect colonies act as a cohesive unit, they are individuated and persist over time (once colonies are formed they do not dissolve or merge with other colonies), they undergo development (as opposed to being formed by the aggregation of a group of solitary insects), and most importantly, colonies can be a reproducing unit because of the reproductive division of labour. Due to this, analogies between eusocial insect colonies and organisms have tempted authors for many years (Emerson 1939: 182-183). However, Wheeler (1911) went further and argued that eusocial insect colonies *are* organisms. He did so for two reasons, firstly eusocial insect colonies matched his definition of an organism and secondly, because of Wheeler's philosophical perspective on biological individuality.

Wheeler (1911: 307-308) understood the concept of organism using a dynamical or processual perspective. He thus defined organisms as:

> An organism is a complex, definitely coördinated and therefore individualized system of activities, which are primarily directed to obtaining and assimilating substances from an environment, to producing other similar systems, known as offspring, and to protecting the system itself […] from disturbances emanating from the environment. (Wheeler 1911: 308).

Importantly, as opposed to other definitions around that time (Pradeu 2016: 805-807), this definition does not mention physical interconnectedness of the parts that form the whole, or body, of the organism. Instead, the key feature of organisms, according to Wheeler, is the integrated set of functions/processes which together form an individuated system. Such a system is an organism if it can maintain itself within its environment and produce other similar offspring systems. Thus, it is easy to see why eusocial insect colonies matched Wheeler's notion of an organism. Even though eusocial insect colonies are not physically interconnected, they are individuated systems that are internally coordinated (in this case, according to Wheeler, primarily for reproduction), they produce offspring (either by swarming or releasing young reproductives which form their own colonies — Cronin et al. 2013) and they maintain themselves against perturbations, e.g. many species have 'soldier' castes or specific defence responses (Wheeler 1928). Therefore, Wheeler's definition of an organism was not limited to physically interconnected systems such as cells and multicellular organisms but also eusocial insect colonies and other biological systems. This is turn, was because of Wheeler's specific philosophical perspective of biological individuality.

Wheeler (1911: 308-310, 1926) was sympathetic to the idea of 'emergent evolution', which, as a non-reductionist position, was opposed to the mainstream reductionism of the materialists during that time. It is from this basis that Wheeler composed his definition of an organism that, as above, did not emphasize physical interconnectedness but instead emphasized functional organization. Based on this, Wheeler (1911: 308-309) argued for a hierarchy of organisms; from cells, cell aggregates (biofilms), multicellular organisms, eusocial colonies, human society, and more. With multicellular organisms as the prototypical organism within this hierarchy. Wheeler (1911: 309, 1926) argued that each token of the different types of organism in this hierarchy are emergent wholes, which are more than just the sum of their parts. In other words, higher-order organisms are emergent wholes constituted by members of some, or one, of the lower-order types of organisms in the hierarchy, for example human societies are formed by multicellular organisms (which are formed by cells). Wheeler was a realist about his hierarchy of organisms, he did not consider it merely as an analogy:

> [But] I believe, nevertheless that all of them [cells, cell aggregates, metazoan, colonies, etc.] are real organisms and not merely conceptual constructions or analogies. (Wheeler 1911: 309).

It appears that it is for this reason that Wheeler (1920: 117, 1926, 1928) later applied the term 'superorganism' to eusocial insects, i.e. he considered that colonies are emergent, second-order, organisms that have the prototypical (multicellular) organisms as their constitutive parts. Or more simply, that colonies are organisms 'in which whole organisms function as the interacting determining parts'; i.e. *super*-organisms whereby the prefix "super" refers to a higher-order rank of organism (Wheeler 1926: 435).

The next leading protagonist in the history of the superorganism[14] concept was A. E. Emerson. Although Emerson was also sympathetic to the notion of emergent evolution, his notion of the superorganism was different to Wheeler's. Consequently, Emerson (1939) also argued for a hierarchy, similarly to Wheeler, but of *biological individuals* rather than of organisms. In other words, based on the notion of emergent evolution, Emerson (1939: 182) also argued for the existence of emergent biological wholes (units) that are the result of interacting lower-level parts, however, not all of these emergent wholes are organisms, even if they are 'relatively independent of other units'.[15]

> Certainly, [a eusocial colony] is a community of organisms as far as the individual components are concerned. When the integrating mechanisms, however, are considered, the community possesses aspects of a single individual. That brings us back to the philosophical discussion of what we mean by the individual. (Emerson 1939: 208).

Therefore, the first major difference between Emerson and Wheeler was that, for the former, a superorganism is a 'social organism' that is *analogous* to an organism (Emerson 1939), whereas for the latter the superorganism *is* an organism but of a higher-order (Wheeler 1911).

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[14] In his later work, Emerson (1952) preferred the term 'supraorganism' rather than 'superorganism', I will continue to use 'superorganism' as for Emerson the two terms are synonymous, and he chose the latter for semantic reasons.

[15] Emerson (1939, 1952) did not specify exactly how a biological individual becomes an organism but his distinction appears to be based on 1) the degree of integration of the parts and 2) physical interconnectedness of the parts. His position, however, appears to anticipate the current debate on biological individuality (see Pradeu 2016).

Moreover, for Emerson (1952), the superorganism concept was primarily a tool for analogical reasoning in the study of eusociality, and sociality more generally (Wilson 1971). Emerson (1952) argued that focusing on the analogies (and dissimilarities) between eusocial colonies and organisms can guide eusociality researchers to discover the processes and integrating mechanisms that enable the emergence of biological individuality at the level of the colony. This is because, Emerson argued, that treating eusocial colonies as superorganisms and consequently comparing them to organisms can lead to the discovery of general biological principles, particularly those pertaining to biological individuality. For example, Emerson argued that one key feature of all biological systems is a drive to increase homeostasis over evolutionary time:

> All levels of organization exhibit homeostasis and the trend of evolution is toward increased homeostasis. (Emerson 1952: 348).

For Emerson, the drive to increased homeostasis leads to the evolution of division of labour and polymorphism within eusocial colonies, just as, he argued, it has led to the evolution of division of labour and cell differentiation in multicellular organisms. Thus, the second major difference between Emerson and Wheeler was that, for the former, the superorganism concept was a tool for analogical reasoning whereas, for the latter, it was a concept with which to classify a type of emergent organism.

In summary, for Wheeler, eusocial colonies are superorganisms because they are organisms formed of organisms (*super*-organisms), for Emerson, eusocial colonies are superorganisms because they are higher-level biological individuals, *but not organisms*, that have analogous traits and properties to organisms. Importantly, however, both authors conceived of the superorganism concept from a physiological notion of individuality. For each author the important point was that eusocial colonies are emergent biological units (individuals), and consequently, one important aim of eusociality research should be to explain how systems that lack physical interconnectedness could achieve the cohesiveness required to enable this emergence. However, by around the 1960s the concept of the superorganism saw a sharp decline in use.

4.1.2. The decline of the superorganism

The decline of the superorganism occurred during the Modern Synthesis and the emergence of the 'gene's eye view', which led to a prominent focus on the gene at the expense of additional focus at the phenotypic level and more holistic, or top-down, approaches (Cronin 1991; Wilson and Wilson 2007; Borrello 2010; Calcott and Sterelny 2011). E. O. Wilson (1971: 317-319) argued that the decline of the superorganism was due to both the focus on reductionist genetic approaches and also the alteration of the superorganism concept by A. E. Emerson (1956). As above, Emerson argued that the superorganism concept should primarily be seen as a tool for analogical reasoning. For Emerson, the aim is to understand how colonies could achieve their cohesiveness and homeostasis and he argued that understanding the common properties or characteristics they share with organisms could aid research into this. Yet, as Wilson (1971) argued, from around the 1960s most eusocial researchers were more interested in using reductionist approaches and explaining eusocial insects from the genetic level, thus the analogical version of the superorganism appeared unnecessary.

Additionally, the superorganism concept, and the colonies-as-individuals argument in general, declined due to the emergence of kin selection. This is because applying kin selection presupposes that a colony is not an individual. Kin selection was developed by Hamilton (1963, 1964a) in order to explain the evolution of cooperation, particularly BA, from a gene's eye perspective, i.e. within the framework of the Modern Synthesis (Hunt 2007: 194; Hölldobler and Wilson 2009: 24-29). According to this perspective, competition between eusocial insect colonies is fully explained in terms of fitness differences of the insects of the whole population; i.e. some colonies are more successful than others because the fitness of each insect in the colony is higher (on average) than those in other colonies. Or in other words, the fitness of a colony is simply the sum of the fitness of each individual in the colony, colonies themselves are not the bearers of fitness. Kin selection, is therefore, primarily a reductionist approach (Okasha 2014).

Moreover, as I showed in chapter 1, Hamilton's (1972) main reason for applying kin selection to the evolution of eusociality was because he rejected the colonies-as-individuals argument. Hamilton, along with many other biologists at the time, considered genetic homogeneity a necessary condition for biological individuality in order to avoid internal conflict (Sturtevant 1938; Hamilton 1972; Santelices 1999).[16] Since eusocial insect colonies are not genetically homogeneous, Hamilton rejected the colonies-as-individuals argument. This, as well as his emphasis on the concept of BA, led Hamilton (1964b, 1972) to view eusocial colonies as social groups and thus he applied the theory of kin selection in order to explain their evolution and maintenance.

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[16] The idea that genetic homogeneity is necessary for biological individuality is still held by authors today (e.g. Detrain and Deneubourg 2006). However, the debate over biological individuality is a prominent one (see Pradeu 2016), and whilst genetic homogeneity may be an important factor for organisms (Arnellos et al. 2014) it may be less important for other forms of biological individuality (Clarke 2010; Dupré 2010).

Kin selection was a groundbreaking theory for evolutionary biology and, consequently, it received much attention by eusocial insect researchers (Bourke and Franks 1995; Alonso and Schuck-Paim 2002). This, in turn, led to many authors to view colonies as groups, for the above reason. Therefore, I argue that the decline of the superorganism, and colonies-as-individuals arguments in general, was due to reductionist interpretations of the Modern Synthesis and due to the introduction of kin selection. However, that is not to say that kin selection is not applicable to eusocial insects at all, but rather, as I argued in the previous chapter, it is more appropriately applied to the evolutionary basal species and the origins of eusociality, i.e. before obligatory eusociality and colony level selection emerge.

Hamilton's huge influence, due to his theory of kin selection, and his focus on the concept of BA, led to more attention being paid to the evolution of eusociality in the decades following his introduction of the theory (Gadagkar 1990: 115; Bourke 1999; Burchill and Moreau 2016). During this period relatively little attention was paid to the maintenance and further evolution of eusocial insects:

> Research on social evolution in insects has concentrated on the origin of eusociality […]. A less well-explored theme is the transition from simple to complex [eusociality] among [eusocial] insects. (Bourke 1999: 245).

The subsequent research into complex eusocial insects — which were traditionally referred to as the evolutionary advanced species (Bourke 1999) — has resulted in evidence for the superorganism argument, which I will review next.

4.1.3. Complex eusociality

Complexity in eusocial insect colonies is broadly defined by the following factors (Hölldobler and Wilson 1990; Bourke 1999; Anderson and McShea 2001; Leonhardt et al. 2016):

- *colony size*, which is measured by the number of members in the colony (not, for example, by the size of the nest);
- *degree of polymorphism*, which refers to the degree of physiological differentiation between the reproductive and worker castes, and if applicable, any possible physiological specialization amongst different worker castes (e.g. soldiers that are physiologically incapable of foraging or feeding themselves);
- *worker totipotency*, which refers to the degree to which workers are specialised to a specific role/set of tasks or are generalists and undertake all tasks (apart from reproduction);
- *communication networks*, which refers to the general degree of interaction amongst the members of the colony, as well as the type of interaction (behavioural, pheromonal, physical, etc.), and how those interactions coordinate the division of labour within the colony.

Together, the *degree of polymorphism* and levels of *worker totipotency* point to the overall division of labour within colonies; for example, if a colony has multiple physiological worker castes (e.g. minor workers, soldiers, etc.) that are each specialised to a small set of tasks (e.g. nest building, foraging, defence, etc.) and therefore have low totipotency, this would point to a high degree of division of labour within the colony as a whole. However, there is no discreet threshold between simple and complex eusocial species, but rather a spectrum from the simplest to the most complex, with varying degrees of complexity across the spectrum. The simplest eusocial colonies are normally relatively small (tens to hundreds of members) with no polymorphism between the reproductive and worker castes (i.e. any worker has the potential to become a reproductive in the event of the queen dying), high totipotency of the worker caste, with relatively simple/minimal communication networks. Consequently, complex colonies are large (thousands to millions of members) with polymorphism (a worker caste that is morphologically different to the reproductive caste, and in some cases, there is also multiple physiological worker castes), the loss of reproductive potential and totipotency in the worker castes, and complex communication systems (Anderson and McShea 2001). For example, honey bees (*Apis mellifera*) are considered a complex eusocial species due to their large colony size, the polymorphism between the reproductive and worker castes, a complex communication system and low totipotency — even though there is a small degree of worker reproductive potential. Honey bee workers do not have spermatheca and cannot mate, but they can produce unfertilized eggs (which due to the haplodiploidy genetic system, can develop into males), but this typically only occurs when the queen dies or loses her influence on the colony (Anderson and McShea 2001; Ronai et al. 2015).

The notion of 'complex' eusociality is not based on arbitrarily chosen parameters. For example, colony size is tightly linked to the degree of organizational complexity. Larger colony size in eusocial insects allows, for example, increased worker specialisation (reduced totipotency); this is because there are more workers available for each task and thus, sub groups of workers can specialise for specific tasks or sets of tasks. Instead, in smaller colonies there are less workers per task and it is therefore more efficient for the colony to maintain generalist workers rather than specialised ones (Fewell and Harrison 2016). Moreover, it has been shown that an increase in colony size (and thus overall mass) affects physiological properties of colonies in an analogous way to increased mass in unitary organisms — for example, mass-specific metabolic rate, germ/soma investment, ontogenetic growth, lifespan, are all effected by increased mass (Hou et al. 2010; Fewell and Harrison 2016). Or in other words, just as in multicellular organisms, larger size is linked with reduced energy use per unit (i.e. per insect in colonies, and per cells in multicellular organisms), as well as slower ontogenetic growth and longer lifespan (Hou et al. 2010).

Moreover, morphological worker castes are only associated with large colonies (Bourke 1999; Anderson and McShea 2001). Complete physical sterility of workers is rare, but it too is also only associated with large colonies (Anderson and McShea 2001). Additionally, in larger colonies increased genetic heterogeneity — by polyandry (multiply mated queens) or polygyny (multiple queens) — can be beneficial to the colony despite the classical predictions from kin selection that extreme cooperation requires high relatedness (Cremer et al. 2007; Oldroyd and Fewell 2007; Wilson 2008b). Increased genetic heterogeneity can lead to increased disease resistance or greater division of labour, but this is not the case for all species and depends on multiple factors (Wilson 2008b). Most importantly, increasing complexity at the colony level is associated with decreasing complexity at the level of the parts, i.e. the insects that form the colony (Anderson and McShea 2001). Or in other words, in complex eusocial insect species, the members of the colony tend to be physically and/or behaviourally specialised and lack totipotency. But at the same time, this results in an increased division of labour and functional integration at the colony level, compared to colonies of more simple species. There is, therefore, evidence for qualitative differences in the organization of colonies in the complex eusocial insect species compared to simple ones.

4.1.4. The revival of the superorganism

As I argued in the previous chapter, the use of the superorganism concept drastically declined around the 1960s. This was not only because Emerson's analogical version of the superorganism was not seen as compatible with the reductionist approaches that became prevalent due to the Modern Synthesis, as E. O. Wilson argued (1971: 317-319). It was mainly due to the emergence of kin selection, a theory which presupposes that colonies are not individuals, and the subsequent widespread attention that it garnered. The concept of the superorganism has since been revived, however, around the late 1980s. The first attempt was by C. J. Lumsden (1982), who, like Wheeler and Emerson, argued for a notion of the superorganism based on a physiological approach to biological individuality. However, Lumsden wanted to move on from the analogical approach developed by Emerson to a more precise theoretical approach. To do this Lumsden (1982) utilised a systems approach and argued for a notion of the superorganism based on models of self-organization and feedback loops. Although self-organization became the mainstream approach when studying the actual organization of eusocial insect colonies, as I have shown in the previous chapter, Lumsden's attempted revival of the superorganism was not so successful.[17] It was not until the work of D. S. Wilson and E. Sober (1989) that the concept of the superorganism can really said to have been 'revived' (Haber 2013).

Wilson and Sober (1989) argued for a revival of the concept of the superorganism, but based on an evolutionary notion of biological individuality. For Wilson and Sober, the defining feature of organisms, and thus superorganisms, is the ability to directly partake in natural selection. Or in other words, what separates organisms from other biological systems/groups is that they are units of selection:

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[17] Lumsden's 1982 article has been cited 41 times, whereas Wilson and Sober's 1989 article has been cited 580 times (according to Google Scholar — February 2019).

> Individuals acquire the exquisite functional organization that justifies their status as organisms by the process of natural selection. (Wilson and Sober 1989: 339).

Wilson and Sober argued that eusocial colonies, as well as other groups of organisms, also exhibit functional organization, and thus should be considered as higher-level organisms (superorganisms). In order to extend their definition of organism to colonies (and other groups of organisms) they relied on the notion of multi-level selection. Wilson and Sober argued that groups (e.g. eusocial colonies) can be considered as superorganisms if they achieve a high degree of internal cooperation (functional organization) such that *between-colony* selection is greater than *within-colony* selection. Or in other words, if colonies qualify as units of selection then they are superorganisms.

Though the key feature of Wilson and Sober's definition of organism, and therefore superorganism, is the notion of functional organization, they do not define precisely what this means. For instance, what is the minimum amount of functions required to achieve functional organization? Wilson and Sober simply argue that functional organization is achieved by natural selection:

> [Natural] selection requires heritable variation. Individuals must differ in their properties, and those differences also must exist to some degree in their offspring. If so, then properties that enhance the relative survival and reproduction of individuals will increase in frequency from generation to generation. The accumulation of these properties *is the functional organization* that allows individuals to successfully survive and reproduce in their environments. (Wilson and Sober 1989: 339-340. Emphasis added).

This could be intentional on the part of Wilson and Sober, as it allows their definition to be more general and applicable to groups as well as organisms (Haber 2013). However, this also has the consequence that their notion of the superorganism does not say anything about how colonies achieve the required cohesiveness and integration in order to become units of selection. In other words, this approach does not focus on the actual organization of colonies but instead on their evolutionary, or phylogenetic, past. This is not necessarily a problem in itself, but it begs the question of how colonies can achieve their cohesiveness and elegant integration.

> The challenge is to understand the complex mechanisms that enable a colony to function *as a single organism*, exactly as imagined by Wheeler so long ago. (Wilson and Wilson 2007: 342. Emphasis in the original).

Despite this issue, the revival of the superorganism concept by Wilson and Sober was relatively successful. Not only is the concept of the superorganism once again a central concept within eusociality research (Wilson and Hölldobler 2009), but it is generally understood using an evolutionary concept of biological individuality (Reeve and Hölldobler 2007; Queller and Strassmann 2009; Haber 2013). This is a direct consequence of Wilson and Sober's (1989) revival of the superorganism, using an evolutionary notion of biological individuality.

A. Hamilton, and colleagues (2009), argued that there are actually two approaches to the superorganism concept in use today. The first is what they refer to as the 'similarity approach', which is essentially an analogous approach whereby eusocial colonies are compared to organisms, and the second is the 'selection approach', which argues that colonies are superorganisms because they are units of selection (Hamilton et al. 2009: 574-576). The similarity approach is similar to Emerson's version of the superorganism and it is argued that Wilson and Sober's account is the key example of this approach (Hamilton et al. 2009). This is because, according to A. Hamilton et al., Wilson and Sober consider colonies as superorganisms because, like organisms, they are functionally organized. Whilst this is true, Wilson and Sober's justification for this is that colonies are units of selection, and therefore their account also falls under the selection approach — a fact with which A. Hamilton and colleagues also agree with (2009: 575-576). However, this highlights the problem with A. Hamilton and colleagues' argument; most contemporary accounts of the superorganism are based on evolutionary notions of biological individuality and thus can be classed as selection approaches. However, they typically also employ analogical reasoning and compare colonies to organisms as further justification (Haber 2013). For example, in their influential book *The Superorganism*, B. Hölldobler and E. O. Wilson (2009) argued:

> [The] term *superorganism* may be applied only to colonies of an advanced state of eusociality, in which interindividual conflict for reproductive privilege is diminished and the worker caste is selected to maximize colony efficiency in intercolony competition. (Hölldobler and Wilson 2009: 9. Emphasis in the original).

Thus, their account could be classed under the selection approach, however, in the glossary section they define a superorganism as: 'A society, such as a eusocial insect colony, that possesses features of organization analogous to the physiological properties of single organisms' (Hölldobler and Wilson 2009: 513). Therefore, additionally, their concept of the superorganism could also be classed under the similarity approach.

This is also true of other authors who use the concept of the superorganism (Reeve and Hölldobler 2007; Eggleton 2011; Haber 2013). Thus, the problem of Wilson and Sober still remains, namely that an evolutionary notion of the superorganism does not say much about the actual organization of colonies. This is demonstrated by the fact that authors typically claim that eusocial colonies are superorganisms because they are units of selection, but they subsequently employ analogical reasoning, comparing colonies to organisms, in order to account for this phenomenon. But defining colony individuality by comparing colonies to multicellular organisms has the potential risk of missing or neglecting the unique and/or important factors that enable *groups of multicellular organisms* to achieve biological individuality at the collective level (Haber 2013). Or in other words, focusing on how eusocial insect colonies are analogous to multicellular organisms (e.g. the reproductive division of labour) potentially focuses the attention of researchers on factors that are less important for colony individuality. For example, unlike prototypical multicellular organisms, eusocial insect colonies lack physical interconnectedness and any form of collective nervous system, which makes the emergence of regulation and control at the collective level a much different prospect than it is in the former. *Eusocial insect colonies are systems that have free-moving multicellular organisms as the constitutive parts, thus the exportation of individuality to the collective level is likely to be very different to that of the transition from unicellular to multicellular individuality.*

Although the superorganism argument went through a sharp decline for almost two decades it is once again at the forefront of eusociality research. Today, however, the argument is mainly made from an evolutionary perspective of biological individuality. Namely, authors use MLS to show that, for many eusocial insect species, colonies are the unit of selection, i.e. evolutionary individuals (Hölldobler and Wilson 2009; Queller and Strassmann 2009;

Strassmann and Queller 2010; Okasha 2014; Helanterä 2016). Yet, whilst the evolutionary aspects of eusocial insect colonies are important (e.g. the transition from selection of reproductives to selection of colonies) the physiological aspects are as equally important. For example, the relations and interactions between the members of the colony are important to understand the proximate causes for the functional integration that enables colony selection (see Arnellos et al. 2014 for an analogous argument for multicellular individuality). However, despite this, the superorganism is rarely approached from a physiological perspective today.

4.2. The self-organization approach to complex eusociality

4.2.1. The problem of hierarchy

As above, research into complex eusociality has only relatively recently gained attention. This is important because the data from this research, particularly the finding that there are qualitative differences in colony organization in the complex species compared to the simpler ones, could point to a form of individuality at the colony level. Indeed, this research led to the revival of the superorganism (Lumsden 1982; Wilson and Sober 1989; Hölldobler and Wilson 2009; Haber 2013). However, unlike in pre-Hamiltonian eusociality research, today the superorganism argument is typically only employed from an evolutionary perspective. In other words, authors use MLS to show that colonies of some eusocial insect species are *units of selection* (Moritz and Fuchs 1998; Detrain and Deneubourg 2006; Reeve and Hölldobler 2007; Hölldobler and Wilson 2009; Queller and Strassmann 2009; Nowak et al. 2010). The superorganism argument from a physiological perspective is, in comparison, currently rarely employed. If it is widely accepted that colonies are evolutionary individuals, why has there been relatively little research into the question of whether colonies are also physiological-like biological individuals? Particularly as this view was made so long ago by Wheeler (1911).

The answer to this question is likely multifaceted, but the same reasons that led to the decline of the superorganism argument are likely to be involved. The prominence of reductionist approaches and a focus on the genetic level, due to the Modern Synthesis, likely reinforced the idea that genetic homogeneity is an essential part of physiological individuality:

> Likewise any metazoan, ant societies are made of units that are differentiated into sterile or reproductive individuals and function as a cooperative unit. Yet the analogy is clearly strained since somatic cells are all *genetically identical* while ants are not. (Detrain and Deneubourg 2006: 165. Emphasis added.)

It is argued that genetic heterogeneity could lead to potential conflict, and thus selection at the lower level would undermine higher-level selection. However, genetic homogeneity is not necessarily required for all forms of biological individuality (see, for example, Dupré 2010).

Not only are eusocial insect colonies not genetically homogeneous but they also lack physical contiguity, i.e. colonies are formed of free-moving insects, and thus do not have clear boundaries as do cells or multicellular organisms. The lack of physical contiguity, as well as genetic heterogeneity, reinforce the intuition that colonies are groups rather than physiological individuals.[18] Moreover, as above, kin selection presupposes that colonies are groups. Thus, the huge focus on kin selection in the decades following its introduction likely had an influence

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[18] Along with genetic homogeneity, physical contiguity has historically also been viewed as important factor for physiological individuality (see Pradeu 2016).

on the current mainstream view that eusocial insect colonies are groups that can be, at most, evolutionary individuals (units of selection).

Finally, another reason for the mainstream view of colonies as groups rather than individuals is that it is commonly argued that top-down hierarchical control does not occur, or is not necessary, in the large colonies of complex species. Arguments are made along the following lines, '[…] their colony as a whole lacks command and control by a still higher-level system. It therefore must be self-organized' (Hölldobler and Wilson 2009: 58). In other words, because colonies lack physical contiguity and any type of organ or nervous system at the collective level (i.e. colony level), such as in multicellular organisms, it is argued that top down hierarchical control does not occur. However, I argue that this view needs to be reassessed, from both a theoretical and empirical perspective. Even though colonies lack physical contiguity and do not have organs, they do have complex communication mechanisms that could enable hierarchical control (Johnson and Linksvayer 2010). In other words, the network of interactions among the members of the colony could result in a higher-order organization that can regulate and control the lower level parts (the insects in the colony) — i.e. a hierarchical-organization — which I will argue for in the next chapter. But the presupposition that hierarchical control does not occur in the large colonies of complex eusocial insects has led to the mainstream view that the coordination and cohesiveness of colonies can be explained by self-organization alone. Current explanatory approaches that focus on the actual organization of colonies are centred around the concept of self-organization (Boomsma and Franks 2006; Detrain and Deneubourg 2006; Fewell et al. 2009). Consequently, even colonies of the most complex eusocial species (with polymorphic castes, complex division of labour, colony selection, etc.) are typically conceived of as *self-organized groups*.

4.2.2. The self-organization approach

The concept of self-organization was developed in thermodynamics to explain how macroscopic patterns/order could spontaneously emerge in previously disordered physical and chemical systems, as a result of distributed local interactions of the microscopic parts (Detrain and Deneubourg 2006). In other words, self-organization was used to explain the phenomenon of emergent order at the macroscopic level without the need of internal or external top-down hierarchical control. The concept of self-organization was thus appealing to eusociality researchers, since as above, it was widely considered that large complex colonies were incapable of hierarchical control but were nevertheless well-organized cohesive complex systems (Bonabeau et al. 1997; Boomsma and Franks 2006; Detrain and Deneubourg 2006; Fewell et al. 2009). This approach, what I refer to as the self-organization (SO) approach, began around the 1980/90s and was developed by E. Bonabeau, S. Camazine, J.-L. Deneubourg, G. Theraulaz, among others (Boomsma and Franks 2006). The main tenet of the SO approach is that complex colony level phenomena can occur in eusocial insect colonies without hierarchical control, instead they are the result of a flat network of locally distributed interactions amongst the parts (in this case the individual insects).

To illustrate this, it will be useful to give a brief example of self-organization in eusocial insects, namely collective decision making. A simple case of collective decision making can occur when there is a choice to be made by the foragers of a colony between two equal sources of food, A and B. At first, each individual forager will randomly choose one of the two choices. Additionally, each forager leaves a pheromone signal to recruit other foragers to their choice. If for any reason more foragers choose A over B, for example, this would cause the pheromone signal at A to be stronger than at B. In turn, the stronger pheromone signal at A will positively feedback on the decision of other foragers, i.e. the stronger pheromone signal will attract more foragers to choose A over B, which will eventually lead to all foragers choosing A over B. Thus, the 'choice' of A over B by the group is a result of a positive feedback loop on initial local random choices of each individual forager (Bonabeau et al. 1997; Detrain and Deneubourg 2006). In other words, in this case the initial decision of option A was randomly caused by more foragers choosing A over B, but this decision was reinforced by a pheromone signal causing a positive feedback on the subsequent individual choices of other foragers. But in other cases, the decision could be less random. For example, if foragers can differentially emit the pheromone signal depending on the quality of the food, then if A is a better quality food source than B, it will attract a stronger pheromone release by foragers, which will feedback on the choice of subsequent foragers entailing that eventually, the whole group will collectively choose A. Consequently, in the context of eusocial systems, the SO approach typically focuses on self-organized phenomena produced by feedback loops (positive or negative) resulting from the multiple locally distributed interactions of the insects in a colony, and the amplification of random fluctuations in those interactions (for more details see Bonabeau et al. 1997).

However, unlike physical systems, the parts that make up complex eusocial insect colonies are not molecules but cognitive agents, and therefore in this context self-organization is sometimes combined with the concept of stigmergy and referred to as stigmergic self-organization (Bonabeau et al. 1997; Holland and Melhuish 1999). Stigmergy, developed by P. P. Grassé, refers to how the behaviour of an agent can be influenced by an environment that was itself affected by earlier behaviour (Hölldobler and Wilson 2009: 479-481). Essentially, stigmergy emphasizes that an agent, in this case an insect in a eusocial colony, can produce complex constructions (e.g. nest, honey comb, etc.) or work without the need of a complete knowledge of the construction or task in hand. Instead, the agent only requires a simple set of behavioural rules. It has been shown that through very simple behavioural rules (or interpretative decision making) complex colony level processes can occur via the insects in the colony responding in accordance to local information, i.e. stigmergic self-organization. For example, Holland and Melhuish (1999) found that robots programmed with a few simple response rules could sort two distinct types of Frisbee in a given space, and put one type into a cluster. The robots achieved this by responding differently to different stimuli, for example; all Frisbees that are not in contact with another Frisbee are picked up, if the robots encountered ringed Frisbees that were in contact with any other Frisbee then they cannot pick them up and move them, but the plain type of Frisbee are always picked up and moved when encountered. After several hours this results in a cluster containing mainly ringed Frisbees. But importantly, for this clustering to occur, no robot required the complete plan the ringed Frisbees should be clustered but not plain ones; they only required simple behavioural rules. The process of clustering different types of objects occurs in certain eusocial colonies, for example brood sorting in some ant species (Holland and Melhuish 1999).

Another factor that is claimed to influence the self-organization of eusocial insect colonies is what is referred to as the ‘response threshold theory’ (Robinson 1992; Page Jr. and Erber 2002). The response threshold theory argues that due to naturally occurring differences among the individual insects in the colony, not every insect will respond at the same time to task stimuli. Some insects will have lower response thresholds for some tasks, say pollen foraging, and will react first to any stimulus for this behaviour (e.g. reduced pollen stores). As they undertake this behaviour the stimulus for it is reduced, consequently, other individuals with a higher threshold for this behaviour will not respond. Therefore, only a subset of the colony responds to the pollen foraging stimulus in this case (unless the stimulus was so high as to also induce a response from individuals with a higher threshold). At the same time, those that did not respond to pollen foraging may have lower response thresholds for other tasks, like water foraging, and so on. The response threshold theory, therefore, also provides a good explanation for how basic division of labour can emerge naturally within groups; namely via differential response thresholds and self-organization dynamics.

Broadly then, the SO approach attempts to explain colony level phenomena by focusing on the interactions of the insects in the colony. The insects in the colony can achieve collective order (i.e. nest constructions, foraging patterns, etc.) simply by acting on local information in a distributed network (Detrain and Deneubourg 2006; Boomsma and Franks 2006):

> The collective behaviour of insect colonies is achieved through feedback mechanisms arising from the activities of individual insects, each following a basic set of rules. (Makinson and Beekman 2014: 2020).

In other words, the SO approach conceives the actual organization of the colony as a flat network of interactions, and that colony cohesiveness emerges through self-organization alone. The SO approach has become the mainstream approach in the study of the actual organization of colonies (specifically the complex species) because of the widely held presupposition that the global behaviour of complex eusocial insect colonies can be explained without resorting to top-down hierarchical control.

The SO approach has been very successful in furthering our understanding of the actual organization of eusocial insect colonies, particularly those collective processes that are based on feedback loops. However, as has been argued by B. R. Johnson and T. A. Linksvayer (2010), coordinating mechanisms or processes are also required in order for the different (self-organized) colony level processes to occur in a cohesive organization. For example, if multiple colony processes were occurring at the same time, then coordinating mechanisms would ensure that enough workers were available for each process, additionally, coordinating mechanisms would be essential to ensure that different colony processes occur in the correct sequence or at the correct time. In the next chapter I will argue that such coordinating mechanisms could be evidence of hierarchical control and regulation. Thus, the claim that there is no hierarchical control and regulation in the large colonies of complex eusocial insects needs to be reassessed. Therefore, in the next chapter I will propose a different approach, that whilst incorporating self-organization, includes forms of hierarchical control. I will call this view the *hierarchical-organizational* approach.

Conclusion

In this chapter I have reviewed the history and current state-of-the-art of the superorganism argument, as well as the study of complex eusociality. To begin with, in section 4.1., I reviewed the history of the superorganism. I highlighted, in 4.1.1., that the concept was originally understood using a physiological and evolutionary perspective of biological individuality. Wheeler, who first applied the concept to eusocial insects, conceived of superorganisms as higher-order organisms. He used an organizational approach to define organisms and argued that eusocial insect colonies fulfilled this definition as equally as multicellular organisms, thus they should be considered as superorganisms. I then highlighted how Emerson, next major protagonist in the history of the superorganism, altered the concept. He argued that the superorganism should be used primarily as a tool for analogical reasoning, in order to discover how eusocial insect colonies can achieve integration and homeostasis at the colony level.

However, he conceived of superorganisms as biological individuals but not organisms. In 4.1.2., I highlighted that the superorganism radically declined in use around the 1960s primarily as a result of the emergence of kin selection. Kin selection is a reductionist approach, with a particular emphasis on the genetic level and population genetics. Moreover, applying kin selection to eusocial insects presupposes that colonies are not individuals because inclusive fitness models posit a personal fitness value to each member of the colony. In other words, kin selection theorists argued that inter-colony competition can be fully explained in terms of the fitness differences of the individuals insects within breeding populations, rather than by colony selection. Thus, with the emergence of kin selection in the 1960s, the concept of the superorganism declined.

However, in section 4.1.3., I argued that the recent research into complex eusocial insect species provided renewed evidence for the superorganism argument. Complex eusocial species are characterised by large colony size, worker specialisation (low worker totipotency), polymorphism, and complex communication networks. As organizational complexity at the colony level increases, the complexity of the members in the colony decreases (Anderson and McShea 2001). In other words, as the division of labour becomes more complex, the members of the colony become more specialised, and as a result, become more reliant on the colony for their development and survival. This empirical evidence, as well as the emergence of new group selection, led to a revival of the superorganism concept. I argued, in section 4.1.4., that the superorganism argument saw a resurgence in the late 1980s due to the work of Wilson and Sober (1989), who were influenced by the increasing research into complex eusociality. However, they conceived the superorganism concept from an evolutionary perspective of biological individuality, using MLS2; colonies are superorganisms when between-colony selection is greater than within-colony selection. As a result, today, the concept is typically understood from an evolutionary perspective of biological individuality; i.e. colonies that are units of selection are superorganisms. Whilst the evolutionary notion of the superorganism is useful from an etiological perspective, it cannot tell us anything about the organizational differences among colonies of different eusocial species.

In sum, despite its revival in the 1980s, the superorganism argument, form a physiological perspective of biological individuality, is less prevalent today than compared to pre-Hamiltonian eusociality research. In 4.2.1., I argued that this is because of the presupposition that hierarchical control does not occur, or is not necessary, in the large colonies of complex eusocial insects. This led to the mainstream view that colony cohesiveness, which enables colony selection in many complex species, is due to the self-organization of the members of the colony alone. In section 4.2.2., I highlighted that, as a result of the presupposition that hierarchical control does not occur, the actual organization of complex eusocial colonies are studied by what I referred to as the self-organization (SO) approach. According to this view, even the most complex eusocial systems can be explained by appealing to a set of local interactions between parts of an initially disordered system, without the need of any hierarchical control. Thus, the SO approach conceives the organization of colonies as flat network of interactions, i.e. a result of self-organization alone. Consequently, authors typically employ the superorganism concept in order to denote a *self-organized group* that is a unit of selection. However, as I will argue next, the mechanisms/processes that coordinate the different (self-organized) colony processes could be evidence of hierarchical control. Therefore, in the next chapter I will challenge the presupposition that hierarchical control does not occur in complex eusocial insect colonies by developing an alternative organizational approach (the *hierarchical-organizational* approach) that assesses if there is hierarchical organization within complex colonies. Moreover, I will argue that such an approach is more suited to assessing the different types of individuality at the colony level in eusocial insects in species from across the eusociality complexity spectrum, using a comparative case study.

Chapter 5 — Revising the superorganism: the hierarchical-organizational approach to complex eusociality

Introduction

In the previous chapter I argued that the superorganism argument, that was prevalent in pre-Hamiltonian eusociality research, saw a radical decline after the emergence of kin selection. This is because kin selection predetermines that colonies are not conceived of as individuals because each member is assigned an (inclusive) fitness value. However, research into complex eusociality (i.e. the more evolutionary derived species with large colonies, polymorphism and worker specialisation, complex communication systems, etc.) influenced a revival of the superorganism. But the superorganism argument is typically employed from an evolutionary perspective today — i.e. colonies that are units of selection are evolutionary individuals and, thus, superorganisms. On the other hand, the idea that hierarchical control is not needed for explaining colony organization in the large colonies of complex eusocial insects, led to the mainstream view that colonies are self-organized groups. Consequently, the study of the actual organization of eusocial colonies is done so using the self-organization approach. According to this view, even the most complex eusocial systems can be explained by appealing to a set of local interactions between parts of an initially disordered system, without the need of any hierarchical control.

In this chapter, I will argue the presupposition that hierarchical control does not occur, or is not needed, in the large colonies of complex eusocial insects needs to be reassessed. I argue that this claim should be assessed theoretically and empirically rather than assumed *a* *priori*. To do so I will develop an alternative organizational approach (the *hierarchical-organizational* approach) that assesses if there is hierarchical organization within complex colonies, that "modulates" (i.e. regulates and controls on) the self-organized dynamics within the colony system; i.e. this approach will be able to assess if colony organization is the result of self-organization only or *also* and *mainly* due to hierarchical regulation and control. I will also argue that this approach would be better suited to assess the issue of whether complex eusocial insect colonies should be considered biological individuals or not. This is because if there are colonies with hierarchical organization then an argument can be made that the colony is in "control" rather than the insects that instantiate it, i.e. the colony organization is not solely the result of self-organization but a higher-level organization that exerts top-down control on its parts. In other words, if there is evidence of hierarchical-organization within colonies of eusocial insects, then this would be evidence for the superorganism from a physiological-like perspective, as well as an evolutionary perspective of biological individuality.

I will begin, in section 5.1., by reviewing a recent physiological approach to colony individuality, namely the "social physiological" approach. I will argue that whilst the social physiology approach is interesting, it may not be suitable for assessing the different types of individuality at the colony level across eusocial insects because it focuses primarily at the genetic level. I then develop the hierarchical-organizational (HO) approach as an alternative to the current explanatory approaches to the actual organization in complex eusocial insects. Taking the colony as a whole, the HO approach will focus on the development of colony organization, in particular assessing the mechanisms and signals that coordinate the collective (self-organized) colony processes. In section 5.2. I will apply the HO approach to three representative case studies of species from across the eusocial complexity spectrum — namely, *Megalopta genalis*, *Vespula vulgaris*, and *Apis mellifera* — in order to assess the presupposition that hierarchical control does not occur. I will review colony development and, where applicable, collective colony processes, and how such processes are regulated. In other words, I will assess if colony organization is the result of self-organization alone, or whether it is due to hierarchical control and regulation. Then in section 5.3., I will assess the types of colony individuality, if applicable, in the three species. Specifically, I will assess whether colonies exhibit individuality at the colony level, and if so, if they can be considered as superorganisms from only an evolutionary perspective (i.e. if they are units of selection), or also from a physiological-like perspective (i.e. if they are hierarchically-organized). Finally, in 5.4., I will highlight how the superorganism argument provides further evidence against the claim that the non-reproductive castes in eusocial insects are examples of BA.

5.1. The hierarchical-organizational approach

As I highlighted in the previous chapter, the SO approach has been very successful in furthering our understanding of the actual organization of eusocial insect colonies, particularly those collective processes that are based on feedback loops. However, the prominent view that the large colonies of complex eusocial insect species are self-organized groups has led to a lack of physiological approaches to the superorganism argument. The superorganism is typically understood as groups that are units of selection, but the evidence from complex eusocial insect colonies points to the fact that they could exhibit colony individuality in a stronger sense. In this section I will develop a physiological approach to the superorganism. I do so by outlining an organizational approach, that whilst incorporating self-organization, does not discard the role of hierarchical control, namely the *hierarchical-organizational* (HO) approach. However, before I do so, I will briefly overview a recent physiological approach to the superorganism that is particularly interesting; the ‘social physiology’ approach (Johnson and Linksvayer 2010).

5.1.1. The social physiology approach

Eusocial insect colonies typically undergo development, are individuated and have relatively clear boundaries (despite lacking physical contiguity), and exhibit (reproductive) division of labour (Eggleton 2011). Moreover, colony selection occurs in many species, particularly in the more complex species, due to the reproductive division of labour (Hölldobler and Wilson 2009). Therefore, in many cases, it is better to view the colony as a single complex system in order to uncover the proximate causes for colony cohesiveness and colony selection. More specifically, the mechanisms and/or interactions that coordinate the different collective colony processes can be studied more accurately if the colony is viewed as a single unit. This is because many factors (e.g. pheromones, behaviours, etc.) that affect or control a specific colony process (e.g. foraging, nest building, caste determination, etc.) derive from different parts or subsets of the colony organization, many of which are not directly involved in that process. Thus, studying a specific colony process in isolation, as has historically been the case, may result in important factors in the emergence and control of that process to be ignored (Smith et al. 2016).

The social physiology approach conceives of colonies as integrated units and focuses on the mechanisms that coordinate the different collective processes in the colony. Following the groundplan theory (West-Eberhard 1996, 2003; Johnson and Linksvayer 2010), the social physiology approach argues that the division of labour (and polymorphism, etc.) is a result of differential expression of the ancient genetic groundplan — which evolved in the solitary ancestors to eusocial insects — in the different members of the colony; i.e. reproductive traits in the queen, non-reproductive traits in workers. The differentiation of the members of the colony, i.e. polymorphisms (queen, worker castes, etc.) and temporal castes (as in honey bees — see below), is what they refer to as 'social anatomy'. The social anatomy is the specialisation (or reduction of totipotency) of colony members that is the basis for the division of labour. The coordinating mechanisms (e.g. pheromones, hormones, etc.) and communication networks that enable integration at the colony level is what they refer to as 'social physiology' (Johnson and Linksvayer 2010). In other words, social physiology are the aspects that regulate the division of labour within the colony.

The main tenet of this approach is that both social anatomy and social physiology are the result of novel regulatory gene networks that are not present in the ancient groundplans of the solitary ancestors. In turn, these novel regulatory genetic networks coordinate the different colony processes, particularly in complex species with polymorphic worker castes:

> We proposed that social physiology, in contrast to the minor alteration of intact genetic networks, is dependent on many formerly independent sensory processes being integrated together into novel gene networks. These novel gene networks then facilitate the coordination of action necessary for collective problem solving. (Johnson and Linksvayer 2010: 73).

Thus, according to this approach, social physiology is the result of emergent novel genetic networks, particularly in complex eusocial insect colonies that have a high degree of polymorphism and polyethism (social anatomy). Consequently, the social physiology approach argues that the whole colony should be treated as a single genome.

The social physiology approach is interesting in that it focuses on the whole colony system and the coordination of colony processes. However, this approach focuses primarily on the genetic level and, consequently, may be less adequate at assessing the types of individuality at the colony level across different eusocial insect species. B. R. Johnson and T. A. Linksvayer (2010: 59-60) did employ broad criteria to distinguish organizational differences between simple and complex colonies; namely 'team-like' and 'factory/machine-like' organizations. Team-like colonies are those that are large enough for collective colony processes, but in which there is little to no polymorphism and workers can generally do most tasks (i.e. high totipotency). Factory-like and machine-like colonies are those with temporal polyethism (factory-like) and/or polymorphic worker castes (machine-like), whereby specific castes specialize in certain sets of tasks. But these criteria essentially rely on the definition of complexity within eusociality and therefore tracks the complexity spectrum across eusocial insect species. The eusocial complexity spectrum is likely to be a good indicator for physiological-like individuality at the colony level, i.e. the most complex species with polymorphic worker castes are likely to be better candidates for physiological-like superorganisms than the less complex species, but this cannot be assumed, concrete criteria are required in order to assess this. Thus, the social physiology approach, in its current form, appears to lack the conceptual tools to determine the differences, at the collective level, of the control and integration of colony processes.

5.1.2. The hierarchical-organizational approach

Unlike the social physiology approach, the HO approach will focus on the organizational factors, at the collective level, that coordinate and control collective colony processes in order to assess how colonies achieve the cohesiveness that enables them to 'function *as a single organism*, exactly as imagined by Wheeler so long ago' (Wilson and Wilson 2007: 342. Emphasis their own). Specifically, taking the colony as a whole, the HO approach assesses if there is hierarchical organization within complex colonies, i.e. an organization that "modulates" (i.e. regulates and controls on) the self-organized dynamics within the colony system. In other words, this approach will be able to assess if colony organization is the result of self-organization only or *also* and *mainly* due to hierarchical regulation and control. Consequently, this approach would be better suited to assess the issue of whether complex eusocial insect colonies should be considered biological individuals or not. This is because if there are colonies with hierarchical organization then an argument can be made that the colony is in "control" rather than the insects that instantiate it, i.e. the colony organization is not solely the result of bottom-up self-organization but also of a higher-level organization that exerts top-down control on its parts. But how can hierarchical control be achieved in the large complex eusocial insect colonies?

The HO approach is derived from the organizational account based on autonomy theory, what I refer to as the Autonomous Perspective (Moreno and Mossio 2015). The key emphasis of the Autonomous Perspective is, as the name suggests, a focus on the autonomous aspects of biological individuals, namely, a focus on how self-determination and self-regulation are achieved. Moreover, autonomy is a key defining feature of biological individuality for this account, i.e. autonomy at the system level is required in order for a biological system to achieve biological individuality (for more details see Moreno and Mossio 2015). Recent work from the Autonomous Perspective has focused on biological individuality in multicellular systems (Arnellos et al. 2014; Arnellos and Moreno 2015, 2016). This approach focuses on the organizational conditions in multicellular systems that allow for autonomy at the collective level. According to this approach, the cells in the system must produce, via the network of interactions, a set of inter-cellular mechanisms that can regulate the development and function of the lower level parts of the system (namely the cells themselves), but at the same time these regulatory mechanisms must be dynamically decoupled from operations of the cells, thus forming a new hierarchical level, enabling autonomy at the collective level. In other words, collectively, the cells themselves must produce a higher-order organization, which is sufficiently dynamically decoupled from the lifespan and operation of each individual cell, such that this higher-order organization is stable enough to hierarchically regulate and control the collective, enabling self-determination at the collective level.

However, analysing the actual organizations of eusocial insect colonies in order to assess the coordination of colony processes, and the degree of hierarchical control, is a difficult task. It must be remembered that eusocial colonies are complex systems that are themselves formed of complex parts (i.e. multicellular insects). Moreover, researchers have typically studied specific colony processes (e.g. foraging, nest building, etc.) in isolation, rather than within the context of the wider colony organization. Consequently, much of the data that is crucial for studying colony organization as a whole is not readily available, or widely published (Smith et al. 2016). Thus, as a first proposal, the HO approach will focus on specific colony processes, within the context of the wider colony organization (where possible), and the critical aspects involved in their control and regulation. To do so, the HO approach will focus on the causal factors, that I refer to as signals, that regulate and coordinate a given colony process. Consequently, signals are defined as any endogenously produced function/constraint (e.g. pheromone, mechanism, etc.) that acts as a causal factor inducing/modulating/inhibiting the development, physiology, and/or behaviour of the colony members or a colony process.

Furthermore, such signals are designated as first-order and second-order based on their dynamical relation to the process that they affect.

First-order signals are those signals that are dynamically coupled to the process that they have a controlling effect on. In other words, first-order signals are both produced by and feedback on the same colony process. For example, if the control of a specific colony process, such as soldier caste determination, is due to a signal that derives from the parts in that process, and furthermore, the signal is only present based on a change in concentration of the constitutive parts — i.e. a high amount of soldiers ensures significant amounts of signal in order to inhibit more larvae developing into soldiers — then this signal is dynamically coupled to the process of soldier development; i.e. the signal controlling soldier caste determination relies on the growth of new soldiers. Whereas, *second-order signals* are dynamically *decoupled* from the process that they regulate. Or more simply, second-order signals, although endogenously derived from the colony, are not derived from the constitutive parts of the specific colony process that they regulate. For example, if the control of a specific colony process, again soldier caste determination, is due to a signal that derives from another part (or subset) of the colony instead of from the constitutive parts of the process (i.e. soldiers), then that signal is a second-order one. In other words, if the signal derives from the queen or another worker caste, the presence of the signal would not be dependent on a change in concentration of the soldiers themselves, it would therefore be dynamically decoupled from soldier caste determination. Thus, second-order signals act *hierarchically* on the processes that they modulate.

By focusing on the type of signals involved in regulating a colony process, researchers can determine if the regulation and/or control of specific colony processes, e.g. caste determination or nest construction, is due solely to first-order signals, and thus is a process of flat self-organization, or due principally to second-order signals, i.e. hierarchical control. If there are second-order signals present in colony organization this would, I argue, be evidence that not all complex eusocial insect colonies are solely the result of flat self-organization. The presence of second-order signals would be evidence that the colony is hierarchically-organized rather than a flat network of distributed self-organization. Consequently, by assessing colony processes within the context of the wider colony organization, researchers can determine whether the organizational cohesiveness is due solely to a flat self-organized network of interactions or due to a hierarchical network; i.e. a hierarchical-organization.

Furthermore, the focus on first- and second-order signals can also be used to assess the type of individuality at the colony level. Specifically, I argue that 1) if a colony has multiple second-order signals in multiple colony processes and 2) if these second-order signals derive from more than one source (i.e. not only the queen but also the brood, different worker castes), then this could be evidence of a form of autonomy at the colony level. This is because premise 1) would point to a high degree of hierarchical control within the colony, i.e. this would point to the possibility of multiple colony processes being hierarchically controlled. Additionally, premise 2) highlights that hierarchical control is distributed at the colony level, rather than emerging from a single part (i.e. the queen). Not only would this result in a more robust hierarchical-organization, since it is not reliant on a single part (i.e. the queen), but it would also point to a higher-order organization that is sufficiently dynamically decoupled from the lower level parts of the system (i.e. each individual insect). This is because the hierarchical-organization, formed by the second-order signals, emerges through a network of interactions rather than emanating from a single part of the colony. Consequently, it operates at a different timescale compared to each individual insect within the colony. Therefore, the presence of multiple second-order signals from more than one source in a colony could be evidence of a dynamically decoupled higher-order organization that hierarchically controls and regulates the lower level parts. Thus, it can be argued that this higher-order organization represents a form of self-determination or autonomy at the collective level; i.e. physiological individuality.

5.2. The application of the HO approach to three representative case studies of species from across the eusocial complexity spectrum

In this section I will apply the HO approach to three representative case studies of eusocial insects in order to assess the types of colony individuality across the complexity spectrum; namely the sweat bee *Megalopta genalis*, the common wasp *Vespula vulgaris*, and honey bees *Apis mellifera*. However, the analysis of these case studies is somewhat limited as many authors do not publish much of the data that is essential for understanding the detailed process of colony organization, i.e. colony size (in terms of insects in the colony), colony developmental details, interactions between different castes and queen, etc. This type of data is referred to as sociometric data, but as many authors/research groups focus on specific colony processes that occur across species (such as types of foraging, nest construction, etc.), as I argued in the previous chapter, then much of these data sets are not assessed or published as it is not seen as relevant to such studies (Smith et al. 2016).

5.2.1. Facultative eusocial bees, Megalopta genalis

Megalopta genalis are a species of sweat bee from the *Halictidae* family that are facultatively eusocial (Kapheim et al. 2016). Reproductive females can either become solitary reproductives or they can produce a eusocial colony (Smith et al. 2007). As with other sweat bee species of the *Halictidae* family, *M. genalis* are on the 'simple' end of the eusocial complexity spectrum (Bourke 1999: 247). They have small colony sizes, from 2-11 bees — but, on average, colonies have around 2-4 member bees (Smith et al. 2003: 15). The only form of polymorphism in *M. genalis* colonies is that workers are smaller than queens, but workers are completely totipotent and have full reproductive potential (Wcislo and Gonzalez 2006; Kapheim et al. 2013). *M. genalis* have gained a lot of attention from researchers because they are facultatively eusocial and can thus be a good analogue for the origins of eusociality (Smith et al. 2003; Kapheim et al. 2015).

M. genalis colonies are typically established by a single female (Wcislo and Gonzalez 2006). *M. genalis* nest in dry/dead wood (e.g. twigs, branches, etc.) that are suspended off of the ground in vegetation. The queen (or solitary female) excavates a tunnel into the wood, which forms the main part of the nest, she then excavates brood cells that adjoin to the central tunnel — the cell entrances are flush with the tunnel walls — (Smith et al. 2003: 15). The entrance to the nest is constricted to a size slightly bigger than the queen's head; this is achieved by the queening adding chewed wood to the entrance hole (Smith et al. 2003: 15).

The division of labour in eusocial colonies of *M. genalis* typically consists of the queen undertaking reproduction and guarding the nest entrance and the worker(s) primarily foraging and feeding other members of the colony via trophallaxis (Kapheim et al. 2016). There are no worker castes or polyethism (specialization) among the workers, instead all workers do the same tasks. This is expected as worker specialization and polymorphic worker castes are only found in the larger colonies of the more complex species (Anderson and McShea 2001). Worker specialization is risky for small colonies since if one of the specialized workers die, before another is produced to replace it, then the colony organization is adversely affected, whereas in large colonies with many workers, the death of individual workers has little effect on colony organization as there are typically many workers of each type (Anderson and McShea 2001; Khoury et al. 2011).

Division of labour in *M. genalis* is determined and maintained via aggression by the dominant queen. Typically, the queen is larger than the workers and this enables the queen to coerce some of her female offspring to become workers (Kapheim et al. 2011, 2013). The smaller size of workers compared to queens is likely due to the queen restricting the amount of nutrition the worker receives during development, i.e. parental manipulation (Smith et al. 2009; Kapheim et al. 2011). After she establishes the nest and before the first workers emerge, the queen will undertake all of the colony tasks. The queen will forage for nectar and pollen which she mixes together and forms into a mass. *M. genalis* are mass provisioners, as opposed to progressive provisioners such as honey bees (*A. mellifera*), which means that eggs are oviposited into brood cells that already contain all the food required for the larval and pupal developmental stages (Wcislo and Gonzalez 2006; Kapheim et al. 2011). The queen will oviposit an egg on a food mass within a brood cell, she will then close the brood cell by plugging the entrance with chewed wood (Quiñones and Wcislo 2015). Thus, for worker-destined brood the queen will deposit less food in the cell prior to ovipositing.

Workers emerge from their brood cells around 35 days post oviposition (Quiñones and Wcislo 2015: 309). Workers then remain in the nest and are fed, via trophallaxis, by the queen for the first 1-14 days (Smith et al. 2003: 15). This is likely due to the young adult workers requiring time to develop their flight muscles. Not only does the queen still undertake the majority of colony tasks during this period, but the queen will also establish dominance during the first 10 days after worker emergence; if it does happen, queen usurpation (i.e. when a worker overtakes the queen as the dominant reproductive) only occurs within the first 10 days, after this queen dominance is secured (Kapheim et al. 2016). The queen establishes dominance over her worker-destined female offspring via aggression, if successful the young female(s) will become the worker(s) and begin foraging and feeding other colony members via trophallaxis, and the queen will then remain in the nest as the only reproductively active member whilst also guarding the nest, when needed, by blocking the entrance with her abdomen (Kapheim et al. 2016).

In established *M. genalis* eusocial colonies, not only is the queen typically larger than the workers but the queen also has higher juvenile hormone (JH) levels and larger ovaries (Kapheim et al. 2013). It has been argued that increased JH levels in the queen increases her ability to dominate some of her female offspring to become workers, since eusocial queens have higher JH levels than solitary reproductives and workers (Smith et al. 2013). However, even though the larger size of the queen enables her to dominate the smaller workers, body size does not determine reproductive potential (Kapheim et al. 2013). If the queen dies, then one of the workers will likely replace the queen and become the new dominant reproductive. Workers that become replacement queens, even though they are smaller in size than typical queens, can be as reproductively fecund as the typical larger queen phenotype (Smith et al. 2009). Thus, the queen inhibits worker reproduction, via aggression, but workers can activate their ovaries in the event of queen death.

There are no collective colony processes in *M. genalis* colonies because of the small size of colonies and the lack of specialization; each task is carried out by an individual. There is, therefore, no higher-order organization in *M. genalis* colonies and, consequently, there are no second-order signals that could coordinate the different collective colony processes within the higher-order organization. Instead, colony organization is based on a dominance hierarchy; the queen coordinates the division of labour via aggression.

5.2.2. The common wasp, Vespula vulgaris

The common wasp (*Vespula vulgaris*) lies around the centre of the eusociality species complexity spectrum; they have relatively large colony size and exhibit polymorphism between the reproductive and non-reproductive castes, but they have no worker castes and relatively simple communication networks (Bourke 1999). Colonies are established in underground nests by a single queen. Nests are constructed from pulp that is created by the wasps from a mix of foraged wood and water. They consist of an outer enclosing layer made up of multiple envelopes, which acts to insulate the interior and create a boundary for the nest, and inside there are multiple layers of horizontal combs (facing down) for rearing the brood, which are also made from pulp (Potter 1964; Steinmetz et al. 2002). The queen builds the first envelopes of the outer layer and the first brood comb. The queen does all colony tasks (i.e. nest and comb construction, foraging, nursing, etc.) before the first worker generation emerges, as in *M. genalis*. Once the first generation of workers emerge and become active the queen focuses only on reproduction, which becomes her main task — her abdomen enlarges, and she loses the ability to fly — whereas workers take over all other tasks (Potter 1964).

V. vulgaris have relatively large colony sizes; around 3000 or more (Potter 1964; Archer 1972). But there are no polymorphic or temporal worker castes, or polyethism,[19] in *V.*

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[19] Polyethism refers to task specialisation in eusocial insects, i.e. that different members of the colony specialise for different tasks. Polyethism can be based, for example, on age or polymorphism: as workers age they may change task specialisation, or workers may develop into different morphological castes (e.g. soldiers for defence). In honey bees workers exhibit the former.

vulgaris. Instead workers are generalists and can typically undertake any worker task after 2-3 days post emergence (Potter 1964).[20] Thus, unlike *M. genalis* colonies, *V. vulgaris* colonies are large enough for collective colony processes to occur, but, as in *M. genalis*, common wasp colonies have relatively little worker specialisation (no polymorphic worker castes or polyethism). Consequently, there are relatively few collective colony processes compared to colonies of the more complex eusocial species, such as honey bees (*A. mellifera*) that I will explore below. I will assess some selected collective colony processes of *V. vulgaris* presently.

Comb construction: Workers overtake comb construction (and envelope construction) from the queen once the first generation of workers emerges, as above. Workers build new comb layers, using pulp, beneath the original horizontal layer that the queen constructed. Workers likely construct the comb via stigmergic self-organization. No single worker needs a complete plan of the comb architecture in her mind, instead multiple workers simultaneously construct the comb each with a set of simple behavioural rules for this process. Since *V. vulgaris* use pulp instead of endogenously produced wax (as in honey bees), comb construction is constrained by the amount of available raw material, as well as the number of workers present in the colony able to forage for wood. This is demonstrated by the fact that comb cells increase in size as a colony grows (Archer 1972; Hunt 2007: 94-95). As a colony grows and produces more workers, there are more workers available to forage for raw material for pulp. Consequently, there is more pulp available for comb construction, and not only do workers produce more comb but in each successive comb layer the brood cells increase in size. Moreover, larger workers are produced as a result of larger worker-cells, and larger workers

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[20] However, during the mature colony state young workers (up to 7 days old) may perform more intranidal tasks and only forage after 7-9 days, but thereafter perform intranidal and extranidal tasks. Moreover, older workers tend to forage less. But in general, all workers can perform all tasks (for more details see Potter 1964).

live longer (Hunt 2007: 94-95). This results in a greater worker-to-brood ratio towards late summer, around the end of the ergonomic stage. It has been argued that the high worker ratio initiates reproductive-comb production (Hunt 2007: 94). However, this hypothesis is not supported by previous evidence. N. B. Potter (1964: 58-63) demonstrated that, for *V. vulgaris* at least, the queen is more important to reproductive-comb production than the worker-to-brood ratio. Potter (1964: 58-63) found that if a queen from a mature colony is transferred to a younger small colony (which has a small worker-to-brood ratio), the workers in the small colony will construct reproductive-comb instead of worker-comb, moreover the opposite was confirmed, if a young queen is transferred to a mature colony in the reproductive stage, the workers destroy any reproductive-comb and instead build worker-comb. This shows that the type of comb constructed is likely controlled by an element of the queen pheromonal mix (QPM) (Potter 1964).

Consequently, for *V. vulgaris*, once the workers take over from the queen in comb construction (and envelope construction) it becomes a self-organized collective colony process. Thus, the self-organized building activities of the workers results from a set of a first-order signals in the collective process of comb construction. Whereas, the QPM modulates this process by ensuring that the workers build worker-comb and reproductive-comb at the optimal time in colony development. The QPM is dynamically decoupled from the comb construction process as it derives from the queen, who is no longer directly involved in the process. Moreover, the queen is a constant presence within the colony and therefore is not reliant on the comb construction process in order to provide the signal that modulates this process. Thus, the QPM acts as a second-order signal on the collective process of comb construction.

Queen/worker caste determination: As above, in *V. vulgaris* there are no polymorphic worker castes but there is a form of polymorphism between queens and workers (Wheeler 1928: 74; Potter 1964; Jeanne 1980). Queens are larger than workers and have larger ovaries and genitalia than workers. Consequently, workers are typically unable to mate with males because of their smaller size and therefore are unable to produce fertilized eggs (Spradbery 1973: 229-234; Jeanne 1980: 376). Workers can produce unfertilized eggs (which produce males) but typically only do so in the case of queen death; in queen-right colonies workers typically do not oviposit (Ross 1985).

Any fertilized egg can develop into a reproductive or a worker (Archer 1972), as in many other wasp, bee and ant species (Schwander et al. 2010). There are, consequently, mechanisms present in the brood stage that determine whether larvae develop into queens or workers; namely, the size of the comb cell and the amount of nutrition. Queens are produced in the larger comb cells of the reproductive-comb and workers are produced in the smaller comb cells of the worker-comb (Spradbery 1971). As above, the type of comb built by the workers is determined by the second-order signal from the queen (the QPM). But the amount of nutrition that larvae receive is dependent on their location in the nest and the number of workers available to forage for food. Differential feeding of larvae does not occur in *V. vulgaris*, however frequency and quantity of food differs between different areas of the nest (Potter 1964: 61). Reproductive-comb are the last comb layers to be produced by the colony, in the mature reproductive stage, and are thus the lowest comb layers and closest to the nest entrance (Potter 1964). Brood cells on the lowest combs are closer to the nest entrance, and the larvae in these cells are the first to be fed by returning foragers (Archer 1972). As above, the colony produces larger workers as it matures, larger workers live longer which results in a greater worker-to-brood ratio in mature colonies (Archer 1972). Moreover, larger workers can collect more nutrition (Richards 1971). Consequently, there are more workers to forage for food in the reproductive stage when queen-brood is produced, and because these workers are large they can forage for greater amounts of food, which results in the queen-brood receiving more food than worker-brood typically do. Increased nutrition causes the queen-brood to grow larger than worker-brood, and the larger comb cells allows space for this increased growth.

Therefore, the process of caste determination in *V. vulgaris* is modulated by two variables in the brood stage; the amount of nutrition and the size of the comb cell. The former variable, nutrition, is ultimately determined by a feedback loop (self-organization). This is because nutrition levels increase as a colony grows (Archer 1972). Consequently, the nutrition variable is a first-order signal on caste determination as it is dynamically coupled to the process itself. In other words, as a colony grows there are more workers available to forage, which positively feedbacks on the amount of nutrition received by the brood. Whereas the other variable, size of the comb cell, is ultimately dependent on a second-order signal in the earlier process of comb construction, above. The type of comb produced is determined by the QPM (a second-order signal).

Worker reproductive inhibition: Reproductive division of labour is underpinned by the caste determination process, above. In other words, the polymorphic differences between the queen and worker castes already ensures that the queen has a greater reproductive potential than workers. Additionally, reproductive division of labour is further ensured by the queen. Specifically, the queen can inhibit worker reproductive potential via her QPM (Van Oystaeyen et al. 2014). Even though workers typically do not mate they do have ovaries (which are typically smaller than those of the queen) and can produce unfertilized eggs (Ross 1985). But typically, workers only have activated ovaries and attempt to oviposit unfertilized eggs when there is no queen, or in the declining stage of the colony when the queen is in senescence (Potter 1964; Ross 1985). A. Van Oystaeyen, and colleagues (2014), demonstrated that this is because elements of the QPM inhibit ovary activation and/or causes oocyte regression in workers. In other words, the queen ensures that workers remain in the non-reproductive caste by inhibiting their reproductive potential.

Consequently, the earlier process of caste determination can be considered as a first-order signal on the reproductive division of labour. This is because caste determination ensures that workers are produced, which are physiologically distinct from the queen, in particular they have less reproductive potential than the queen. But the QPM from the colony's queen can be considered as a second-order signal on reproductive division of labour. This is because the QPM further influences the caste determination process by inhibiting adult worker reproductive potential, but this signal is dynamically decoupled from this process. As above, this is because, unlike the workers, the queen is a constant presence in the colony (Potter 1964). Thus, the QPM works at a different timescale to the operation of worker development, i.e. the queen lives as long as the colony and, thus, can constantly produce her QPM, whereas there are many generations of workers throughout the colony cycle (Potter 1964).

5.2.3. Honey bees, Apis mellifera

Honey bees (*A. mellifera*) are a well-studied complex eusocial insect species (Bourke 1999). Like *V. vulgaris*, they have large colony sizes and polymorphism between the queen and worker castes, but additionally, they exhibit (temporal) worker castes (Lyko et al. 2010; Smith et al. 2016). *A. mellifera* colonies are initiated from swarms, rather than a single queen as in *V. vulgaris*, above (Cronin et al. 2013). This entails that, from their inception, honey bee colonies exhibit division of labour; i.e. reproductive division of labour and task specialisation are involved in all stages of *A. mellifera* colony development. Colonies reproduce, via swarming, in late spring/early summer (in temperate climates). The parent colony — the old queen with around two thirds of the worker population (primary swarm) — leave the old nest in order to establish another nest in a new site. What is left behind in the old nest is one third of the parent colony (workers and, sometimes, drones) along with young queens (still in the brood stage), which have the potential to form an incipient colony — a new queen plus workers inherited from the parent colony — (Lee and Winston 1987; Beekman et al. 2006; Grozinger et al. 2014; Smith et al. 2016). This cycle is repeated yearly (Smith et al. 2016).

Colonies nest within suitable cavities — those with enough space for the comb to be produced but with a single entrance that can be guarded by the bees — typically in tree trunks or logs (Seeley and Morse 1976; Simone-Finstrom and Spivak 2010; Hepburn et al. 2014). Nests contain vertical layers of comb, which is the main element of the nest; it is where the larvae develop into adult bees, it is used to store honey and pollen, and it is the central hub for communication (Seeley and Morse 1976; Tautz 2009). Unlike *V. vulgaris*, honey bee comb is made from endogenously produced wax, from special glands in workers. Honey bee colonies are large, containing tens of thousands of bees; 10,000-20,000 in feral colonies and 40,000+ in domesticated colonies (Harris 2008; Smith et al. 2016). Colony organization is more complex compared to that in *V. vulgaris*, consequently, there are more collective colony process in *A. mellifera*. As above for *V. vulgaris*, I will presently assess selected colony processes for *A. mellifera*.

Temporal polyethism and worker castes: As above, unlike *V. vulgaris*, workers in honey bee colonies exhibit a further division of labour. *A. mellifera* workers undergo a temporal polyethism schedule and, consequently, within colonies there are temporal worker castes. The worker castes of *A. mellifera* are the following:

nurses, specialise in feeding and attending the brood (and queen), as well as feeding the queen and other members of the colony;

nest workers,[21] specialise in other intranidal (inside the nest) tasks such as comb construction and maintenance, ventilation, receiving nectar and processing it into honey, storing honey and pollen, and more;

foragers, specialise in extranidal (outside the nest) tasks, such as foraging for nectar, pollen and water (Seeley 1982; Johnson 2008).

Adult worker bees transition through the different castes as they age. Thus, not only do the workers in each castes specialise for specific tasks, additionally, workers of each caste are physiologically tuned to their task set, e.g. *nurses* have large activated hypopharyngeal glands that they use to produce jelly to feed the brood/queen, whereas in *nest workers* these glands produce invertase in order to process nectar into honey, and *foragers* have inactive hypopharyngeal glands (Johnson 2003, 2008). Typically, during the active months (spring to autumn), the temporal polyethism schedule is the following; workers are *nurses* from around 2-11 days old, *nest workers* 11-18 days old, and *foragers* around 18+ days old (Johnson 2008). But this temporal polyethism schedule is plastic and can be manipulated by the colony in response to environmental conditions, as I explain presently.

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[21] I propose the term ‘nest workers’ for the middle-aged worker caste as they specialise in construction and housekeeping tasks, as well as food storage (Johnson 2008). ‘Nurses’ are commonly so-called because they specialise in feeding other members, particularly the brood, and likewise ‘foragers’ as they specialise in foraging.

The temporal polyethism of each individual worker bee is controlled, *internally*, by juvenile hormone (JH) and the glycolipoprotein vitellogenin (Vg). It has been proposed that, within each worker bee, JH and Vg form a regulatory network — or 'double repressor' network (Amdam and Omholt 2003: 451) — since they mutually inhibit one another. Typically, levels of Vg are high after first eclosion (adult emergence from larva) and naturally decrease with age, high levels of Vg delay the biosynthesis of JH. As Vg decreases this allows for the biosynthesis of JH, and as JH levels increase this inhibits further Vg expression (Nelson et al. 2007). This is important because Vg is associated with the ability of nurses to produce proteinaceous jelly that they feed to other members of the colony. Whereas JH biosynthesis causes the further development of adult workers, and their progression through the worker castes. For example, increasing JH levels induce change within the hypopharyngeal glands of the worker such that they go from producing jelly for feeding other colony members (a process which relies on Vg) to, instead, producing enzymes for processing nectar into honey, thus causing the switch from the *nurse* to *nest worker* caste. However, there are external signals, which derive from the colony, that also affect the temporal polyethism within each worker.

Signals from the queen, brood, and the forager caste also affect the temporal polyethism schedule in each worker, and therefore also the ratio of workers within each caste (**Figure 1**). *Firstly*, the queen has an inhibitory effect on JH biosynthesis in workers via her pheromone mix (QPM).[22] It has been demonstrated that, in the presence of QPM, workers have significantly delayed JH biosynthesis compared to those not exposed to QPM (Kaatz et a. 1992; Pankiw at al. 1998). *Secondly*, the brood release signals that affect the polyethism schedule of workers. Young brood emit E-β-ocimene — a volatile pheromone that is transmitted into the

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[22] I use the term 'queen pheromone mix' as it has been shown that queens produce pheromones from multiple sources — not only their mandibular glands as has been the main focus previously — that act as signals in the colony (Slessor et al. 2005; Masionnasse et al. 2010a).

nest aerially — that appears to target nest workers and causes increased development in them so that they transition to foragers sooner, probably by increasing JH biosynthesis. However, older brood emit brood ester pheromone, which is transmitted on contact, that targets nurses, delaying their development, most likely by inhibiting the biosynthesis of JH (Maisonnasse et al. 2010b). *Finally*, the forager caste release a signal which affects the temporal polyethism schedule of younger workers. Foragers produce ethyl oleate which gets transmitted via trophallaxis when foragers pass their nectar loads to nest workers, who deposit nectar in the comb. It has been shown that ethyl oleate inhibits the nest workers from developing into the forager caste (Leoncini et al. 2004).

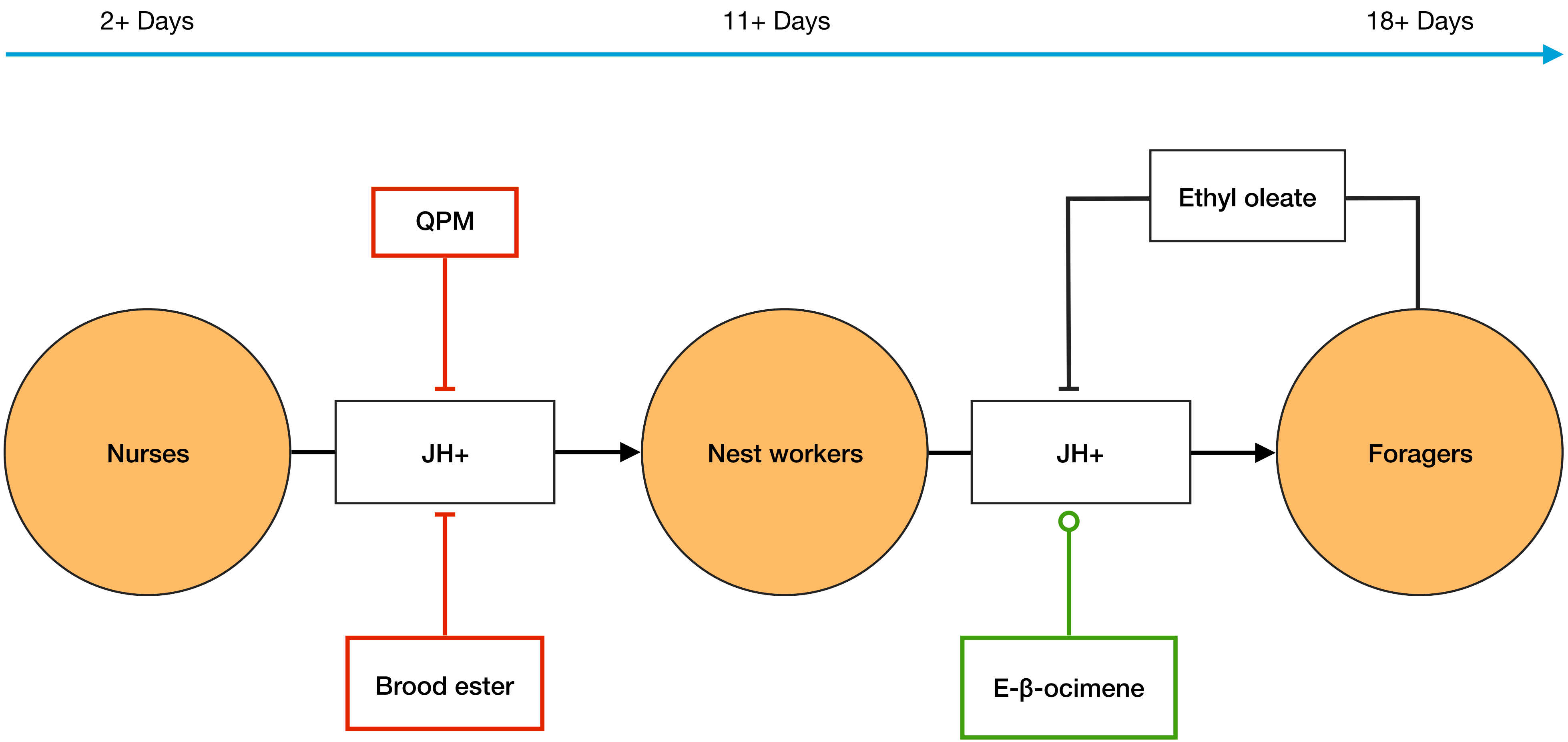

Fig. 1. Temporal polyethism. Worker bees, in *A. mellifera*, transition between the temporal worker castes, *orange circles*, as internal levels of juvenile hormone (*JH*) increase, *represented as JH+*. JH biosynthesis is affected by external factors, including inter-member signals: *QPM, brood ester, E-β-ocimene,* and *ethyl oleate*. QPM, brood ester, and ethyl oleate inhibit JH biosynthesis, *flat-ended lines*, and E-β-ocimene promotes JH biosynthesis, *circle-ended line*. The inter-member signals allow the ratio of the temporal worker castes to be controlled at the colony level, *see text for more details*. The timeline represents the typical age of workers in each caste in the active summer period.

JH and Vg can be considered as first-order signals on the temporal polyethism schedule within each worker. They form an interactive mutual inhibitory network within each bee — high Vg levels inhibit JH biosynthesis and high JH levels inhibit Vg biosynthesis — but, moreover, their effects are limited to the worker in which they are produced. JH and Vg are thus dynamically *coupled* to the internal development system of each worker bee. Added to this, the inter-member signal *ethyl oleate* from the forager caste[23] can also be considered as a first-order signal. This is because the inhibitory effect of ethyl oleate on the nest worker caste is due to a negative feedback loop, i.e. the presence of foragers inhibits the development of nest workers into the forager caste, but the absence of foragers allows nest workers to develop into foragers. Moreover, workers only begin to produce ethyl oleate at significant enough levels to act as a signal when they reach the forager caste (Leoncini et al. 2004). Thus, the operation of ethyl oleate on this process is tightly coupled to the internal constraints of the individual workers, i.e. there must be older workers (foragers) present in order for ethyl oleate to act as an inhibitory signal on younger workers' (nest workers) development.

However, the inter-member signals *QPM*, *brood ester*, and *E-β-ocimene*, can be considered second-order signals on the temporal polyethism schedule (**Table 1**). This is because they are dynamically decoupled from the systems that they modulate, i.e. the internal developmental systems of individual workers. All of these signals affect the temporal polyethism schedule of workers — QPM and brood ester slow worker development and E-β-ocimene induces worker development — but they operate at different timescales. The queen is, typically, a constant presence in the colony and therefore the presence of QPM and its influence on the temporal polyethism schedule of the workers is not reliant on a change in

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[23] Ethyl oleate is also produced by the queen, brood and other workers. However, it has been argued that only forager-derived ethyl oleate affects the temporal polyethism schedule within workers (Leoncini et al. 2004; Slessor et al. 2005).

concentration of the workers and/or on a direct feedback loop, as is the case with forager-derived ethyl oleate. The same is true of brood ester and E-β-ocimene, since they derive from the brood, which are not a part of the temporal polyethism or the worker castes.

	Signal	Source	Target	Role
First-order signals				
	JH	Internal to each worker	Internal to each worker	Increased JH levels induce worker development to next worker caste
	Vg	Internal to each worker	Internal to each worker	High Vg levels are required for nursing, additionally high Vg levels inhibit JH biosynthesis
	Ethyl oleate	Foragers	Nest workers	Inhibits nest workers transitioning to the forager caste
Second-order signals				
	QPM	Queen	Nurses and nest workers	Inhibits JH biosynthesis and thus worker development
	Brood ester	Old brood	Nurses	Inhibits JH biosynthesis and thus worker development
	E-β-ocimene	Young brood	Nest workers	Induces worker development (nest worker to forager), possibly by inducing JH biosynthesis or inhibiting Vg biosynthesis

Table 1. *Temporal polyethism and caste ratio control*

The presence of second-order signals (QPM, brood ester, and E-β-ocimene) on the temporal polyethism of the workers allows for the worker caste ratio to be controlled at the level of the colony (i.e. hierarchically). This is because, the control of the ratio of workers within each caste is not solely reliant on the self-organization of the workers themselves; i.e. it is not solely reliant on a signal (ethyl oleate) from the foragers inhibiting the development of nest workers via a negative feedback loop. Instead, in addition to the self-organization dynamics of the workers, there are second-order signals (QPM, brood ester, and E-β-ocimene) that modulate the development and temporal polyethism schedule within each worker. In other words, *the control and regulation of the ratio of workers within each caste is not dependent on a change in concentration of the workers themselves (i.e. the growth of new workers) but instead on second-order signals that can modulate the former process and, thus, the existing workers*. For example, when a colony reproduces via swarming, the queen and a large proportion of the workers, from all castes (i.e. of different ages), will leave the old nest in order to establish a new nest site (Smith et al. 2016). However, since it takes at least 3 weeks for the colony to produce new workers after it establishes a new nest, the current worker population will be predominately formed of older workers, i.e. the majority of the workers will be older than is typical for the nurse caste (Robinson et al. 1989; Smith et al. 2016). It has been shown that old workers (even those that have been foragers) can revert back to the nurse caste, with these ‘reverted’ nurses even having low JH levels and regenerated hypopharyngeal glands in order to feed the brood (Robinson 1992). This developmental reversion could be due to the presence of second-order signals. Specifically, older workers can revert to the nurse caste due to *QPM* and *brood ester* inhibiting JH biosynthesis, and consequently allowing Vg biosynthesis and the reactivation of the hypopharyngeal glands. Additionally, *E-β-ocimene* would counteract this by promoting JH biosynthesis to ensure that not too many workers revert to nurses and, thus, ensuring an equal balance between the worker castes. Thus, the plasticity of the temporal polyethism is likely to be controlled by the second-order signals that act on the internal development systems of the workers, consequently allowing *the colony* to regulate the ratio of workers in each caste.

But this is not the case for all eusocial insect species that exhibit worker castes. For example, in *Pheidole* ants, soldier/minor worker caste determination does not appear to involve second-order signals. *Pheidole* ants do not exhibit temporal castes but many exhibit physical worker castes, typically minor worker and soldier castes (Lillico-Ouachour and Abouheif 2017). Caste determination in *Pheidole* ants is determined during the larval stages. There is a developmental switch early in larval development; larvae with high JH levels activate the queen developmental programme and those with low JH levels activate the worker developmental programme. Those larvae that activate the worker developmental programme face a further developmental switch, into either a soldier or minor worker. This soldier/minor worker developmental switch is internally mediated by levels of JH; worker-larvae with high JH levels develop into soldiers and worker-larvae with low JH levels develop into minor workers. But crucially, Lillico-Ouachour and Abouheif (2017) found that this secondary developmental switch in worker-larvae is also affected by an inter-member signal, a pheromone from adult soldiers. They found that when adult soldiers are present in the colony, they inhibit worker-larvae developing into soldiers, possibly by the *soldier pheromone* inhibiting JH biosynthesis within each worker-larvae. Conversely, when the number of adult soldiers decreases (e.g. due to mortality) this induces worker-larvae to develop into soldiers as the inhibitory effect of the soldier pheromone will also decrease.

However, similarly to the operation of the ethyl oleate in *A. mellifera*, the inhibitory effect of the soldier pheromone is also dependent on a change in the concentration of the soldiers themselves, hence its action on worker-larvae development is dynamically *coupled* to worker-larvae development; i.e. the activation of the inhibitory effect of the soldier pheromone relies on the growth of new soldiers. Thus, the soldier pheromone can be considered as a first-order signal on soldier/minor worker caste determination. The soldier pheromone does allow for the ratio of the morphological worker castes (soldiers and minor workers) to be controlled collectively in *Pheidole*. But this type of collective control is localised to the soldier caste themselves via the negative feedback effect of the soldier pheromone. This is in clear contrast to the case in *A. mellifera*, whereby, due to the presence of second-order signals (**Table 1**) regulation of the temporal worker castes is hierarchically controlled at the collective colony level.

Reproductive/worker caste determination: Colony level control of the temporal polyethism schedule of workers is important for *A. mellifera* colonies because the presence of worker castes allows for further second-order signals; i.e. a more complex higher-order organization compared to common wasp colonies. This is clear in the case of queen production, as I will explain presently.

Similarly to *V. vulgaris*, in *A. mellifera*, queen/worker caste determination is not genetically predetermined, i.e. any fertilized egg can be used to produce a queen or a worker (Wang et al. 2015). There are, consequently, signals and mechanisms present in the brood stage that determine the development of a particular larva into either a queen or worker (**Figure 2**). Queen-brood require large vertically-protruding comb cells, that are produced by nest workers. This is because in the larval and pupal stages, queen-brood are much larger than worker-brood, and so the increased volume of the larger comb cells is essential for their proper growth (Wang et al. 2015).

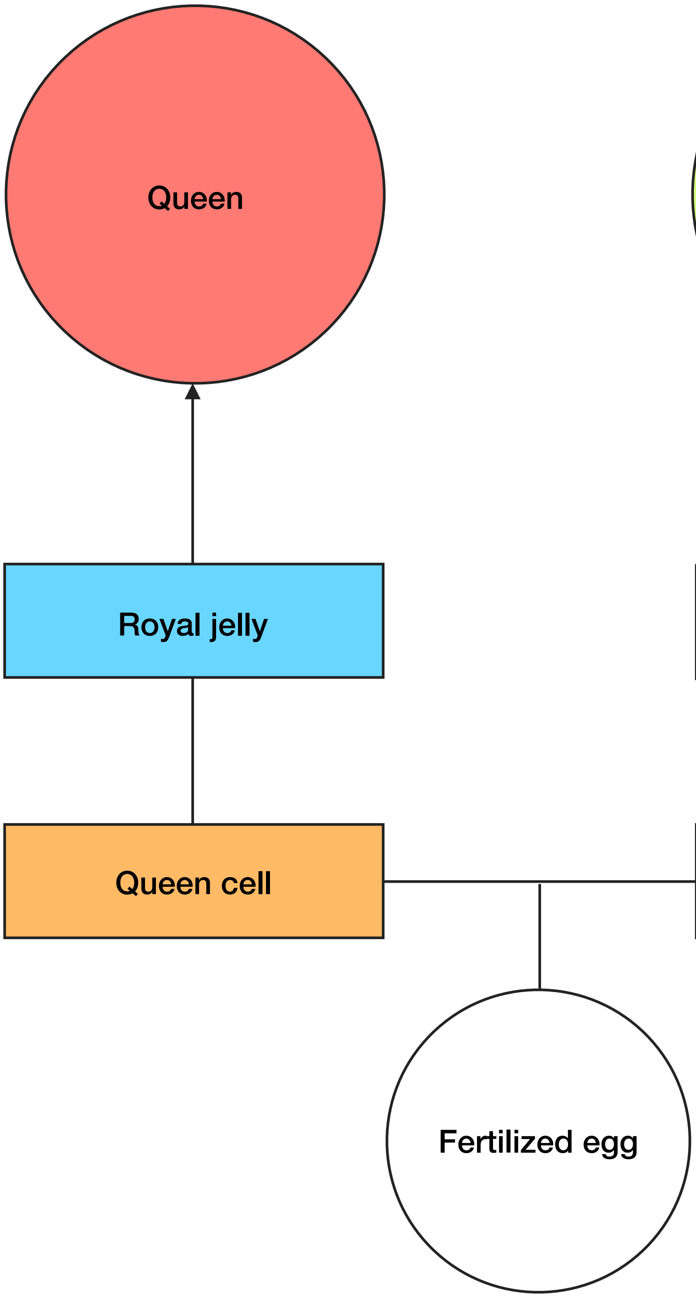

Fig. 2. Queen/worker production. Any fertilized egg can develop into a queen or worker in *A. mellifera*. The type of comb cell, *orange squares*, and diet, *blue squares*, determine the development of larvae. Large queen cells and royal jelly cause larvae from fertilized eggs to develop into queens, whereas small comb cells and brood food cause equivalent larvae to develop into workers. Royal jelly induces an epigenetic change within the larvae. The size of the comb cell constrains larval growth. *See text for more details*.

However, it is not only the size of the comb cell that determines the development of fertilized eggs into queens or workers, the type of diet that the brood receives in the larval stages is also an important factor. Nurse workers will begin feeding the larvae as soon as they hatch (eggs hatch after 3 days); worker-larvae receive ‘brood food’ — which is a mixture of jelly, honey and pollen — whilst queen-larvae receive a specialised diet of royal jelly and pollen (Wang et al. 2015). This is significant because it has been experimentally shown that newly hatched larvae (from fertilized eggs) that are fed a diet exclusively of royal jelly during the larval stage will develop into queens, whereas larvae fed with brood food will develop into workers (Page Jr. and Peng 2001; Wang et al. 2015). Lyko, and colleagues (2010), found that it is not just the higher nutritional value of the royal jelly that affects the larvae development. As well as accelerating metabolism and increasing growth, elements of the royal jelly (most likely phenyl butyrate) affect DNA methylation in the developing larvae by silencing DNA methyltransferase 3 (DNMT3). Royal jelly, therefore, induces an epigenetic change in the developing larvae.

As I have shown above, the different worker castes are maintained by the colony, via second-order signals, despite individual workers transitioning between castes. As a result of this, the *nurse* and *nest worker* castes are a constant presence in the colony, consequently, they can produce their respective signals for larvae development when required. Specifically, nest workers produce queen cells either in the event of the death of the queen or, more commonly, when the colony begins to prepare to swarm (Grozinger et al. 2014).[24] The queen will then oviposit fertilized eggs within queen cells and once the larvae emerge, nurse workers will supply them with royal jelly as needed (Beetsma 1979).[25] It can thus be argued that royal jelly and queen cells are dynamically decoupled from the process of reproductive caste

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[24] It is unclear exactly what initiates the colony into swarm preparation, but multiple cues are likely to be involved (Grozinger et al. 2014). But as I discuss below, for the specific case of queen cell production, a change to, or lack of, QPM may be key.

[25] It is likely that the size of comb cells acts as a cue for the nurses (Beetsma 1979), i.e. nurses may respond according to the type of cell in the following way: for larvae in queen cells deposit royal jelly, for larvae in worker cells then deposit brood food.

determination, i.e. the presence of the nurse and nest worker castes, in order to provide these signals, are not directly dependent on the process that they affect. Therefore, both queen cells and royal jelly can be considered as second-order signals on reproductive caste determination (**Table 2**).

	Signal	Source	Target	Role
First-order signals				
	Internal developmental constraints of larvae	Internal to each larva	Internal to each larva	Internally controls the development of larvae
Second-order signals				
	Queen cells	Nest workers	Queen-larvae	Larger comb cell volume allows for the increased growth of queen-larvae
	Worker cells	Nest workers	Worker-larvae	Smaller comb cell restricts growth of worker-larvae
	Royal jelly	Nurses	Queen-larvae	Induces the queen developmental programme by causing an epigenetic change
	Brood food	Nurses	Worker-larvae	Induces the worker developmental programme by not causing an epigenetic change

Table 2. *Reproductive caste determination*

Thus, queen/worker caste determination is more complex than in *V. vulgaris*. As above, there are second-order signals involved in queen production in *V. vulgaris* but to a lesser degree than in *A. mellifera*. It can be argued that in *V. vulgaris*, queen production is practically determined by the queen — the state of the QPM determines the production of reproductive-comb, and, even though nutrition levels increase due to self-organization, worker foraging is induced by the presence of the queen (Potter 1964: 50). Instead, in *A. mellifera* the production of queens is determined by the higher-order collective organization. Royal jelly, which causes an epigenetic change in queen-larvae, acts as a second-order signal; it is independent of the internal development systems of the developing larvae that it modulates. Also, this second-order signal derives from the nurse temporal caste (rather than from the queen). Moreover, the production of reproductive-comb is not dependent on the QPM in the same way as it is in *V. vulgaris*, as I will show presently.

Comb construction: The comb is an essential element of a colony's nest (Tautz 2009), it is where food (honey and pollen) is processed and stored, it is necessary for the production of brood (and therefore colony members), and it is essential for colony communication — for example, bees use the surface of the comb to do their communication dances, and vibrating its surface adds additional information to these dances (Hölldobler and Wilson 2009: 169-178). The comb is built and maintained by the nest worker caste (Johnson 2008). To do this nest workers secrete wax from glands in their abdomens, which they collect and use to construct the comb (Hepburn et al. 2014). Typically, only nest workers have activated wax glands (Johnson 2003). Comb construction is most likely the result of stigmergic self-organization (Oldroyd and Pratt 2015). This is because there is no need for any individual nest worker to have the complete plan of the comb in their mind, instead each cell of the comb can be constructed by multiple nest workers, each with a set of simple behavioural rules. Each nest worker will react with the appropriate construction task based on the current state of any particular part of the comb as they come across it (for more details see: Oldroyd and Pratt 2015). However, the size and type of comb produced is influenced by QPM (Maisonnasse et al. 2010a). It has been shown that nest workers construct less comb when there is no queen present in the colony as compared to when a queen is present. Moreover, when there is no queen present nest workers produce more drone-sized cells and queen cells in preparation for swarming rather than suitable comb for producing workers (Maisonnasse et al. 2010a). Therefore, an element of the QPM of the queen acts as a signal to the nest workers, affecting their building activity when constructing the comb. This signal ensures the correct type of comb is built at the correct time, i.e. worker-comb in the founding and ergonomic stages of colony development (Smith et al. 2016).

	Signal	Source	Target	Role
First-order signals				
	Stigmergic building	Nest workers	Comb	Construction of comb
Second-order signals				
	QPM	Queen	Nest workers	Induces nest workers to build more comb and predominately worker-comb

Table 3. *Comb construction*

It can be argued that stigmergic building by the nest workers is a first-order signal on comb construction in *A. mellifera* (**Table 3**). The role of the nest workers in this process is essential, without which no comb will be produced, and the colony cannot grow and maintain itself. However, QPM can be considered as a second-order signal on comb construction (and therefore colony development). This is because it is not essential in order for comb to be produced, instead it acts as a modulator on this process, i.e. it is dynamically decoupled from it. QPM acts indirectly by affecting the nest workers during comb construction; with QPM present nest workers produce more comb and primarily worker-comb, with a reduction (or loss of) QPM present nest workers produce less comb and significantly more reproductive-comb.

In *V. vulgaris*, reproductive comb production is also regulated by the QPM, as above, but not in exactly the same way. In *V. vulgaris* comb construction ceases in queenless colonies (Potter 1964), but this is not the case for *A. mellifera*. Furthermore, in honey bees, the production of reproductive-comb in the absence (or lack) of QPM appears to suggest a colony level response to a perturbation. The absence of QPM could be due to the death of the queen, for example, and without a queen no workers can be produced, and the colony cannot grow and maintain itself. Put simply, a colony without a queen will not survive for long. If queen death occurs, the workers of the colony will attempt to produce a new queen (if there is young worker-brood, less than 3 days old,[26] to convert into queen-brood by extending their comb cells into *queen cells* and feeding them *royal jelly*) and/or produce drones to send out to mate with young queens from other colonies (Free and Williams 1975; Tautz 2009: 135-139; Naeger et al. 2013). Therefore, it could be argued that the absence of the second-order signal (QPM) during comb construction causes a switch in the constitutive organization of the colony. The colony switches from normal growth and self-maintenance to a state of attempting to produce reproductives, in order to 1) replace the queen — to once again enable colony growth and self-

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[26] Queens can be produced from worker-larvae that are under 3 days old (Beetsma 1979). However, the age at which worker-larvae are switched to queen-larvae (via extended comb cells and royal jelly) affects the reproductive potential of the resultant adult queen: queens produced from the youngest worker-larvae have the highest reproductive potential as adults (Rangel et al. 2013).

maintenance — and/or 2) produce drones — in an attempt to reproduce in case of colony failure.

Worker reproductive inhibition: In *A. mellifera* workers cannot mate as they lack genitalia, but they do have ovaries and have the potential to produce unfertilized eggs that develop into males (Ronai et al. 2015). As in *V. vulgaris*, worker reproductive potential is inhibited in *A. mellifera* colonies by the QPM; it causes oocyte regression in workers (Ronai et al. 2015). But unlike *V. vulgaris* colonies, worker reproduction is also inhibited by signals from the brood, namely brood ester and E-β-ocimene (Maisonnasse et al. 2010b). QPM, brood ester and E-β-ocimene can all be considered as second-order signals on worker reproductive inhibition as again, they are dynamically decoupled from this process. The QPM derives from the queen and brood ester and E-β-ocimene derive from the brood, therefore their presence and effect on worker reproductive inhibition is not directly dependent on that process.

5.3. Comparison of colony level individuality in three eusocial insect species

In the previous section I applied the HO approach to three representative case studies — *M. genalis*, *V. vulgaris*, and *A. mellifera* — in order to assess the organizational differences between colonies of different species across the eusocial complexity spectrum. I showed that of the three, only *A. mellifera* exhibits second-order signals, a form of hierarchical control, from multiple sources; *V. vulgaris* has only one known source of second-order signals (the queen) and *M. genalis* colonies are too small for collective colony processes and, consequently, lack any collective organization with second-order signals. I will now conclude by comparing the types of colony individuality (**table 4**), if applicable, in each of these eusocial insect species.

As above, *M. genalis* are on the very simple end of the eusocial complexity spectrum. Colonies of *M. genalis* are too small for collective colony processes; each task is done by an individual bee. They therefore lack the type of collective organization possible for second-order signals. Instead, colony organization is controlled by the queen via aggression. Moreover, workers are fully totipotent and have full reproductive potential, but they typically do not reproduce due to the aggression of the queen. Consequently, selection is likely to be operating at the individual level only, rather than at the collective colony level (Kapheim et al. 2015; Johnson and Linksvayer 2010). In other words, colonies are not units of selection in *M. genalis* and consequently, colonies are not evolutionary individuals in this species. Additionally, colonies of *M. genalis* are not physiological-like individuals either since they have no higher-order organization and second-order signals. Instead, they are groups with a dominant reproductive, similar to many mammal social groups (e.g. meerkats), and if anything happens to the dominant reproductive, then any other female member can take her place.

In comparison, colonies of both *V. vulgaris* and *A. mellifera* have large colonies that exhibit collective colony processes. Moreover, they both exhibit second-order signals that hierarchically control and coordinate the collective processes. However, *A. mellifera* colonies have second-order signals from multiple sources whereas *V. vulgaris* only have one known source of second-order signals, namely the queen. This has implications for the hierarchical-organization within colonies; colony organization in *V. vulgaris* is likely to be much less stable than *A. mellifera*. This is demonstrated in the event of queen death, i.e. the absence of the sole source for second-order signals in the common wasp.

In *V. vulgaris* colony organization breaks down when the queen dies, which typically happens after the colony has produced young reproductives in the autumn (Potter 1964). Workers begin to oviposit unfertilized eggs, although they are rarely successful because oviposition is relatively unorganized — multiple workers oviposit eggs in the same comb cell — and foraging almost completely ceases without a queen present, thus there is little food for any worker-laid brood. Moreover, workers begin to cannibalise any brood present due to the lack of foraging. Consequently, due to the lack of colony cohesiveness and lack of food, the colony dies (Potter 1964: 34).

Whereas *A. mellifera* colonies have discreet temporal worker castes, which allows for more sources of second-order signals than in *V. vulgaris* colonies. Consequently, colony organization is not reliant on once source of second-order signals and is, therefore, more robust. Unlike in *V. vulgaris*, colony organization does not break down in the case of queen death, instead *A. mellifera* colonies will attempt produce a new replacement queen. The *nest worker* caste will adapt the comb cells of suitable larvae (from fertilized eggs) into queen cells (a second-order signal), and the *nurse* caste will then feed these larvae exclusively with royal jelly (a second-order signal), thus allowing the colony to produce a replacement queen.

The presence of multiple sources of second-order signals in *A. mellifera* colonies results in a more complex hierarchical-organization whereby hierarchical control and regulation is distributed at the collective colony level, as opposed to *V. vulgaris* whereby the hierarchical control and regulation is centralized around the queen, resulting in a more minimal form of hierarchical-organization. Consequently, it can be argued that the network of interactions, particularly between the parts that produce second-order signals, forms a new hierarchical level of organization in *A. mellifera* colonies. A hierarchical level that is dynamically decoupled from the lower level colony parts (the bees) but at the same time is capable of modulating and controlling on those lower level parts. In comparison, in *V. vulgaris* colonies the hierarchical-organization is more tightly coupled to the operation of the lower level parts because the second-order signals derive from a single source (the queen). Thus, colonies of both species exhibit hierarchical control in the coordination of colony organization, but in *V. vulgaris* this is determined at the lower level (i.e. the queen) whereas in *A. mellifera* this is determined at the collective level, by the higher-order organization.

	Evolutionary individuality	**Physiological-like individuality**
M. genalis	No	No
V. vulgaris	Yes	No
A. mellifera	Yes	Yes

Table 4. *Types of colony level individuality in three eusocial insect species*

Therefore, it can be argued that there is a form of physiological-like individuality at the colony level in *A. mellifera* but not in *V. vulgaris*. In *V. vulgaris* colonies can, at most, be considered as phenotypic extensions of the queen. Or, perhaps more likely, simply as groups with a minimal form of hierarchical-organization. In other words, *V. vulgaris* colonies may represent an intermediate stage of colony individuality because they have not quite achieved physiological-like individuality at the colony level — there is only a minimal form of hierarchical-organization — but colonies are units of selection and, thus, there is evolutionary individuality at the colony level. Whereas colonies of *A. mellifera* are arguably superorganisms in both senses; i.e. there is arguably physiological-like individuality as well as evolutionary individuality at the colony level in honey bees.

5.4. The concept of BA and the superorganism

What do these conclusions entail for the use of the concept of BA within eusociality research? Out of the three species assessed in the comparative case study, BA is only theoretically possible in *M. genalis* because there is no form of individuality at the colony level. However, as I have shown above, it is quite clear that offspring do not develop into the non-reproductive worker caste because of an internal trait that they possess, i.e. BA. Instead, they are coerced into that role by the queen. Thus, they do not become workers in an attempt to increase their inclusive fitness (BA), instead they are under parental manipulation (Kapheim et al. 2015).

In the case of *V. vulgaris* and *A. mellifera*, the concept of BA is not applicable to the workers because colonies are superorganisms. In *V. vulgaris*, colonies are units of selection, and thus evolutionary superorganisms. The evolutionary approach to the superorganism is based on MLS2, as I argued in chapter 3, which argues that selection occurs at multiple levels simultaneously. However, in the case of *V. vulgaris*, and other similarly organized eusocial insect species, selection is primarily occurring between-colonies (Hölldobler and Wilson 2009). Thus, in such cases the insects within colonies are not evolutionary individuals in their own right, their fitness is derived from the colony level (Okasha 2014). Moreover, as I have highlighted above, *V. vulgaris* also exhibit a minimal form of hierarchical control, based on second-order signals from the queen. Individuals develop into non-reproductive workers due to mechanisms in the brood stage (comb cell size and amount of nutrition), which are both ultimately regulated by the second-order signals from the queen. Not only do wasps require the colony in order to develop and survive, offspring develop into workers — have their reproductive potential inhibited — by hierarchical control. Therefore, the claim that workers in *V. vulgaris* are biological altruistic (according to the definition I proposed in chapter 3), as many authors do (e.g. Ratnieks and Wenseleers 2006, 2008), is incorrect.

In *A. mellifera*, colonies are superorganisms in the fullest sense. Not only are colonies units of selection (i.e. evolutionary superorganisms), due to their hierarchical-organization they are also physiological-like superorganisms. Not only are workers not evolutionary individuals in their own right (because the colony is the unit of selection), like in *V. vulgaris*, they are also lower level parts in a higher-order system. Because there are multiple sources of second-order signals, there is a more complex form of hierarchical-organization within *A. mellifera* colonies. As above, the network of interactions form a hierarchical level that is dynamically decoupled from the lower level colony parts (the bees) but at the same time is capable of modulating and controlling on those lower level parts. Therefore, not only are individual bees not evolutionary individuals, they are determined into their roles within the colony (e.g. queen or worker) due to the complex hierarchical-organization. Thus, workers in *A. mellifera*, and similarly organized species, cannot be examples of BA; a trait which is only applicable to biological individuals.

Conclusion

In this chapter I have challenged the presupposition that hierarchical control does not occur in complex eusocial insects. Using the HO approach, I argued that there is evidence that hierarchical control occurs in at least two complex eusocial insect species (i.e. *V. vulgaris* and *A. mellifera*). Furthermore, I applied the HO approach to three representative case studies in order to assess the types of colony individuality in eusocial insects.

To begin with, in section 5.1., I proposed an organizational approach that incorporates self-organization, but focuses on the possible hierarchical control within colonies, namely the HO approach. The HO approach focuses on the coordinating signals that control and regulate the collective colony processes (e.g. caste determination, nest construction, etc.). Specifically, the HO approach assesses whether colony processes are controlled solely by first-order signals, thus flat self-organization, or by second-order signals, thus a hierarchically controlled self-organization. Additionally, I argued that there is a form of physiological-like individuality at the colony level if 1) a colony has multiple second-order signals in multiple colony processes and 2) these second-order signals derive from more than one source (i.e. not only the queen but also the brood, different worker castes). This is because, premise 1) points to the fact that the colony is hierarchically-organized. Whereas premise 2) highlights that hierarchical control is distributed at the colony level, rather than being reliant on a single part (i.e. the queen), therefore resulting in a higher-order organization that is sufficiently dynamically decoupled from the lower level parts of the system (i.e. each individual insect). A dynamically decoupled higher-order organization could be evidence of physiological-like individuality.

In section 5.2., I applied the HO approach to three representative case studies; a species representing the most simple eusocial insects (*M. genalis*), a species from the mid-range of the eusocial complexity spectrum (*V. vulgaris*), and a species representing the more complex species (*A. mellifera*). *M. genalis* colonies are too small for collective colony processes, thus they lack a collective organization possible for second-order signals. Whereas, both *V. vulgaris* and *A. mellifera* colonies are large enough for collective organizations and, furthermore, both exhibit hierarchical-organization due to the presence of second-order signals. However, there is only one known source of second-order signals in *V. vulgaris* colonies, namely, the queen.

Whereas, in *A. mellifera* colonies, there are multiple sources of second-order signals; the queen, the brood, and the temporal worker castes.

In section 5.3., I analysed the types of individuality in eusocial insect colonies. Based on these case studies, it is likely that in the most simple species of eusocial insects, represented by *M. genalis*, there is no form of individuality at the colony level. Instead, in species like *M. genalis*, colonies are groups with a dominant reproductive, i.e. the queen, who maintains colony cohesiveness via aggression. Whereas, as organizational complexity increases within eusocial insect species, colony individuality also emerges — as colonies evolved to be more complex, the insects that instantiate them became more specialised and, thus, they became individually less complex (Anderson and McShea 2001). Colonies of species on the middle range of the eusocial complexity spectrum, as represented by *V. vulgaris*, are units of selection due to the complex reproductive division of labour, and are consequently evolutionary superorganisms. However, *V. vulgaris* exhibit a minimal form of hierarchical-organization as the queen represents the unique source of second-order signals in the colony. Thus, in *V. vulgaris*, and similar species (around the centre of the eusocial complexity spectrum) with a minimal hierarchical-organization in colonies, there is no physiological-like individuality at the colony level. However, in the more complex species, as represented by *A. mellifera*, there are multiple second-order signals from multiple sources, which forms a higher-order organization that is dynamically decoupled from the lower level parts. Consequently, colonies in such species are not only evolutionary superorganisms, but also superorganisms in a physiological-like sense; as argued by Wheeler so long ago.

Finally, in section 5.4., I assessed the consequences of these findings for the use of the concept of BA within eusociality research. I argued that the BA is only theoretically possible in one of the three species analysed in 5.2., namely *M. genalis*. This is because colonies of *M. genalis* are not superorganisms, in either sense. Moreover, as I highlighted in chapter 3, selection takes place primarily at the individual level in this species. However, it is clear from the case study that there is no evidence that individuals in *M. genalis* become non-reproductives because of an internal trait that they possess; i.e. individuals are not attempting to increase their inclusive fitness by becoming workers (i.e. BA). Instead, they are coerced into becoming workers by the queen (i.e. parental manipulation). Furthermore, I argued that BA is not even theoretically possible in *V. vulgaris* and *A. mellifera*. This is because colonies in both species are superorganisms. In *V. vulgaris*, colonies are evolutionary superorganisms (units of selection). Moreover, they exhibit a minimal form of hierarchical-organization. Not only are the workers not evolutionary individuals in their own right, they develop into non-reproductive workers due to hierarchical control, which is ultimately reliant on the queen. In *A. mellifera*, colonies are superorganisms in both an evolutionary and physiological-like sense. Colonies exhibit a complex hierarchical-organization that is dynamically decoupled from the lower level parts, but which at the same time is capable of modulating and controlling on those lower level parts. Thus, not only are individuals in *A. mellifera* not evolutionary individuals, they develop into non-reproductive workers due to hierarchical control of the collective organization. Therefore, workers in both *V. vulgaris* and *A. mellifera* are not biologically altruistic.

Eusociality researchers should, therefore, explore alternative approaches that do not rule out the possibility of hierarchical control in complex eusocial insects, such as the HO approach that I have developed in this chapter. As well as investigating the superorganism from an evolutionary perspective, and assessing which species exhibit colony selection, researchers should also approach the superorganism from an organizational perspective in order to assess which species can also be considered physiological-like individuals. It has been shown that many species of eusocial insects exhibit colony selection, due to the evolution of obligate eusociality in these species (Hölldobler and Wilson 2009). Therefore, many species are likely to qualify as evolutionary superorganisms, such as in *V. vulgaris*. But some species, such as *A. mellifera* and other highly complex species, are also likely to be physiological-like superorganisms because of hierarchical-organization within these colonies. But more empirical research needs to be carried out by eusociality researchers in order to assess this. The concept of BA would not be applicable to the non-reproductive castes in those species in which colonies are superorganisms in any sense, as I argued above. Thus, the current widespread use of the concept of BA within eusociality research is not justified. It is only theoretically possible in the most simple species whereby colonies are not superorganisms in any sense; i.e. likely the facultative eusocial species such as *M. genalis*. However, as I argued in chapter 3, there is currently no direct evidence that the concept of BA is the correct description of the behaviour of the non-reproductive castes in these species. Moreover, applying the concept of BA to species such as *V. vulgaris* and *A. mellifera*, obscures important and interesting biological factors in the evolution and maintenance of superorganisms; i.e. hierarchical-organization.

Conclusion

> [The] earliest evolutionary steps towards eusociality are most favoured if mediated through *maternal manipulation*. (Kapheim et al. 2015: 5. Emphasis added).

The aim of this thesis was to provide a critical analysis of the use of the concept of BA within eusociality research from a historical and philosophical perspective. Specifically, I addressed the following questions:

A. Is the concept of BA a correct description of the behaviour of the non-reproductive castes in eusocial insect colonies?
B. Has the widespread use of the concept of BA been problematic for eusociality research?

I addressed these questions in the previous chapters by challenging the following claims about the concept of BA and eusociality research that are made within the literature:

(1) That BA *is* a fundamental issue in eusociality research
(2) That BA *has been* a fundamental issue in eusociality research since Darwin
(3) Darwin discussed and/or developed the concept of BA and its associated paradox

In chapters 1 and 2, I challenged claims (2) and (3). In chapter 1, I traced the history of the concept of BA within eusociality research. Contrary to claim (2), I argued the concept of BA was developed by Haldane (1932) seven decades after Darwin first published *On the Origin of Species*. Additionally, I argued that the concept did not become widely used within eusociality research until around the 1960s, a century after Darwin published the *Origin*. This was due to the emergence of kin selection. Hamilton applied kin selection theory to the explanation of the evolution of eusociality because a) he rejected the superorganism argument that was previously widespread and b) he already considered eusocial insects as an example of BA prior to developing the theory of kin selection. But the reason why Hamilton applied the concept of BA has received little attention within the literature, and this is problematic because Hamilton's influence led to the mainstream view that BA is necessarily required in order for eusociality to evolve. I argued that the Hamilton applied the concept of BA to eusocial insects because of the Sturtevant-Hamilton problem of sterility. Following Sturtevant, Hamilton argued that worker BA must evolve in order for eusociality to evolve. But the Sturtevant-Hamilton problem of sterility does not necessarily entail that BA is essential for the evolution of BA, it only entails that the non-reproductive castes evolve. This could occur due to worker BA or it could occur due to parental manipulation, for example. However, this point went relatively unnoticed due to the lack of reassessment into the original argument for the sterility problem by Sturtevant. As a consequence, the majority of authors conceptualised the evolution of eusociality as the evolution of BA. Alternatives to BA, such as the superorganism, dominance, etc., that were in use in pre-Hamiltonian eusociality research, declined as a result of the widespread use of BA.

In chapter 2, I argued that contrary to claim (3), Darwin did not discuss and/or develop the concept of BA. Darwin's concept of morality, in the *Descent of Man*, was more similar to psychological altruism than BA. Eusocial insects did initially pose a serious problem for Darwin when he was developing his theory of natural selection, which he referred to as the "special difficulty". But the "special difficulty" was not to do with BA but, rather, the fact that the non-reproductive castes have evolved to be different to the reproductives. Thus, I argued that Darwin did not discuss and/or develop the concept of BA.

I challenged claim (1) in chapters 3, 4, and 5, which I will summarise below. Simultaneously, I will highlight how I addressed the two main questions of this thesis. I will then address some implications of the findings of this thesis.

Has the widespread use of the concept of BA been problematic for eusociality research?

Hamilton applied the concept of BA to eusociality due to the Sturtevant-Hamilton problem of sterility, and he used kin selection theory in order to explain the evolution of eusocial insects; i.e. he argued that eusociality evolved due to the evolution of biologically altruistic worker castes. Due to the fact that kin selection theory was so groundbreaking, Hamilton had an enormous influence on the field. As a consequence, the majority of authors conceptualised the evolution of eusociality as the evolution of BA, following Hamilton. But this conceptual monism of BA, post-Hamilton, was problematic for eusociality research. Firstly, the widespread use of BA led to inaccurate historiographies of eusociality research, e.g. claims (2) and (3). In chapter 2, I argued that authors have often viewed the history of eusociality research to be centred around the problem of BA, due to the current conceptual monism of BA in post-Hamiltonian eusociality research. This led to the inaccurate historical claims (2) and (3), above. I argued that this is not only a problem for historical accuracy, however. Claims (2) and (3) have the effect of justifying the current widespread use of the concept of BA, by adding historical weight to the use of the concept. In other words, the claim that authors, including Darwin, have conceptualised the evolution of eusociality as the evolution of BA throughout history, supports the current conceptualisation of the problem in the same way.

Moreover, the widespread use of the concept of BA, and the subsequent inaccurate historiographies of eusociality research, led to a lack of focus on possible alternatives. Some alternatives, such as the superorganism, dominance, trophallaxis, etc., were already in use prior to Hamilton, as I highlighted in chapter 1. Others, such as parental manipulation, were proposed after Hamilton introduced kin selection, but received relatively little attention compared to the concept of BA. This is extremely problematic because, as I highlighted in chapter 3, recent empirical data supports the view that parental coercion led to the evolution of the reproductive division of labour, *not* biological altruistic workers.

The conceptual monism of BA was also problematic because it resulted in multiple definitions of the concept in use, as I argued in chapter 3. Because of the view that BA was necessarily required for the evolution of eusociality, authors typically altered the concept to fit their theoretical models rather than seeking alternatives. Group selection theorists developed the concept of weak BA, but I argued that this is not true BA because it defines the fitness consequences relatively. Moreover, weak BA can only evolve by increasing the focal individuals absolute fitness. Kin selection theorists defined the fitness consequences in terms of absolute fitness. But the evidence for parental coercion has often been interpreted as evidence of worker BA by kin selection theorists due to the fitness consequences definition of BA (BA_f) — a trait that cause negative selection to the focal individual and positive selection to the recipient individual(s). I argued that both worker BA *and* parental coercion can fit this definition; both traits cause negative selection to the focal individual (the worker). Thus, the evidence of coercion has either been interpreted as BA, or in some cases as “enforced BA”. Therefore, I proposed a definition of BA, closer to the original notion from Haldane, that stipulates that the cause of the fitness consequences is due to a trait possessed by the focal individual: BA = a trait possessed by the focal individual, that causes it to benefit others at a long-term cost to itself, resulting in negative selection on the focal individual and positive selection on the recipient(s).

Is the concept of BA a correct description of the behaviour of the non-reproductive castes in eusocial insect colonies?

In chapter 3, I assessed the role of BA within current evolutionary studies of eusocial insects. I argued that only kin selection is compatible with the concept of BA that I proposed; group selection is only compatible with weak BA, which is a form of mutualism not BA. However, I argued that there is a lack of evidence that eusociality evolved due to worker BA. Recent evidence supports the parental manipulation perspective; that eusociality evolved due to parental coercion. Therefore, there is a lack of empirical support for the claim that the non-reproductive castes of eusocial insects are biologically altruistic. Thus, not only is it incorrect to claim that BA is a fundamental problem for eusociality research (claim (1)), it is likely that *BA is not even the correct description of the behaviour of the non-reproductive castes*.

In chapters 4 and 5, I explored the superorganism concept, in order to further highlight that, for many species, the concept of BA is an incorrect description of the behaviour of the non-reproductive castes. The superorganism argument was prevalent prior to Hamilton but underwent a radical decline due to the emergence of kin selection and the concept of BA. Research into complex eusociality led to a revival of the superorganism in the late 1980s. However, I argued in chapter 4, that today the superorganism is typically understood from an evolutionary perspective of biological individuality; colonies that are units of selection are evolutionary superorganisms. But, I argued, in pre-Hamiltonian eusociality research the superorganism was originally conceived from a physiological perspective; defining colonies as emergent higher-level biological individuals. Currently, authors rarely employ the superorganism concept from a physiological perspective due to the presupposition that hierarchical control is not possible in the large colonies of complex eusocial insects. Consequently, colonies of complex eusocial insect species are typically conceived of as self-organized groups that are units of selection. However, I argued that there is evidence that hierarchical control is not only possible but actually exhibited in some colonies. Thus, in chapter 5, I proposed an organizational approach, that whilst incorporating self-organization, does not presuppose that hierarchical control in not possible, namely the *hierarchical-organizational* (HO) approach. The HO approach focuses on the coordinating signals that control and regulate the collective colony processes (e.g. caste determination, nest construction, etc.). Specifically, the HO approach assesses whether colony processes are controlled solely by first-order signals, thus self-organization, or by second-order signals, thus hierarchical control.

I applied the HO approach to three representative case studies in order to assess the types of colony individuality across species of eusocial insects. I argued that colonies of the most simple eusocial insect species (e.g. *M. genalis*), that exhibit facultative eusociality, are not superorganisms in any sense. Colonies of species in the mid-range of the complexity spectrum (e.g. *V. vulgaris*), are likely to be evolutionary superorganisms because they are units of selection, but not physiological-like superorganisms because they exhibit only a minimal form of hierarchical-organization. But colonies of the most complex species (e.g. *A. mellifera*) are likely to be superorganisms in the fullest sense, i.e. evolutionary and physiological-like individuals, due to their hierarchical-organization. Importantly, if a colony is a superorganism (in an evolutionary and/or physiological sense) then the concept of BA is not applicable to the members of the colony. This is because the concept of BA, is by definition, only applicable to individuals that are (potentially) evolutionary individuals; i.e. individuals that are the targets of natural selection. If a colony is an evolutionary superorganism, the colony is the unit of selection and thus the members of the colony do not have personal fitness values that BA could have consequences on. Additionally, if a colony is also a physiological-like superorganism, the members of the colony are lower level parts in a higher-order system. Therefore, the workers are determined into their role via hierarchical control at the collective colony level. The concept of BA would not be applicable to the non-reproductive castes in those species in which colonies qualify as superorganisms.

By using the HO approach to assess the development and maintenance of the actual organization within colonies, it is clear that members of the colony develop into the non-reproductive worker role due to coercion and/or hierarchical control; they do not do so because of a trait that they possess (i.e. BA) that causes them to attempt to increase their inclusive fitness by becoming non-reproductive workers.

Eusociality without BA? Implications of the thesis

In chapter 3, I argued that the evolution of eusociality likely involved two phases. Phase 1 is the evolutionary origins of eusocial insects. In this phase colony selection did not occur because eusociality evolved from solitary ancestors, thus kin selection likely drove the evolution of eusocial insects. As obligate eusociality emerged, colony selection likely occurred. Colony selection drove the evolution of further organizational complexity within colonies, resulting in the evolution of hierarchically-organized colonies. Thus, phase 2 is characterised as the evolution of the superorganism, via MLS. Crucially, worker BA is only possible in phase 1, prior to colony selection, but there is currently no evidence of worker BA. Instead, it is likely that the reproductive division of labour evolved in phase 1 due to parental manipulation. In phase 2 colony selection occurs and thus BA is not applicable. This argument has potential implications for the debate over the evolution of eusociality. A prominent debate today persists over whether kin selection or group selection (MLS2) is the best explanation for the evolution of eusociality (Hölldobler and Wilson 2009; Nowak et al. 2010; Abbot et al. 2011). Instead of being viewed as competing theories, they should be seen as complementary processes in the different evolutionary phases of eusociality.

It cannot be assumed that eusocial insect workers are biologically altruistic simply because they do not reproduce but cooperate for the colony; this could occur due to BA or coercion, for example. The use of BA must be empirically supported; it must be shown that this behaviour is due to a trait that the focal individual possesses. Not only is there currently no empirical evidence for BA, but I have shown that the concept of BA is not necessarily required in the evolution of eusociality. Moreover, the conceptual monism of BA is not supported by historical claims; the concept only became widely used in the 1960s. Therefore, researchers should pay more attention to the alternatives to the concept of BA, such as the HO approach, coercion, the superorganism, phenotypic plasticity, and more.

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