

Darwin's special difficulty: the evolution of “neuter insects” and current theory

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Abstract In the *Origin of Species*, Darwin discussed several challenges that worker insects presented to his theory of natural selection. Complex instincts such as building of combs of hexagonal cells were one problem and were explained by showing plausible intermediate stages. A more serious challenge was posed by the multiple worker castes seen in many ants. How could sterile individuals continue to evolve? A careful reading of the *Origin* suggests that Darwin was not primarily concerned by the evolution of worker sterility itself, which he considered a minor difficulty. Some modern commentaries on Darwin and insect workers seem to be cases of present interests interfering with the interpretation of the past. From a modern perspective, the evolution of a worker caste, and its corollary altruism, are evolutionary puzzles inasmuch as natural selection normally favors greater, not lesser,

individual reproduction. These puzzles were resolved by Hamilton's theory of inclusive fitness. We now have a good functional understanding of how natural selection can cause both the origin of workers and their elaboration into greater levels of sterility and multiple morphological castes. Mechanistic understanding of morphological castes is also increasing via research into alternative developmental pathways. When the *Origin* was written, genetics did not exist and it would have been virtually impossible for Darwin to elaborate such ideas. However, the *Origin* probably addressed the main questions in the minds of Victorian readers in relation to insect workers. Darwin was prescient in having insights with close relationships to modern-day interests and the key principles involved, including kinship and benefits to the colony, even if these are not exact precursors to modern thinking.

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Introduction

“It is common in evolutionary circles to trace the lineage of one's position to the first and greatest evolutionist of them all, thereby investing one's view with the imprimatur of authority, sometimes with justification, other times less so.” (Alcock 2001, p. 17)

In 2009, the bicentenary of his birth and the 150-year anniversary of the *Origin of Species*, Charles Darwin was still a potent influence in the working life of the modern evolutionary biologist. Lewens (2007, page 5) comments that “Darwin is still a part of modern Darwinian biology in a way that Einstein is not a part of modern physics,” that

modern biologists have read Darwin's works, often refer to themselves as Darwinians, and that “When biologists differ over issues in modern science, they often try to claim Darwin for their team. Darwin is still regarded as a quotable biological authority, and struggles go on between biologists over how his views should be interpreted.” Alcock (2001, page 17, see above) makes a similar point.

One reason for Darwin's enduring influence is the broad scope of his work. Darwin studied and wrote on topics ranging from pollination biology to sexual selection, from the formation of vegetable mould to human emotions. But of greater importance than breadth was Darwin's ability to recognize and develop key issues. Evolutionary psychology and human cultural evolution, two recent and rapidly developing areas of evolutionary biology, both include and build on many ideas first elaborated by Darwin. In short, reading Darwin is both relevant and useful.

Another area addressed by Darwin is social evolution. The *Descent of Man* (1877) is a later and major source for his thinking in this area and lays the groundwork for several modern topics. To give one example, he pondered the stimulus to developing virtue caused by “the praise and blame of our fellow-men” (Darwin 1871 p.164), commenting that “it is hardly possible to exaggerate the importance during rude times of the love of praise and the dread of blame” (p. 165). Darwin did not explain how praise and blame are converted into individual fitness. Modern theorists have devised game theoretical models to address these issues and the results tend to confirm the importance of reputation (e.g., indirect reciprocity models, Nowak and Sigmund 2005; see also Alexander 1979).

Darwin presents what is probably his best-known discussion of social evolution in Chapter 7, *Instinct*, of the *Origin of Species* when he addresses the “special difficulty” (see below) posed by insect workers to his theory of natural selection. Many evolutionary biologists will be aware of Darwin's difficulty with worker insects as it is frequently referred to. However, there is a wide range of opinion as to what exactly he was addressing and what his insights show. On the one hand, the difficulty has been seen as that posed by worker altruism and later solved by Hamilton (1964). In this vein Dugatkin (1997 p. 5; see also Dugatkin 2006) writes “In a characteristic flash of brilliance, however, Darwin resolved the paradox by outlining inclusive fitness theory more than 100 years before Hamilton (1964)”. Similarly, Wilson (1975 p. 117) writes “...the concept of kin selection...was originated by Charles Darwin in the *Origin of Species*.” On the other hand, some see Darwin as addressing the more general problem of adaptive evolutionary change in workers, that is, change in individuals that do not have offspring, rather than the more specific case of worker altruism. As an example of this, Williams (1993, p. 412), in his review of *The ant and the peacock* (Cronin 1991), writes “...her [Cronin's]

reading of Darwin's perception of the challenge of the social insects (pp. 198–199) was exactly mine. The modern literature is full of statements to the effect that Darwin saw a special difficulty in the altruism of workers. He did not. His worry was about how the workers could develop adaptations that none of their ancestors had.” Hunt (2007) also comes down firmly on this side. West-Eberhard (1996 p. 290), acknowledges the link between Darwin's difficulty and altruism but focuses on a “usually overlooked” aspect of the “dilemma,” namely the important general issue of the evolution of alternative developmental pathways allowing multiple phenotypes (e.g., workers and queens) to arise from a single genotype.

The discussion of Darwin's difficulty with insect workers clearly contains elements of what Lewens (2007, p. 6) refers to as “...progressive history...which focuses selectively on those elements of the past that are important from the perspective of today's best science...” The evolution of altruism is certainly a topic of great interest in modern-day evolutionary biology and is a genuine Darwinian paradox inasmuch as natural selection generally favors individuals that reproduce more rather than less, as do worker insects (Trivers 1985). As a result, and given that few biologists (ourselves included) are also trained historians, Dugatkin's possible over-enthusiasm (Dugatkin 1997, 2006) for equating Darwin's difficulty specifically with the evolution of altruism is understandable and is by no means unique. For example, Herbers (2009), in celebration of Darwin 200, begins “He [Darwin] actually was more concerned by the challenge of extensive variation among workers themselves...” but a few sentences later notes the progressive tendency by writing “Darwin's special difficulty has since been generalized as the problem of altruism.”

Hunt (2007 p. 184) points out that significant interest in altruism dates only from the early 1970s, and that the first quotation of Darwin's “special difficulty” was by Wilson (1971). Hunt (2007) uses this to downplay altruism as a significant question in evolutionary biology. An alternative viewpoint would be that it took the work of Maynard-Smith (1964), Williams (1966) and especially Hamilton (1964) to bring altruism to the forefront by showing that it was a real evolutionary paradox. Prior to this, species-advantage thinking (Wynne-Edwards 1962; see also Dawkins 1976; Trivers 1985) may have led to the problem being obscured. Fisher and Haldane came close to making the breakthrough eventually made by Hamilton (Dugatkin 2006) but neither did so. Perhaps this was because they did not consider altruism as a significant problem and so did not follow up on their insights (Ratnieks and Helanterä 2009; see also Trivers 1985 p. 46).

In this article we first review what Darwin wrote about insect workers (see also Figs. 1 and 2) with the aim of shedding light on the challenge that he felt that they

presented to his theory of natural selection and the logic behind his attempts to include them within the theory. To do this we use quotations from the first edition of the *Origin of Species* (Darwin 1859). Although sometimes quite lengthy, we believe that this will enable the reader to evaluate both Darwin's difficulty and his argument in an objective manner. (As scientists, we leave a fuller treatment involving Darwin's notebooks, correspondence and detailed comparison of the six volumes of the *Origin* to those who are trained in historical methods.) We then do turn to the present and briefly summarize some current ideas relevant to the worker insect difficulties discussed by Darwin. Here it is clear that we are arguing from the present, rather than from a historical perspective. To the modern biologist, Darwin's difficulties with insect workers can lead to an impressively wide range of questions, including alternative developmental pathways, animal breeding, the origin of eusociality, parental manipulation, intra-colony conflicts, division of labor, optimization theory, colony level selection and others. We have focused our attention on two of these: (1) How can natural selection favor the evolution of sterile workers? (2) How can natural selection produce morphologically distinct worker castes? In the [Appendix](#), we also provide some discussion of theoretical issues.

Brief background to Darwin's theory of natural selection

Darwin lacked a clear understanding of the mechanism of inheritance. Although at the time of the *Origin* Mendel was studying inheritance in peas, and published his results in 1866, it was not until 1900 that his work became widely known and not until several decades later that Mendelian genetics would be united with Darwin's theory of natural selection to form the neo-Darwinian synthesis. Nevertheless, Darwin knew that traits were passed across generations from his studies of animal and plant breeding. From this, and from his realization that in the “struggle for life” only a “small number can survive,” he deduced that beneficial traits would increase over many generations via natural selection.

Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual ... will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving, for, of the many individuals of any species which are periodically born, but a small number can survive (Chapter 3 “Struggle for Life” page 61).

In discussing his theory, Darwin emphasized that evolution by natural selection would proceed gradually, in small steps.

Natural selection can act only by the preservation and accumulation of infinitesimally small inherited modifications... (Chapter 3 “Natural Selection” page 95).

Darwin was confident that his theory could explain the evolution even of complex adaptations, such as the eye, by the accumulation of many beneficial small changes over many generations.

To suppose that the eye, with all its inimitable contrivances ... could have been formed by natural selection, seems, I freely confess, absurd in the highest possible degree. Yet reason tells me, that if numerous gradations from a perfect and complex eye to one very imperfect and simple, each grade being useful to its possessor, can be shown to exist; if further, the eye does vary ever so slightly, and the variations be inherited, which is certainly the case; and if any variation or modification in the organ be ever useful to an animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, can hardly be considered real (Chapter 6 “Difficulties on Theory” page 186).

Why were worker insects a “special difficulty” for Darwin?

To Darwin the evolution of a complex eye by the gradual accumulation of inherited changes was relatively straightforward. In contrast, the two major themes of his theory—inheritance of beneficial traits and gradual modification—seemed to be seriously challenged by the existence of worker insects. Here, individuals occurred in each generation that were very different from their fertile parents. This seemed to counter the idea of gradual changes. And even worse, these individuals were sterile and so unable to pass on their traits to the next generation: there seemed to be no scope for inheritance, which was a key part of natural selection.

In the second half of the first paragraph of the section on *Neuter Insects* (Chapter 7, Instinct, page 236) Darwin writes

I ...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.

In the next paragraph (pages 236–7) he makes it clear that the “*special difficulty*” was not the origin of the sterile workers themselves. This is seen as no more difficult to explain by natural selection than some striking change in morphology or instinctive behavior. He was also untroubled as to how natural selection could favor worker sterility, which he attributed to selection on the colony.

...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 it had 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. But I must pass over this preliminary difficulty.

Darwin's “great difficulty” lay in how these traits could be inherited and how an individual radically different from its fertile parents could arise by natural selection:

The great difficulty lies in the working ants differing widely from both the males and the fertile females in structure, as in the shape of the thorax and in being destitute of wings and sometimes of eyes, and in instinct... If a working ant or other neuter insect had been an animal in the ordinary state, I should have unhesitatingly assumed that all its characters had been slowly acquired through natural selection; namely, by an individual having been born with some slight profitable modification of structure, this being inherited by its offspring, which again varied and were again selected, and so onwards. 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

A few pages later (p. 238) Darwin comes to the “climax of the difficulty,” which is to explain the situation, found in various ants with which he was familiar, in which distinct worker castes occur.

...but we have not as yet touched on the climax of the difficulty; namely, the fact that the neuters of several ants differ, not only from the fertile females and males, but from each other, sometimes to an almost

incredible degree, and are thus divided into two or even three castes. The castes, moreover, do not generally graduate into each other, but are perfectly well defined; being as distinct from each other, as are any two species of the same genus, or rather as any two genera of the same family...

Darwin solves this problem to his satisfaction in the next paragraph (p. 239) and in a subsequent paragraph (p. 241). Because workers are profitable to their parents, the parents produce offspring workers of different morphologies. In some species this may be through producing a range of worker types. In some of these it is the extreme forms that are the most useful to the community. In this way we can have the evolution of morphologically distinct worker castes. The special difficulty was solved. Figure 2a shows workers of *Pheidole oxyops*. *Pheidole* are a large genus characterized by distinct major and minor workers without intermediates. Figure 2b shows worker *Atta*. Mature *Atta* colonies have workers with an approximately 200-fold range in mass, but with all sizes represented. Workers of different sizes perform different activities, including guarding and cutting fruit (the largest workers), cutting and transporting leaf fragments (medium-sized), and tending the fungus garden (smallest) (Fig. 2) (Helanterä and Ratnieks 2008; Hölldobler and Wilson 1990, 2009).

It will indeed be thought that I have an overweening confidence in the principle of natural selection, when I do not admit that such wonderful and well-established facts at once annihilate my theory. In the simpler case of neuter insects all of one caste or of the same kind, which have been rendered by natural selection, as I believe to be quite possible, different from the fertile males and females, in this case, we may safely conclude from the analogy of ordinary variations, that each successive, slight, profitable modification did not probably at first appear in all the individual neuters in the same nest, but in a few alone; and that by the long-continued selection of the fertile parents which produced most neuters with the profitable modification, all the neuters ultimately came to have the desired character...

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



Fig. 1 Food pots in the stingless bee *Tetragonisca angustula* (a). The egg-shaped pots are often built close together with adjoining walls and can hold pollen or honey. In this example, six pots encircle a seventh pot that, as a result, has a hexagonal shape. Inside a nest of *Melipona beecheii*, referred to as *M. domestica* in the *Origin* (b). The food pots are the larger egg-shaped cells to the left and lower sides. The square shows a group of five pots encircling a pentagonal pot. The pots are arranged irregularly. By contrast, the brood cells, upper right, form regular combs of hexagonal cells. After being constructed, a brood cell is filled with food, the queen then lays an egg, and the cell is sealed. This gives a developing female larva some control over her caste fate as the same sized cells are used for rearing males, workers, and queens, one per cell. Photos taken by F. Ratnieks at Fazenda Aretuzina, São Simão, São Paulo, Brazil (a), and Merida, Yucatan, Mexico (b)

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...

In the above two paragraphs Darwin refers to natural selection for workers acting on the parents, not on the workers themselves. Earlier (p.237) he had already set out an argument, based on the correlation of characteristics in relatives, by which natural selection could modify the traits

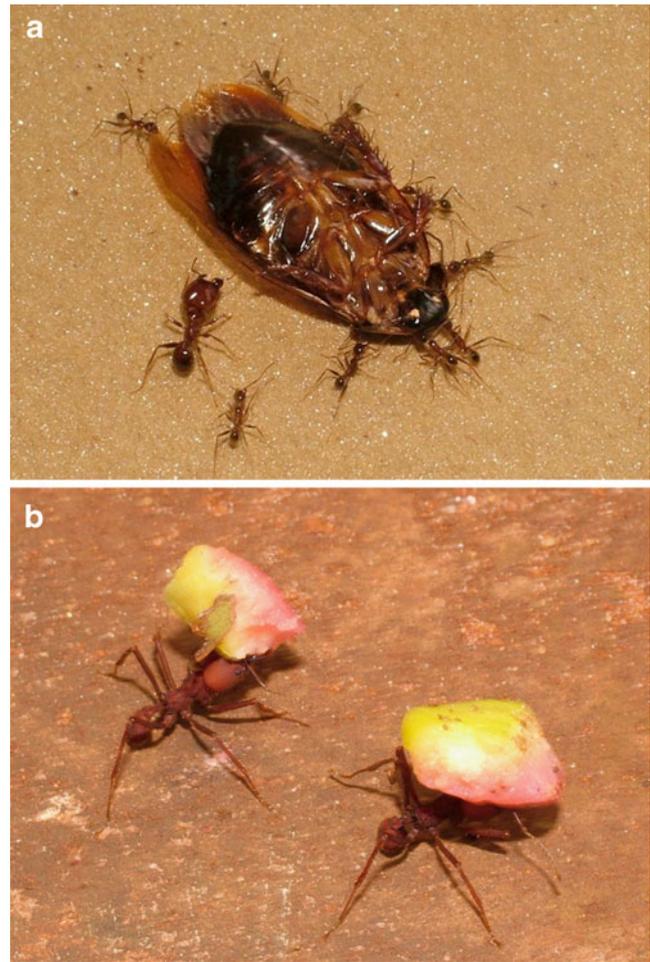


Fig. 2 Workers of *Pheidole oxylops* (a). *Pheidole* generally have a bimodal distribution of worker sizes. Shown are a group of minor workers retrieving a dead insect while a major looks on. The main role of the majors is defence. Medium-sized *Atta* workers carrying cut fruit pieces back to the nest (b) (Helanterä and Ratnieks 2008). *Atta* workers have a 200-fold range in body mass. Larger workers are defenders and also cut fruit, while the smallest workers tend the fungus garden inside the nest. Photos taken by F. Ratnieks at Fazenda Aretuzina, São Simão, São Paulo, Brazil

of sterile workers by selection at the level of the family, that is by selection on relatives.

...Hence I can see no real difficulty in any character having become correlated with the sterile condition of certain members of insect-communities: the difficulty lies in understanding how such correlated modifications of structure could have been slowly accumulated by natural selection.

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 to the individual, and may thus gain the desired end. Thus, a well-flavored vegetable is cooked, and the individual is destroyed; but the

horticulturist sows seeds of the same stock, and confidently expects to get nearly the same variety; breeders of cattle wish the flesh and fat to be well marbled together; the animal has been slaughtered, but the breeder goes with confidence to the same family...

The above are not the only social insect difficulties presented in Chapter 7. Earlier in this chapter, Darwin singles out two instincts of social insects, slavery in ants and comb building in the honey bee as especially noteworthy, including some information he himself collected by observation and experimentation at his home.

The opening sentence of Chapter 7 makes it clear that comb building was something that he felt he would have to address, because it would be so well known to his readers and perhaps because it could easily be considered an example of divine creation "... so wonderful an instinct as that of the hive-bee making its cells will probably have occurred to many readers, as a difficulty sufficient to overthrow my whole theory." Darwin notes that the honey pots of stingless bees, specifically the tropical American *Melipona beecheii* (referred to him as *M. domestica*), provide an example of an intermediate stage between the building of spherical cells, as in bumble bees, and hexagonal cells, as in honey bees (see Fig. 1). Comb-building could thus progress through intermediate stages and, by needing less wax than spherical cells, would be beneficial to the colony "Hence the saving of wax by largely saving honey must be a most important element of success in any family of bees." And later "Thus, as I believe, the most wonderful of all known instincts, that of the hive-bee, can be explained by natural selection having taken advantage of numerous, successive, slight modifications of simpler instincts;"...and later "The motive power of the process of natural selection having been economy of wax; that individual swarm which wasted least honey in the secretion of wax, having succeeded best, and having transmitted by inheritance its newly acquired economical instinct to new swarms, which in their turn will have had the best chance of succeeding in the struggle for existence." The discussion of comb building in honey bees and slavery in ants takes several pages and is resolved by showing that these instincts can reasonably be seen as having evolved through intermediate stages and in having benefits to the colony.

Current thinking

Darwin's treatment of the special difficulty posed by worker insects raises two major questions. His first and lesser difficulty was how natural selection could favor the evolution of sterile individuals. In current terminology, this

is the problem of explaining the origin of eusociality. That is, the origin of altruistic individuals who help others to reproduce and have reduced direct reproduction as a result. His second and greater difficulty was morphologically distinct worker castes, as found in many ants and termites. Inclusive fitness theory (Hamilton 1964) provides insight into both questions (see also the Appendix). In the two following sections we discuss some current thinking on these.

Question 1: how can natural selection favor the evolution of sterile workers?

How natural selection can favor an individual giving up personal reproduction to increase the reproduction of another was answered 100 years after the *Origin*. In his seminal twin papers, Hamilton (1964) explained the evolution of reproductive altruism through benefits to kin. His inclusive fitness theory is a general extension of natural selection theory to include the effects on gene frequencies of social interactions. The theory is based on probabilities of sharing genes identical by descent, relatedness, and therefore builds on genetic concepts unavailable to Darwin and which were developed for use in animal breeding (Malécot 1948).

Genes in a helping individual that allow parents, or other relatives, greater reproduction can increase in frequency in the population provided that the help results in sufficient additional kin being reared to compensate the cost to the helper's direct reproduction. Put another way, a helping individual can have higher inclusive fitness despite having lower direct fitness (direct reproduction). According to Hamilton's rule, helping your parents is favored by natural selection when $br_s > cr_o$, where b is the increase in the number of siblings, c the reduction in own offspring, and r_s and r_o the relatednesses of the helping individual to siblings and offspring. For a worker helping to rear full siblings both these relatedness terms are 0.5. (In haplodiploids with female workers, such as bees, wasps and ants, 0.5 is the mean of 0.75 to full sisters and 0.25 to brothers. For clonal organisms both relatedness terms are 1. See also the Appendix.) In this situation the inclusive fitness of a helper is the same when helping instead of reproducing, provided that helping to rear siblings is as efficient as rearing offspring. Comparative study of modern-day species of eusocial Hymenoptera (ants, bees, and wasps) indicates that monandry, and hence high kinship, prevailed when eusociality originated (Hughes et al. 2008). This provides general support for the prediction that altruism is favored by high relatedness. Multiple mating by queens, which reduces relatedness, is common in modern day eusocial insects, including the honey bee and leafcutter ants, but is a derived characteristic (Hughes et al. 2008). Furthermore, it

is only common in species with non-totipotent workers, which, therefore, cannot opt out of social life and set up their own nest. (Other factors such as the superseding of a mother queen by a sister and multiple queens can also reduce relatedness of workers to the queen's offspring.)

The above argument shows how inclusive fitness theory can be used to evaluate the interests of helping individuals, or any other party of interest in the social group including the parents, to determine whether selection will favor or disfavor helping. How does this compare to Darwin's scenario? Darwin's comments in the *Origin* such as “profitable to the community” and “natural selection, by acting on the fertile parents, could form a species which should regularly produce neuters” and “... if such insects had been social, and it had 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” show that his focus was predominantly on the interests of the parents or the whole colony, rather than that of the helping individual. The interests of the helper were overlooked even though his theory of natural selection normally emphasizes benefits to the individual, as shown by his statement “Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual ...” (page 61).

From a modern-day perspective, Darwin was prescient in focusing on benefits to kin. However, Darwin switches from individual benefits to benefits to the colony or parents without justifying this. Although any individual will receive an inclusive fitness benefit by helping its parents or kin, we now realize that there are conflicts involved. As a result, individuals may not always do what is in the best interests of their colony because there are also benefits to be gained from manipulating colony reproduction, such as when workers attempt to reproduce instead of working (Ratnieks et al. 2006). We also now understand that coercion, whether from the queen (Chamov 1978) or other workers (Ratnieks 1988), plays an important role in causing individuals to act altruistically in modern-day species (Ratnieks and Wenseleers 2005; Ratnieks et al. 2006). However, it is unlikely that coercion was important at the origin of eusociality because coercive behaviors, such as killing worker-laid eggs or restricting the food of female larvae to cause them to develop into workers, have little relevance until eusociality has evolved (Ratnieks and Wenseleers 2008), although egg-killing could be adaptive in non-eusocial species with brood parasitism.

Darwin also writes “...some insects and other articulate animals in a state of nature occasionally become sterile” suggesting that his scenario for the origin of workers is one in which sterility occurs early in the evolution of eusociality, even initially. However, it is more likely that the loss of full reproductive potency in workers occurred

after the origin of eusociality. In many extant lineages of social insects (e.g., halictid bees, *Polistes* wasps, *Microstigmus* wasps) the working individuals are reproductively totipotent and need only mate (or, as in many termites, also to metamorphose) in order to be able to lay eggs of both sexes and to head a colony. More generally, the terms “neuter” and “sterile” are also inaccurate in an important way. In the majority of eusocial Hymenoptera the workers, which are always female, are morphologically distinct from the queens and have lost the ability to mate, yet retain functional ovaries and can lay unfertilized eggs. These normally give rise to males if reared. In only a few genera of ants, stingless bees, and higher termites, are the workers fully sterile.

Question 2: how can natural selection produce morphologically distinct worker castes?

In his discussion of insect workers, Darwin's greatest difficulty was in explaining the derived situation in which workers and queens are distinct morphological castes. This situation has arisen several times independently (e.g., in termites, ants, Apidae bees, Vespinae wasps) and includes the most familiar and abundant social insects. Oster and Wilson (1978) devoted much of their book to worker caste ratios in ants, including the conditions under which morphologically distinct worker castes may be selected for via benefits to the colony. Hasegawa (1997) provides empirical support by showing that the presence of majors, in addition to minors, aids the success of *Colobopsis* ant colonies.

Oster and Wilson's (1978) optimization logic is simple. For a given cost of production, the ratio of worker castes that is ergonomically most beneficial to the colony as a whole will be selected for. This is as predicted by inclusive fitness theory provided that workers have no option other than to help, and assuming there is no other constraint on the production of multiple castes. If the workers are fully sterile and if developing larvae also have no control over their caste fate, this will be the case. In this situation a developing larva or an adult worker can best enhance its inclusive fitness by becoming or doing what most helps the colony to survive, grow, and ultimately to reproduce.

Darwin's explanation for the evolution of worker castes “profitable to the community” and “natural selection, by acting on the fertile parents, could form a species which should regularly produce neuters” are in keeping with Oster and Wilson (1978). However, the argument leaves out the potentially confounding role of intracolony conflict. If insect workers are not fully sterile then opportunities for direct reproduction may interact with and even act against the evolution of multiple castes. The workers in most species of eusocial Hymenoptera cannot mate but retain

ovaries and can lay unfertilized eggs that develop into males if reared. If workers' sons are frequently reared, then workers belonging to the caste that has the greater opportunity to lay eggs will have greater inclusive fitness. Female larvae may, therefore, be selected to develop into this more-reproductive worker sub-caste in the same way as there is also conflict over queen versus worker caste fate (see below; Bourke and Ratnieks 1999; Ratnieks et al. 2006).

Oster and Wilson (1978) themselves raised this issue. On page 23 they write "...the evolution of caste...is guided by natural selection at the colony level...The interaction of individual-level and colony-level selection complicates the evolution of caste in ways that are just beginning to be explored." They also provided some evidence suggesting that individual-level selection is a significant constraint on the evolution of multiple worker castes by showing that ant genera with fully sterile workers are more likely to have more than one worker caste than are genera whose workers retain functional ovaries. Subsequently, additional ant genera have been shown to have sterile workers. For example, worker leafcutter ants, *Atta*, retain ovaries but can lay only sterile trophic eggs (Dijkstra et al. 2005). *Atta* also have very great within-species diversity in worker morphology (Oster and Wilson 1978; Hölldobler and Wilson 1990, 2009).

Different worker castes may have different reproductive ability. In the Australian ant *Myrmecia gulosa* (Dietemann et al. 2002) workers have a bimodal size distribution. The larger workers have more ovarioles per ovary than the smaller workers (7.1 versus 4.3). In colonies with a queen, worker-laid eggs are "trophic" serving as a means of transferring food among adults and to larvae, which may be of considerable importance as this species is unable to share food by regurgitation, trophallaxis, as can many ants. But in queenless colonies many workers lay viable eggs. The reproductive opportunities of the two worker castes can be estimated from (proportion laying viable eggs) \times (number of ovarioles) \times (eggs per ovariole) as $0.165 \times 7.1 \times 0.42 = 0.49$ for large workers and $0.39 \times 4.3 \times 0.21 = 0.35$ for small workers, indicating that large workers have only a modest advantage. The difference is much greater in the Arizonan ant *Crematogaster smithi*, in which approximately half the colonies have specialized reproductive workers. These constitute approximately 1% of the workforce (Heinze et al. 1999), are much larger than the other workers, and have considerably greater reproductive capacity with 6–12 ovarioles per ovary versus 2. In colonies with a queen most worker-laid eggs are fed to larvae or eaten by the queen. In queenless colonies, however, worker-laid eggs are reared into males. Under queenless conditions the large workers are approximately 20 times as fecund, per ant, as the small workers.

In *C. smithi* the large workers have much greater reproductive capacity, although this may only be advantageous to them in queenless colonies. Could this difference in reproductive capacity hinder the evolution of two worker castes? That may depend on which caste evolved first. If the large workers are more recently evolved, then their increased reproductive capacity would aid their origin when considering individual level benefits. Heinze et al. (1999) speculate that large workers may also benefit the colony by converting incoming food into a form, eggs, which can act as storage. If this is the case, then selection at both individual and colony levels could favor the evolution of large workers in *C. smithi*.

The fact that different castes may have different reproductive opportunities and that this causes potential for conflict is a general phenomenon in social insects because it applies not just to differences among worker castes, which are found only in some ants (Wheeler 1926; Oster and Wilson 1978) and termites (Wilson 1971; Shellman-Reeve 1997), but also to the worker-queen caste difference that is extremely widespread and which also occurs in many bees and wasps (Wilson 1971). Theory shows that female larvae will often be selected to develop into workers even when this is not in the interests of other colony members due to reduced colony performance (Bourke and Ratnieks 1999; Ratnieks 2001; Wenseleers et al. 2003). In particular, if individual larvae control their own caste fate ("self-determination" Bourke and Ratnieks 1999) this can result in the overproduction of queens, thereby reducing the number of workers reared and causing reduced colony growth, survival and reproduction. In most species queen overproduction is prevented because adult workers can control the food that larvae receive and thereby prevent larvae from developing into queens, which are generally larger than workers. In this way the ratio of workers to young queens reared is that which is most beneficial to the colony as a whole. However, queens are overproduced in a few species, such as *Melipona* bees. Brood rearing in *Melipona* is unusual as queens are not larger than workers and larvae are reared in sealed cells on a provision mass. Under these exceptional conditions female larvae have the power to control their own case fate (Bourke and Ratnieks 1999; Ratnieks 2001; Wenseleers and Ratnieks 2004).

When workers can control larval feeding, female larvae will normally enhance their inclusive fitness by acquiescing to the fate intended for them by the adult workers, who enforce the interests of the colony as a whole. Thus, a honey bee larva in a worker cell probably has no real choice other than to develop into a worker (Ratnieks et al. 2006; Wenseleers et al. 2004; Ratnieks and Wenseleers 2005). If she develops into a worker she will work and help to rear relatives, thereby increasing her inclusive fitness. If she attempts to develop into a queen she will likely die,

either as a result of being directly killed by the workers or because the food supply and size of a worker cell is insufficient to allow her to develop into a queen. Note that female larvae do, in principle, have a choice over their caste fate because worker-queen caste in most eusocial Hymenoptera is not genetically determined. In the honey bee, females retain the developmental flexibility to become either a worker or a queen until midway through the larval stage (Wheeler 1986).

These latter examples closely match Darwin's comment about the origin of eusociality "and if such insects had been social, and it had 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." However, they occur not at the origin of eusociality but in highly derived species in which female larvae have relinquished control over their caste fate to others in their colony.

Final thoughts

Darwin's "special difficulty," the climax of which is the evolution of multiple worker castes, is no longer considered a major evolutionary problem. But our current understanding indicates that the conditions favoring the evolution of multiple worker castes may often be absent. In addition to cases where multiple castes are not beneficial to the colony as a whole (Oster and Wilson 1978), it may also be disfavored at the individual level. From a modern perspective, Darwin's analysis lacks the individual-level and gene-level understanding on the evolution of social traits given by Hamilton (1964, 1972) and Dawkins (1976).

Perhaps the biggest advance between Darwin and Hamilton is that it was Hamilton, not Darwin, who saw that the evolution of altruistic behavior was a major evolutionary problem. However, in promoting his new theory Darwin was addressing a readership who would be more likely to challenge him on how honey bee workers could build exquisite combs of hexagonal cells and how non-reproducing individuals could themselves be modified by natural selection, rather than on worker sterility and altruism. Yet in addressing these concerns Darwin had far reaching insights that have close relationships to modern-day interests and the key principles involved in social insect evolution, including kinship and benefits to the colony, even if these are not necessarily the exact precursors to modern thinking.

The questions that we have discussed above are only two of the many that could have been chosen, and relate mainly to functional/ultimate concerns. A mechanistic area that is now rapidly developing concerns the genetic underpinnings

of alternative developmental pathways (West-Eberhard 1996). An understanding of genetics, specifically population genetics, was necessary for Hamilton to formulate his theory, as shown by the title "The genetical evolution of social behaviour" of his twin papers (Hamilton 1964). An understanding of genetics, specifically gene regulation, is also necessary to understand how a single genotype can give rise to one of several very different morphologies. If Darwin were alive today there would be many areas in which he could be updated in relation to the evolution of worker insects. But few of these would not include some important point of contact with his own thinking from over 150 years ago.

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Appendix theory...and query

The underlying theory for understanding the conditions under which natural selection will favor the evolution of social acts that affect the lifetime reproduction of actors was developed by Hamilton (1964). Recent discussions of social evolution theory include Foster (2009) and Wenseleers et al. (2010). See also Marshall et al. and other contributions to this Darwin 200 collection of papers.

Selfish and mutualistic/cooperative acts do not present a Darwinian puzzle as both increase the lifetime fitness of actors (Ratnieks 2006; West et al. 2007). Altruism, which by definition causes reduced lifetime reproduction, is, however, a Darwinian puzzle inasmuch as natural selection normally favors only traits that increase an individual's reproduction. Hamilton's theory of inclusive fitness, sometimes referred to as kin selection (Maynard-Smith 1964), shows how traits that reduce lifetime production of offspring can be favored by natural selection when help is directed to kin. How closely related actor and recipient need to be depends upon the cost to the actor's reproduction versus the benefit to the recipient's reproduction, and is summarized in Hamilton's rule ($rb > c$, see also main text). Where costs and benefits are equal, the minimum ratio of relatedness to the recipient required is 1. That is, the altruist must be as related to the collateral kin helped as to its own offspring. This equality is provided in a family in which

altruists help rear full siblings instead of offspring or in a clonal society. Note that clonal reproduction does not provide a greater incentive for altruism as the relatedness ratio is also 1 (1:1), the same as for diploid (0.5:0.5) and haplodiploid $(0.5:(0.75+0.5)/2)$ family groups with a single parent of each sex. At the level of genes and population genetics, it is easy, in general terms, to see how helping kin at a cost to one's own reproduction can be favored by natural selection. Helping results in fewer of the altruist's genes being passed on directly, but more being passed on indirectly, leading to an overall increase in the frequency of genes that cause altruism.

Social insects have an important relationship with Hamilton's theory of inclusive fitness. On the one hand the altruism of insect workers is the defining characteristic of the eusocial insects. Reproduction in insect societies has provided important tests of inclusive fitness theory itself (see examples in Foster et al. 2006a, b) and the theory has predicted novel features of reproductive and social biology such as queen-worker conflict over sex allocation and worker policing (the mutual inhibition of reproduction by workers) (Ratnieks et al. 2001; Ratnieks et al. 2006).

Over the past few years the importance of Hamilton's theories in understanding insect social evolution have been questioned by the distinguished ant biologist and sociobiologist Edward O. Wilson and colleagues (Nowak et al. 2010; Wilson 2008; Wilson and Hölldobler 2005). These criticisms are wide ranging, and many have been responded to (e.g., Foster et al. 2006a,b; Crozier 2008; Foster 2009). Here, we address a few that are of relevance in the context of this paper.

Wilson (2008) writes “Virtually all of it [research on social insects] has been guided by the concept of group selection, in other words, selection that targets traits emerging from the interaction of colony members [p. 22].” It is true that much research on social insects can be guided by the general and readily apparent fact that workers normally work together for the good of the colony, and can seek explanations for much of what goes on in an insect society on this basis. Observation of any insect colony will readily show examples of cooperation (Ratnieks et al. 2006), such as communication and coordination in defense, nest building and foraging (Dyer 1992; Seeley 1995). What is less obvious to the casual observer is that insect societies are also subject to conflict among nestmates (Ratnieks 2006). By virtue of the intermediate levels of relatedness found in families, the individuals in insect societies are subject to strong altruistic and selfish incentives. They also have opportunities for both altruism and selfishness.

Inclusive fitness theory helps us to understand these opposing tendencies towards altruism and selfishness and their diverse outcomes. The application of the theory is not entirely straightforward (Ratnieks and Wenseleers 2008).

One of the main complications comes from the fact that several “forces” normally act at one time. Thus, the level of altruism (the proportion that do not lay eggs) seen in the workers in a colony is affected by multiple factors. One is the direct effect of relatedness on the tendency towards acting altruistically. Another is the effect of relatedness on the tendency for workers to prevent each other from reproducing. Both are significant and yet they work in opposite directions (Wenseleers and Ratnieks 2006; Ratnieks and Wenseleers 2008). High relatedness directly favors altruism. Conversely, low relatedness favors altruism indirectly, by favoring the mutual policing of worker reproduction thereby causing reduced worker production of males.

Where it is the main relevant variable, the predictive power of relatedness can be very high. In queenless colonies the proportion of workers that act altruistically (do not have active ovaries and so are not laying eggs) increases with worker-worker relatedness as expected from Hamilton's rule. This one parameter explains 67% of the variance in the proportion of egg laying workers among 10 species in which relatedness ranges from 0.3 to 0.75 (Wenseleers and Ratnieks 2006). By contrast, the average amount of variance explained by the main factor of interest in ecological and evolutionary studies is much less, only 4% (Møller and Jennions 2002).

Counter-intuitively, in many species including the honey bee, conflicts within the society actually lead to effective coercion that unifies the individuals to a common interest—the good of the colony—by restricting opportunities to act selfishly (Ratnieks and Helanterä 2009). Thus, conflict can cause altruism. But in some other species, such as *Melipona* stingless bees, the conflicts are not resolved and the society is subject to ongoing conflicts over queen versus worker caste fate that are costly to the colony given that resources are wasted rearing excess queens instead of workers (Ratnieks and Wenseleers 2005). As both types of bees are equally colony living, with perennial nests founded by swarms, it is clear that colony-level selection is not a sufficient explanation for the differences in social harmony between them.

It could perhaps be said that inclusive fitness theory is, among other things, the theory that enables us to understand the degree to which individual versus group-level interests prevail. Multi-level selection models can also be used for this purpose, and can be interchangeable with inclusive fitness models (Wenseleers et al. 2010). However, modeling the relatively complex reproductive opportunities of different individuals and their kinship can generally be carried out more easily and naturally with an inclusive fitness approach. For example, when workers reproduce they normally contribute only to male production, whereas the costs to the colony of having reduced work effort affect

both male and female (young queens, swarms) production. In addition, several degrees of relatedness to males must be considered including relatedness to sons, brothers, grandsons (workers' sons from the queen's perspective), and nephews (other workers' sons). Of these, relatedness of workers to nephews is itself variable as it depends upon the number of males mated to the mother queen (Ratnieks 1988).

When being used to predict and understand social insect reproduction, theory alone is not sufficient as it needs to be applied in a manner that pays attention to many relevant details of natural history. It is an art (the phrase “a feeling for the organism” comes to mind) as well as a science to know which of these are important, especially as there is relevant variation among social insect taxa at all possible hierarchical levels from order to subspecies (Beekman and Ratnieks 2003; Ratnieks et al. 2006). Thus, differences between honey bees and stingless bees in the way that brood are reared, via progressive versus mass-provisioning respectively, are highly significant in terms of the outcome and resolution of reproductive conflicts within colonies (Bourke and Ratnieks 1999; Ratnieks and Wenseleers 2005; Ratnieks et al. 2006; Wenseleers et al. 2004).

Wilson (2008) writes “Kin selection theory is not wrong; it is simply relatively ineffective, even inapplicable in its present form to most empirical research [p.23].” No theory is universally applicable and the apparent utility of any theory will also depend on individual interests. A researcher studying, for example, the honey bee waggle dance might never need to work with inclusive fitness theory. Dyer's review on the dance language has 126 references, but Hamilton (1964) is not among them (Dyer 1992). Following Wilson's logic one could argue that important twentieth century theories in physics such as quantum mechanics and relativity are ineffective and inapplicable inasmuch as many physicists and engineers do not use these theories in their own particular work. Nevertheless, these theories underpin the whole discipline and represent our best understanding of the workings of nature.

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