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Opinion piece

Darwin's 'one special difficulty': celebrating Darwin 200

Darwin identified eusocial evolution, especially of complex insect societies, as a particular challenge to his theory of natural selection. A century later, Hamilton provided a framework for selection on inclusive fitness. Hamilton's rule is robust and fertile, having generated multiple subdisciplines over the past 45 years. His suggestion that eusociality can be explained via kin selection, however, remains contentious. I review the continuing debate on the role of kin selection in eusocial evolution and suggest some lines of research that should resolve that debate.

The origin of species stands unparalleled in the biological literature for its scope and subsequent impact. Indeed, its central thesis that species are mutable and that life evolved through the process of natural selection has achieved the status of theory. Darwin (1859) took particular care to address phenomena that appeared incongruous with natural selection, especially 'one special difficulty':

> I…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 male and fertile females, and yet from being sterile they cannot propagate their kind.

Darwin was referring to insect societies with a strong reproductive division of labour. For the hymenopteran social insects (ants, bees and wasps), the sterile workers are all female, whereas in termites both males and females can be workers. In *The origin of species*, Darwin likened neuters to somatic tissues, thereby dismissing the apparent challenge to his theory (and, incidentally, eliminating the argument for inheritance of acquired characters). He actually was more concerned with the challenge of extensive variation among workers themselves. For example, army ant colonies can contain a million individuals; some are large defensive soldiers with specialized jaws, while others are small workers that care for larvae. Darwin considered at length how such variation among all-sterile individuals could evolve, and developed an argument that relied on 'selection on the family'. Darwin's special difficulty has since become generalized as the problem of altruism, or the evolution of a trait disadvantageous to its bearer but advantageous to another.

Scientific criticism from Darwin's contemporaries essentially ignored his 'one special difficulty' and, instead, focused on the mode of inheritance. Blending inheritance was the accepted model and Darwin's theory required tweaks in successive editions of *The origin of species* to align his ideas with that presumed mechanism. Difficulties presented by blending inheritance were resolved with the rediscovery of Mendel's work. The ensuing neo-Darwinian synthesis incorporated particulate inheritance into mathematical models of selection, giving birth to the field of population genetics. Its primary architects Fisher, Haldane and Wright all grappled with the problem of altruism, but no general formal solution to Darwin's special difficulty emerged from their work. Verbal arguments that described how altruistic traits might persist if they enhanced group survival were effectively dispelled by Williams (1966).

Hamilton's two landmark papers (1964*a*,*b*) at last presented a coherent theory grounded in genetic principles to explain the evolution of altruism. Hamilton's breakthrough insight was that genes are shared with relatives and therefore altruistic traits can evolve if they preferentially benefit relatives. The first paper formalizes that simple concept and offered a proof of what we now call Hamilton's law:

$$\text{altruism can evolve if } rb > c,$$

where b is the benefit to the recipient of the altruistic act; c is the cost to the bearer; and r is the degree of relatedness between them. This simple equation is extraordinarily robust: it is has been re-derived numerous times under different biological conditions (Queller 1985; Lehmann & Keller 2006). Furthermore, its simplicity has tremendous heuristic value; students with a modicum of genetic knowledge can appreciate how natural selection might work on the extended genotype to increase what Hamilton called inclusive fitness via the process dubbed 'kin selection' (Maynard Smith 1964).

Hamilton's second paper outlined an application of inclusive fitness for the social hymenoptera. Throughout the order Hymenoptera, females develop from fertilized eggs and males from unfertilized eggs. Hamilton explicated a cascade of relatedness oddities that ensue from haplodiploid sex determination. For example, a male derives all his genes from his mother and thus $r_{\text{son–mother}} = 1$; however, the mother queen gives half her genes to her son through meiosis and thus $r_{\text{mother–son}} = $ one-half. Most striking, sisters share three quarters of their genes with each other but only half with their potential offspring, thereby making sterility a good strategy for getting copies of genes into the next generation—because $rb > c$ is relatively easily satisfied.

The ensuing 45 years of research inspired by Hamilton's papers have been extraordinarily fruitful, giving rise to subdisciplines such as kin recognition and levels of selection theory. Yet the central issue of Darwin's special difficulty—the origin of eusociality—remains an area of active research today. There is at present no consensus on how the three traits that define eusociality (reproductive division of labour, overlapping generations and sterile workers; Wilson 1971) arose across disparate taxa.

Table 1. Characteristics of eusocial taxa.

taxon	sex determination	type of development	nesting habits	worker characteristics	food source
Hymenoptera (ants, bees and wasps)	haplodiploid	holometabolous	constructed or excavated	female only, adults	outside the nest
termites	diplodiploid	hemimetabolous	constructed or excavated	both sexes, immatures and adults	inside the nest
aphids	diplodiploid	hemimetabolous	induced	both sexes, immatures	inside the nest
thrips	haplodiploid	hemimetabolous	induced	both sexes, immatures	inside the nest
snapping shrimp	diplodiploid	post-larval juveniles resemble adults and are workers	excavated	both sexes, immatures	inside the nest
naked mole rats	diplodiploid	juveniles resemble adults and can work	excavated	both sexes, immatures and adults	inside the nest

Hamilton's second paper generated the 'haplodiploidy hypothesis' that haplodiploid sex determination predisposes lineages to eusociality due to relatedness coefficients that confer an advantage to female sterility. The appeal of his formulation is immediate and obvious: the relatedness coefficients predict not only sterility of females, but also lack of sterile castes among males (since they are related to their offspring by 1 but to siblings by at most one-half). A burgeoning interest in the evolution of eusociality was accelerated with the appearance of Trivers and Hare's landmark paper (1976) that linked Hamiltonian inclusive fitness with parent–offspring conflict (Trivers 1974). Trivers and Hare pointed out that coefficients of relatedness can increase a worker's inclusive fitness only if the sex ratio of fertile females to males becomes female biased (with an equal sex ratio, the advantage of the increased relatedness to sisters, three-quarters, is exactly counterbalanced by their reduced relatedness to brothers, one-quarter). Trivers and Hare predicted that the operation of kin selection within eusocial colonies could best be studied by examining the conflict of interest between the workers who rear the brood (and are best served by a 3 : 1 investment biased towards sisters) and the queen who lays the eggs (whose inclusive fitness is maximized by a Fisherian 1 : 1 sex ratio). Their analysis of existing data gave a strong indication that, in fact, sex ratios within hymenopteran societies reflect that conflict.

Together, the Hamilton and Trivers–Hare papers generated an enormous amount of research on conflict within social insects and other systems (cf. Crozier & Pamilo 1996). Indeed, the prediction of such conflicts is considered a more fertile outcome of Hamilton's papers than the literature on cooperation (Queller & Strassmann 1998). Genetic conflicts-of-interest theory has illuminated sociality in unexpected contexts, including the behaviour of slime moulds that form chimeric fruiting bodies and social bacteria that form biofilms. Predictions generated from consideration of relatedness among social interactants have included options for the evolution of cheating and retaliation, honest signalling and partitioning of reproduction.

Most certainly, Hamilton's solution of Darwin's 'one special difficulty' has proved fertile. However, that begs the question of whether Hamilton was in fact right. Are the coefficients of relatedness inherent

in haplodiploidy a sufficient explanation for the evolution of neuters? Eusociality has evolved independently multiple times (table 1), and haplodiploid sex determination is not universal. Even among haplodiploid species, most are solitary (sawflies, parasitic wasps, solitary bees and most thrips) and others show a form of sociality that falls short of eusociality. All other groups have diplodiploid sex determination (table 1): eusociality in termites, aphids, naked mole rats and snapping shrimp is difficult to explain via coefficients of relatedness. Therefore, haplodiploidy is neither a necessary nor a sufficient condition for the evolution of eusociality.

The haplodiploidy hypothesis is incomplete because it treats just one of the three variables in Hamilton's rule. In addition to r, Hamilton's rule includes c and b. The costs and benefits associated with any altruistic trait must depend on the local environment, and thus are inherently ecological. There is no question about the dominance of coefficients of relatedness, r, in the literature on kin selection: we have many estimates for r within social groups but estimates for b and c are rare.

I offer two explanations for the primacy of r-values in the literature on kin selection. First, a focus on relatedness has provided a rich research agenda for studying both cooperation and conflict. By examining situations in which r varies within a reasonably constant ecological background (thus holding b and c relatively constant), scientists have been able to show repeatedly that variation in r predicts variation in an output variable that reflects conflict or cooperation. For example, within hymenopteran societies, worker inclusive fitness is enhanced via males produced by fertile sisters ($r=$ three-eighths) rather than those produced by their mothers ($r=$ one-quarter)—if the queen has mated exactly once. Worker policing, whereby workers selectively destroy eggs laid by their worker sisters, is predicted when queens mate two or more times (Ratnieks 1988), and clever experiments have verified that prediction. Similarly, the predicted outcome of queen–worker conflict can depend on queen mating frequency, worker laying, etc., and numerous studies have borne out those predictions in the field. Clearly, analysis of r and its covariates has proved a productive research agenda.

A second reason for an over-focus on coefficients of relatedness is they are easy to estimate. Good

algorithms and a proliferation of molecular markers allow calculation of r-values in short order, and those values can be compared across colonies, populations and taxa. By contrast, estimating costs and benefits of *any* trait, including altruism, requires concentrated ecological work. Understanding ecological context for a focal species takes a combination of good natural history and experimentation, which themselves are time-intensive (Hunt 2007). Furthermore, there is precious little universality in ecology; a hard-won explanation for one population or species may not offer explanatory power for a second. Science far prefers generality to unique solutions, yet for the operation of kin selection, we must expect different explanations in different ecological contexts. Given the returns on investment and generality of results from r-focused research, it is not surprising that b- or c-focused research is under-represented in the kin selection literature.

The imbalance in our understanding of the three variables in Hamilton's rule fuels a simmering debate in the literature about the primacy of kin selection as an explanation for the evolution of eusociality. That debate takes two forms. The first objection is raised for the reason stated above—overemphasis on relatedness coefficients to the exclusion of costs and benefits (Hunt 2007). With considerably more emphasis on c and b, this objection can be overcome. The second objection rejects kin selection altogether in favour of competing hypotheses for the evolution of altruism. What are the alternatives proposed to Hamiltonian kin selection for the evolution of eusociality, and how successful are they? Early alternatives proposed (such as parental manipulation) can be subsumed into a kin selection framework, leaving a form of group selection as the primary mechanism still under debate. Selection on groups can override countervailing selection on individuals (indeed, that is the primary mechanism for the major transitions described by Maynard Smith & Szathmary (1995)), but the scenarios specifically proposed for the evolution of altruism (Wilson 2005) also fit within a kin selection framework (Lehmann *et al*. 2007; Crozier 2008).

At present then, we have no viable general alternatives to Hamiltonian kin selection for the origin or proliferation of eusociality. Our overemphasis on r-values has led the field down several blind alleys (e.g. fruitless searching for a mechanism to elevate coefficients of relatedness in diplodiploid species). We now accept that eusociality in diplodiploid species must depend on the relative costs to workers of being sterile as well as the benefits of that sterility for their fertile nest-mates. Furthermore, measurements of b and c are likely to yield different scenarios for different evolutionary origins.

Here I suggest some promising research agendas. The major groups exhibiting eusociality are shown in table 1, along with salient features of their biology. A crucial distinction is that hymenopteran societies have holometabolous development while other insect taxa have hemimetabolous development. This distinction provides very different options for division of labour within societies. Among ants, bees and wasps, larvae and pupae are altricial and can do no active work; only adults can forage, tend the brood and clean the nest. By contrast, nymphs of aphids, thrips and termites resemble adults morphologically and can perform many tasks essential to social cohesion. Brood care workers, cleaners and even soldiers can be immature forms that retain the developmental plasticity to become reproductive themselves. This striking difference in developmental pattern across taxa surely has consequences for calculation of b and c in Hamilton's rule, yet developmental options have largely been ignored by advocates of kin selection (Hunt 2007).

A second important distinction involves population density and nest structure within which societies function, considered key to determining b and c (Korb & Heinze 2004; Hunt 2007). The hymenopteran eusocial insects build nests from which they venture out to find resources, whereas the other taxa live on or inside their food: aphids and thrips live within the galls produced by their host plants, while termites excavate galleries in wood; snapping shrimps live within their sponge hosts; and naked mole rats live in subterranean tunnels, foraging on roots that grow through the roof. Remaining within a fortress that provides food produces a premium on resource defence and hygiene, whereas the open system of species that forage externally requires enhanced communication and defence strategies for individuals. Again, the import of these fundamental differences for the b and c variables in Hamilton's rule is obvious.

The task ahead, then, is to fully incorporate the costs and benefits of evolutionary options into our analysis of the multiple origins of eusociality. While research driven by variable values of r will continue to produce important insights, a comprehensive solution to Darwin's 'one special difficulty' awaits integration of those values with the overridingly important costs to altruists and benefits to recipients.

Despite disagreements about the relative importance of coefficients of relatedness versus costs and benefits of sociality, there is abundant evidence that 'selection on the family' is an important mechanism of eusocial evolution. The re-emergence of the superorganism concept explicitly identifies family groups as the unit of selection (Korb & Heinze 2004). Thus, Darwin's conjecture in *The origin of species* appears to be fundamentally correct, and Hamilton's calculus enlightens the explicit mechanisms underlying Darwin's conjecture. A resolution of the debate over origins of eusociality can only be achieved upon full explication of all three components of Hamilton's rule.

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