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Kin selection, genomics and caste-antagonistic pleiotropy

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Kin selection is a fundamentally important process that affects the evolution of social behaviours. The genomics revolution now provides the opportunity to test kin selection theory using genomic data. In this commentary, we discuss previous studies that explored the link between kin selection and patterns of variation within the genome. We then present a new theory aimed at understanding the evolution of genes involved in the development of social insects. Specifically, we investigate caste-antagonistic pleiotropy, which occurs when the phenotypes of distinct castes are optimized by different genotypes at a single locus. We find that caste-antagonistic pleiotropy leads to narrow regions where polymorphism can be maintained. Furthermore, multiple mating by queens reduces the region in which worker-favoured alleles fix, which suggests that multiple mating impedes worker caste evolution. We conclude by discussing ways to test these and other facets of kin selection using newly emerging genomic data.

1. William D. Hamilton and kin selection theory

William D. Hamilton revolutionized the study of sociality [1]. Arguably, Hamilton's most important work focused on the process of kin selection. Kin selection occurs when alleles for social behaviours are selected because these behaviours affect the fitness of relatives [2]. Fundamentally, the idea underlying kin selection is that an allele can be transmitted not only through personal reproduction, but also through the reproduction of kin.

Kin selection is responsible for the evolution of many of the remarkable actions displayed by social animals, such as the extreme helping behaviours displayed by social insects (figure 1) [3–4]. Kin selection also underlies the social actions of microbes, including the production of public goods [5]. Remarkably, even plants show evidence of kin-selected 'behaviours', such as competition through root growth, which may vary based on kinship [6]. Indeed, the evolution of many of the cooperative actions among entities at all levels of biological organization relied on kin selection-like processes [7]. Thus, kin selection represents a fundamentally important mechanism governing biological group formation.

2. Kin selection and molecular evolution

Kin selection theory has been primarily applied to explain the evolution of social behaviours at the phenotypic level. However, the signatures of kin selection should be seen at the genomic level as well. For example, Linksvayer & Wade [8] and Hall & Goodisman [9] determined the effects of kin selection on molecular evolution. They showed that the strength of kin selection, measured as the probability of fixation of a newly arising allele experiencing directional selection, could equal that of direct selection, but only when relatedness was high. As relatedness declined, so too did the strength of kin selection (figure 2a). Consequently, genes experiencing kin selection and direct selection may exhibit different rates of molecular evolution depending on the social system of the species in question.

Figure 1. The behaviours of social insects, such as (*a*) the honeybee (*Apis mellifera*), (*b*) the fire ant (*Solenopsis invicta*) and (*c*) the yellowjacket wasp (*Vespula maculifrons*) have been shaped extensively by the process of kin selection. Social insects often exhibit phenotypically distinct castes, the evolution of which may be hampered by caste-antagonistic pleiotropy, particularly in species where queens mate with multiple males such as *A. mellifera* and *V. maculifrons* (see text for details). (Online version in colour.)
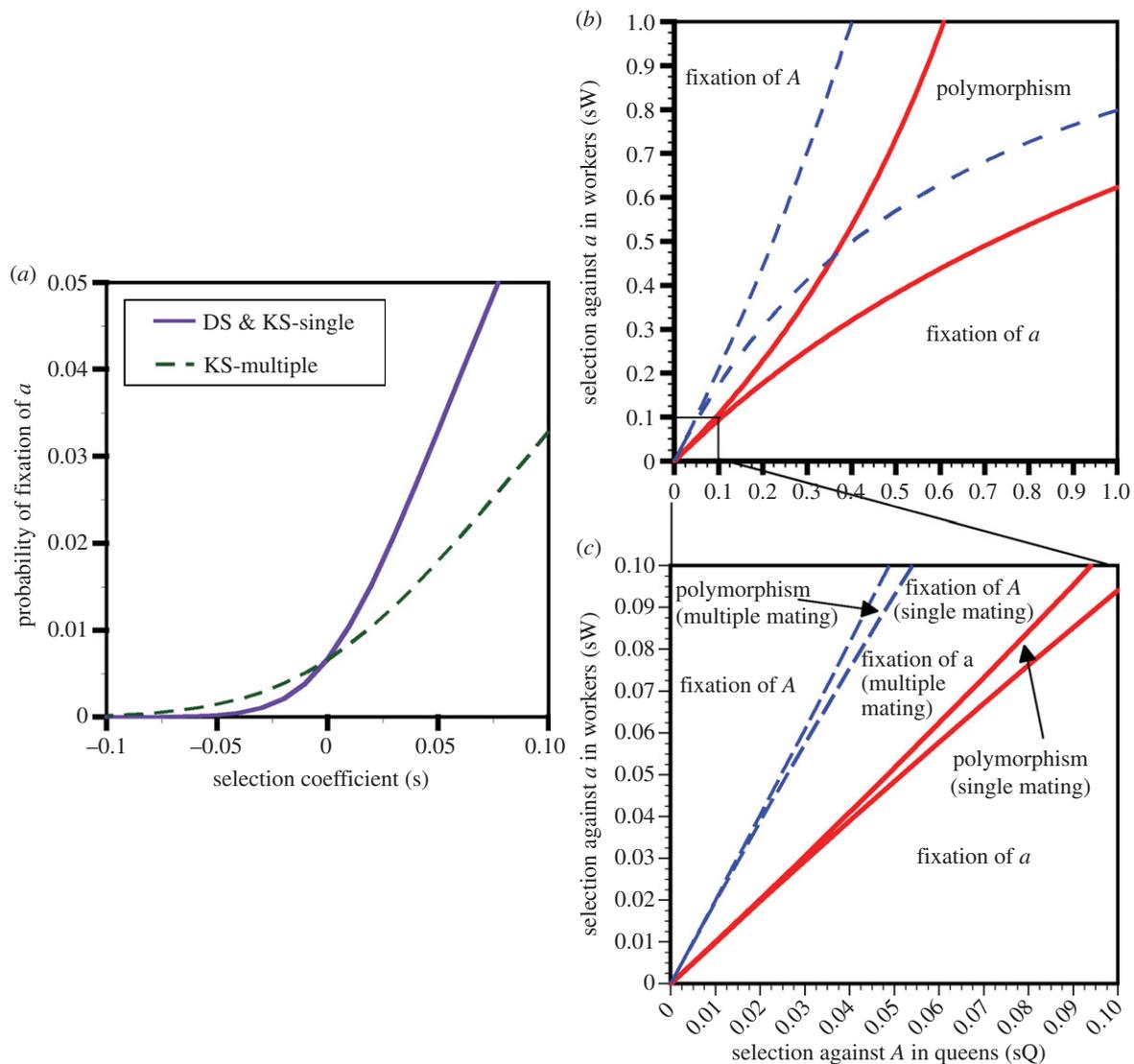

Figure 2. The outcome of selection for genes experiencing directional selection or caste-antagonistic selection. (*a*) The probability of fixation of newly arising additive alleles as a function of the strength of selection is identical under direct selection (DS) on queens or kin selection (KS) on workers when queens are singly mated (KS-single). However, when queens are multiply mated, beneficial alleles ($s > 0$) fix at lower rates and deleterious alleles ($s < 0$) fix at higher rates, when they are subjected to KS in workers (KS-multiple). (*b,c*) Regions in which antagonistic selection results in fixation of the queen-favoured *a* allele, the worker-favoured *A* allele or polymorphism. Solid lines and dashed lines delineate regions for singly and multiply mated queens, respectively. sQ and sW represent the strength of selection on performance against alleles *A* and *a* in queens and workers, respectively. In (*b*), all possible combinations of selection coefficients are shown, whereas panel (*c*) expands the region with more realistic, weaker selection. (Online version in colour.)

This prediction was tested using data in two social insects, the fire ant *Solenopsis invicta* and the honeybee *Apis mellifera* [9] (figure 1*a,b*). The queens of these two species mate different numbers of times; fire ant queens mate once, whereas honeybee queens mate multiply. Thus, the rates of evolution of queen- and worker-biased genes were predicted to be different in the honeybee but similar in the fire ant. Queen- and worker-biased genes did evolve at significantly

different rates in the honeybee and non-significantly different rates in the fire ant, consistent with expectations [9]. Thus, these studies began to link molecular and genome evolution with theoretical predictions of kin selection.

3. Caste-antagonistic pleiotropy in social genomes

Extending Hamilton's ideas to genome evolution requires the development of theory to predict how kin selection affects patterns of genetic variation. Of particular relevance for highly social species, such as social insects, is the case of antagonistic selection between castes [10], which occurs when distinct castes have different phenotypic optima for the same trait (cf. [11]). If this trait is controlled by the same gene(s) in both castes, then alleles favoured in one caste may be disfavoured in another. For example, wing muscle development may be beneficial for queen ants, which partake in mating flights, but is unlikely to be beneficial for worker ants, which do not fly. Thus, an allele that increases wing muscle development would potentially be subject to antagonistic selection across castes.

We determined the outcome of antagonistic selection arising from caste-antagonistic pleiotropy in haplodiploid social insects. Here, we present the special case where gene effects were additive at a single locus that affected caste 'performance', which in turn affected colony fitness (details in the electronic supplementary material). In this model, queens reproduced and were subject to direct selection, whereas workers were incapable of reproduction and subject exclusively to kin selection. We assumed that allele a was favoured in queens and allele A was favoured in workers. We then determined the combinations of selection coefficients in which either allele was fixed or both alleles were maintained as a polymorphism. Our interest was in understanding whether kin selection in workers was overwhelmed by direct selection acting in the opposite direction in queens, and whether caste-antagonistic pleiotropy was likely to lead to detectable genetic patterns within the genomes of social species.

We found that the region of the parameter space in which the queen-favoured allele fixed was the same size as the region in which the worker-favoured allele fixed, but only when queens mated once (figure 2b,c). By contrast, when queens mated with multiple males, the region of the parameter space in which the worker-favoured allele fixed was substantially smaller, and the region where the queen-favoured allele fixed was substantially larger (figure 2b,c). These differences arose because kin selection operating on workers was weaker than direct selection operating on queens when queens mated many times. Regardless, in both cases, the region of the parameter space allowing polymorphism was limited, especially when selection coefficients were realistically small (figure 2c).

4. Outlook: kin selection and social insect genomics

The revolution in social insect genomics [12–14] now allows rates of evolution and levels of polymorphism to be determined for all loci across multiple genomes. Thus, population genetic predictions arising from kin selection theory can be tested using newly emerging genomic data.

The model presented here makes three predictions. First, antagonistic selection across castes is unlikely to maintain polymorphism. Consequently, loci affecting traits in multiple castes are not expected to show high levels of polymorphism compared with other loci. Overall, this suggests that factors other than caste-antagonistic pleiotropy may be responsible for the maintenance of genetic polymorphism in social species.

Second, the model predicts that the evolution of antagonistic alleles that are favoured in workers, but disfavoured in queens, is impeded by multiple mating by queens. Such worker-beneficial alleles are strong candidates for alleles that would lead to distinct worker phenotypes. Consequently, these results suggest that phenotypic differentiation between the queen and worker castes, or within the worker caste, could have evolved more easily in species with singly mated queens, and that multiple mating hinders the evolution of caste differences.

Interestingly, currently available empirical data suggest that hymenopteran social insects that have genetically diverse colonies (e.g. are headed by multiply mated queens) have more phenotypically diverse workers [15]. If phenotypic differentiation in workers is due to selection in workers, then available data are inconsistent with our theoretical expectations, suggesting that caste-antagonistic pleiotropy is not a pervasive force. However, caste-antagonistic pleiotropy may have been important in the early evolution of sociality, when castes were first evolving and gene expression patterns in proto-queens and workers were similar. Subsequently, caste-antagonistic pleiotropy could have been resolved through the evolution of differential expression of genes between castes [16–19], allowing worker phenotypic differences to result from genes under selection (e.g. expressed) in workers only.

Third, our model predicts that adaptive evolution of genes that function in both queens and workers is more likely to be due to fixation of alleles that give queen-favoured phenotypes in species with multiply mated queens. By contrast, adaptive alleles are expected to be just as likely to give worker-favoured as queen-favoured phenotypes in species with singly mated queens. If adaptive evolution in social species is driven primarily by selection on performance of workers, then genes that function in both queens and workers should show higher rates of adaptive evolution in species with singly mated, rather than multiply mated, queens. Conversely, if adaptive evolution is driven by selection on queen performance, the opposite pattern is predicted. Thus, the patterns of molecular evolution may give insight into whether selection acts primarily on worker or queen performance.

In conclusion, models for interpreting genomic data have great potential for testing kin selection theory by determining how social evolution affects molecular evolution (e.g. [20–27]). Moreover, these investigations provide further inspiration for the development of new theory aimed at generating predictions regarding how genes should evolve under direct and kin selection. With several large-scale sequencing projects in progress, the genomes of social animals offer a natural playground for data and theory to come together in testing kin selection theory and providing insight into the evolution of social behaviours.

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