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Social wasps as models to study the major evolutionary transition to superorganismality

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The major evolutionary transition to superorganismality has taken place several times in the insects. Although there has been much consideration of the ultimate evolutionary explanations for superorganismality, we know relatively little about what proximate mechanisms constrain or promote this major transition. Here, we propose that Vespid wasps represent an understudied, but potentially very useful, model system for studying the mechanisms underpinning superorganismality. We highlight how there is an abundance of behavioural data for many wasp species, confirming their utility in studies of social evolution; however, there is a sparsity of genomic data from which we can test proximate and ultimate hypotheses on this major evolutionary transition.

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Introduction

Life on earth has been shaped by a series of rare but important events termed major evolutionary transitions [1]. The hallmark of a major transition is a change in the way that biological information is stored and transmitted, leading to a new level of biological organisation in life's hierarchy. Major transitions are predicted to develop in a series of stages under specific types of ecological conditions [2,3] but we know little about the mechanisms by which they occur. In recent years sociogenomics (the study of sociality in molecular terms [4]) has transformed our understanding of the molecular basis of sociality, raising the likelihood that we will soon be able to understand the kinds of molecular mechanisms that promote or constrain major transitions.

The evolution of superorganismality (Box 1) among some social hymenopteran (bees, wasps and ants) insect lineages is one of the most striking examples of a major transition [5]. Whilst there has been much empirical research on insect species that have already undergone the major transition to superorganismality (e.g. the honeybee *Apis mellifera*, the fire ant *Solenopsis invicta*), we still know relatively little about what happens at the molecular level during the earliest and intermediate stages of a major transition [6,7]. Here, we make the case that Vespid wasps (Box 1) provide unique opportunities for testing hypotheses about the molecular mechanisms underlying the transitional stages in a major evolutionary transition.

The importance of studying the early and intermediate stages of the major transition to superorganismality

A major evolutionary transition is predicted to occur in several stages [2,3]. Firstly, natural selection must favour lower-level entities to come together to form a cooperative group. Secondly, a cooperative group must be irreversibly transformed into a cohesive whole that can be considered a new higher-level entity or 'individual'. The process of a major transition therefore marks important changes in the level at which natural selection predominantly acts, and the types of adaptations it is predicted to give rise to.

Traditionally, most research on major transitions has focused on identifying the ultimate evolutionary explanations for their origin [2,3]; in recent years there have been a growing number of empirical studies attempting to understand their underlying proximate mechanisms [6,8••]. To date, these empirical studies in insects have, however, tended to focus on species which have already undergone a major transition to superorganismality, for example [9,10,11••]. A potential limitation of these studies is that the kinds of adaptations that occur before the transition are unlikely to be the same as those that happen after the transition [12]. Ancestral traits that were present before the major transition to superorganismality may have been lost, altered, or masked by the emergence of novel traits once a major transition has occurred. It may be the case, therefore, that we need to look to species exhibiting characteristics of being at early or intermediate stages in the evolution of superorganismality, rather than solely superorganisms themselves, if our goal is to understand the mechanistic details underlying this major transition. Figure 1 highlights how

Box 1 Glossary of terms

Superorganism: A concept proposed by Wheeler [5] to suggest that some social insect colonies represent an entirely new type of higher-level organism. The idea behind this is that irreversible caste differentiation in social insects is akin to the germline and soma split among cells of multicellular organisms. See [12] for full review.

Vespidae: The family Vespidae (order: Hymenoptera, suborder: Aculeata, superfamily: Vespoidea) contains the subfamilies Vespinae, Polistinae, Stenogastrinae, Eumeninae and Masarinae [13,14]. Of these subfamilies, only the Vespinae, Polistinae and Stenogastrinae exhibit sociality.

Inclusive fitness theory: A framework focussing on how the reproductive interests of individuals depend both upon the impact of their behaviour on their own reproductive success, (direct fitness effects) and on that of individuals to whom they are related (indirect fitness effects) [29,65]. Often used to explain adaptations to social environments [28,66].

proximate mechanisms and the stages of the transition to eusociality may evolve. It is important, however, to stress that our suggestion here is not that species exhibiting these characteristics are necessarily on an evolutionary trajectory towards greater complexity, but rather that these species might provide important clues about the mechanisms that were present in the ancestors of modern day superorganisms.

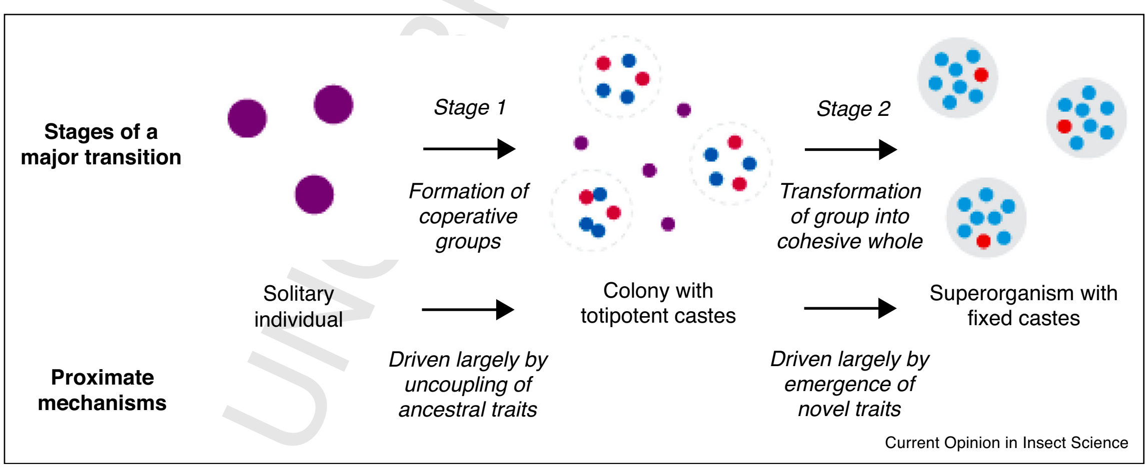
Vespid wasps as a model system

Here we discuss how the Vespidae provide an excellent phylogenetic context for testing hypotheses about the major transition to superorganismality. Wasps are a relatively understudied group, but they play important ecological roles and exhibit a remarkable diversity in social complexity, from species with the simplest of social groups (where all individuals can reproduce, but some act as helpers; for example, *Polistes* paper wasps) to species with the most complex societies in which the colony can be considered an individual (super)organism in its own right (where division of labour is fixed during development, irreversibly; for example, *Vespula* yellow-jacket wasps) [13].

Crucially, new genetic data has confirmed that sociality has evolved twice in the Vespidae; once in the Stenogastrinae and once in the sister group Vespinae + Polistinae [14,15••]. This recent revelation brings the Vespidae into sharp focus as a model group for understanding the evolution of sociality as they provide two independent evolutionary events of the same set of innovations [13,16]. Moreover, there are many species from both lineages, representing different stages, whose ecology and behaviour have been well studied. These species and the innovations they display provide exciting opportunities for future sociogenomic research, and the potential to help reconcile ultimate and proximate explanations for the major evolutionary transition to superorganismality.

In Table 1 we provide examples of social behaviours in Vespidae that may represent important adaptations in the early and intermediate stages of the major transition to superorganismality. We highlight how little is known about the underlying molecular mechanisms of these behaviours.

Figure 1



The two key stages in the major transition to superorganismality (following West *et al.* [2,28]) are likely to be associated with shifts in the underlying proximate molecular mechanisms. Stage 1 represents the shift from solitary to group living, where group members retain the full behavioural and physiological totipotency of their solitary ancestor; this stage is predicted to be driven by the uncoupling of conserved molecular processes associated with ancestral traits and rearrangement of ancestral genes and gene networks. Stage 2 represents the shift from totipotent group membership to superorganismality, whereby group members have reduced totipotency, emergence of committed reproductive and non-reproductive castes and thus the group functions as a new level of individuality; the novel phenotpyic traits that emerge having passed through this stage are likely to be underpinned by novel molecular processes (e.g. *de novo* genes, neofunctionalisation).

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