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

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Abstract

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.

Box 1: Glossary of terms

Superorganism: A concept proposed by Wheeler [1] 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 [2] for full review.

Vespidae: The family Vespidae (order: Hymenoptera, suborder: Aculeata, superfamily: Vespoidea) contains the subfamilies Vespinae, Polistinae, Stenogastrinae, Eumeninae and Masarinae [3,4]. 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) [5,6]. Often used to explain adaptations to social environments [7,8].

Introduction

Life on earth has been shaped by a series of rare but important events termed major evolutionary transitions [9]. 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 organization in life's hierarchy. Major transitions are predicted to develop in a series of stages under specific types of ecological conditions [10,11] but we know little about the mechanisms by which they occur. In recent years sociogenomics (the study of sociality in molecular terms [12]) 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 [1]. 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 [13,14]. 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 [10,11]. 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 [10,11]; in recent years there have been a growing number of empirical studies attempting to understand their underlying proximate mechanisms [13,15]. To date, these empirical studies in insects have, however, tended to focus on species which have already undergone a major transition to superorganismality, e.g. [16–18]. 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 [2]. 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 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; e.g. *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; e.g. *Vespula* yellow-jacket wasps) [4].

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 [3,19]. 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 [4,20]. 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.

Social innovations in Vespid wasps

Evolution of group living from a solitary, ancestral state

At the very early stages in social evolution is the shift of individuals coming together to form groups [10,11]. From the highly plastic, solitary phenotype, in which individuals display the full repertoire of behavioural traits, the first conversion to sociality involves a decoupling of behaviours between the reproductive ('queens') and those that delay or abstain from reproduction altogether ('workers') [21] Facultatively social species, such as members of the Stenogastrinae [22,23], are excellent models for studying this innovation as all individuals have the ability to initiate their own nest and become the reproductive. There is, however, usually a single dominant egg-layer in these societies [24,25]; most female offspring choose to remain on their natal nest as adults, as non-egg-laying helpers [22] although they retain the capacity to develop their ovaries throughout their life, and thus the option to disperse and found a nest alone. This reproductive strategy is likely to have arisen due to ecological constraints on independent founding [24], and the high fitness payoffs from indirect reproduction [24,25]. An outstanding question (which has been broached in halictid bees [26]), is what molecular processes are required for the shift from solitary living to facultative group living? Most simply, differences in the timing of expression of the molecular processes regulating the reproductive and provisioning subsets of the solitary phenotype could explain this innovation; alternatively modification in the use of genes or gene networks may be required [12–15] (Figure 1).

Evolution of altruistic behaviour from ancestral, selfish behaviour

From an ultimate perspective, the evolution into group living involves a shift from direct to indirect fitness for non-reproductive group members (Box 1). This shift is best studied in the very simple social societies, as exhibited by the Stenogastrinae [24,27] and some Polistinae [28–30], where helpers can inherit the nest when the dominant females dies. When this happens, the inclusive fitness interests of an individual changes from indirect (when they refrain from reproducing and engage in the cooperative brood care of siblings) to direct (when they produce their own offspring). Who becomes queen during this process is determined by a reproductive hierarchy which can either be age- [29,31], or dominance-based [29]. Individuals who never get the opportunity to inherit the nest are said to behave ‘altruistically’ [8], since their inclusive fitness interests can only be met through indirect fitness benefits. Hamilton [6] explained how natural selection can lead to the evolution of such behaviours (reviewed in [8]), but we continue to know very little about their molecular basis [12]. The search for genes encoding altruistic behaviours has been attempted in several species, including the honeybee, ants and termites (reviewed in [32]). In the context of understanding the processes by which the major transition to superorganismality arises, however, we need to look for evidence of a molecular basis of altruism in the first stages of group living, where altruism first evolves.

Loss of reproductive plasticity

One of the hallmarks of the major transition to superorganismality is the loss of plasticity with respect to reproduction [2]; specifically, this is the evolution of a commitment to reproductive potency (as a queen) or reproductive sterility (as a worker). In the simplest social groups, individuals retain both behavioural totipotency, and reproductive potential. The interesting question, therefore, is when, why and how a loss of reproductive plasticity arises. During the major transition, the point at which plasticity is lost (or ‘commitment’ [2]) is pushed back in the developmental time of individuals, from adulthood (e.g. in species that show a loss of reproductive potential *during* their adult life, as in some Polistinae [33,34]) to brood development (e.g. in species with pre-imaginal caste determination, effective sterility is committed during larval development in the Vespinae wasps). To understand the process by which plasticity is lost at the outset of this innovation, species which exhibit a loss in reproductive potential within adult life are potentially important models. Documentation of such losses are rare as they require behavioural experiments to test of reproductive capacity; however, there is evidence of this in *Metapolybia* sp. and also *Polistes canadensis,* where replacement queens are drawn from the youngest females on the nest, and where experiments show that females are incapable of taking advantage of egg-laying opportunities as they age [28,34]. This loss of plasticity, and of reproductive potential, marks the mechanistic basis for the initial shift from direct to indirect fitness (Box 1), and transcriptomic data shows that differences between queens and workers significantly increase at this stage (Taylor et al. unpublished). Analyses of the molecular processes that regulate this loss of plasticity during adulthood would provide insights into the first stages of this critical innovation. These changes may involve epigenetic processes that impose limitations on the reversibility in the expression of molecular pathways [35].

Pre-imaginal caste differences

The most recognisable, and most studied, shift in sociality is the so-called ‘point of no return’ at which true superorganismality emerges [2]; distinct morphological castes are exhibited in species living in complex societies of wasps, such as some Polistinae [36–38] and Vespinae [39]. This innovation marks the commitment of individuals during development to a fixed reproductive or non-reproductive role, where ultimate investments in direct or indirect fitness are sealed by mechanistic processes (Figure 1). The nutritional basis of caste-determination has been studied in species across all levels of social complexity (reviewed in [40]), with the differential feeding of queens and workers causing significant molecular changes in gene expression [41], and the epigenetic mechanisms that regulate gene expression [17,42]. While the evolution of pre-imaginal caste differentiation is well studied in the bees and ants, a long-standing question is whether molecular processes underpinning fixed caste commitment are the same across social lineages and ecological life-histories [13,43]. Remarkably, we lack any large-scale studies on the molecular basis of pre-imaginal caste differentiation in the wasps. The Vespines are the obvious model clade for this analysis, where worker reproductive potential is limited by the inability to mate and strong differences in morphology, physiology and behaviour. The Polistinae are less well studied, but some species show evidence of allometric caste differentiation (e.g. *Agelaia* and *Brachygastra* [37,38]), suggesting pre-imaginal commitment of individuals to specific social roles. The gradient of pre-imaginal caste differentiation in the Polistines therefore may provide valuable insights into the *process* of this key innovation.

Mutual dependence in the life cycle - Evolution of swarm founding behaviour

Independent nest founding is the ancestral state of social insects. This requires significant levels of behavioural plasticity from the founding queen, as she is required to found, build and maintain a nest, and provision her brood. A key alteration once superorganismality has evolved, therefore, is the reduced ability by reproductive females to independently found a nest, and instead evolve mutual dependency on group founding (with a cohort of workers or other potential reproductives), as a swarm. Swam-founding is a key trait in many bee species (e.g. honeybees; stingless bees) where a single queen leaves the natal nest to found a new nest, accompanied by a group of workers. In ants another form of reduction in behavioural plasticity is found in the claustrally-founding queens, who must build a nest, but then use their own body's resources to raise the first brood, thus precluding the need to provision. In the wasps, swarm-founding is a key behavioural trait of the Epiponini in the Polistinae [4,44,45]. In multi-queen colonies, swarm founding has the benefit of maintaining high relatedness through cyclical oligyny, whereby only a single queen is present at the time of sexual reproduction [46]. Swarm founding is obligatory in these species: the queens have lost the ancestral behavioural repertoire required to successfully initiate their own nest. This behaviour may therefore have evolved as: a) a novel trait to maintain high relatedness within the colony, and b) a loss of ancestral plasticity and complete co-dependence of queen and worker castes. This trait may therefore be underlain by both novel genes for swarm-founding behaviour (as seen in *Apis* spp. [16]) (Figure 1) and regulation by the epigenetic processes which limit behavioural plasticity [35].

Mutual dependence in the life cycle - Reproductive control

Reproductive control is determined through queen-worker communication across all levels of social complexity (see [47,48] for reviews). It differs, however, significantly with group size, and by extension, social complexity; in small, simple societies, queens retain dominance through aggressive interactions and visual cues, while in large, complex societies, suppression of worker reproduction is controlled by queen pheromones [49–52]. The hydrocarbons which act as a sterility-inducing queen pheromone are highly conserved [53]. This same pheromone has been found to also signal egg maternity, enabling workers to destroy worker-laid eggs in a selective manner (worker policing) [54]. Worker policing occurs in species with multiply-mated queens because a worker force that is derived from two or more fathers is more closely related (on average) to the male offspring of their mother (brothers) than they are to the average worker-laid male [55]; worker policing can also evolve in singly-mated species if it increases colony efficiency [49,55]. Multiple mating and worker policing has evolved in many species of bees and ants [56,57]. To date, however, there have been no genomic studies examining the molecular processes by which these innovations have evolved.

Among the wasps, the Vespinae are the only group known to be multiply-mated: within this clade, there are species that exhibit low (e.g. *Vespa crabro* [58]) and high (e.g. *Vespula* sp. [59]) levels of multiple mating, and associated levels of worker policing. This group is therefore an excellent model system for studying the molecular processes that regulate the innovations of multiple mating and worker policing.

Conclusions

The last few years have heralded significant theoretical and empirical progress in understanding the evolution of superorganismality [2,60], yet we still lack information on the mechanisms which precede the major transition. Here we summarise examples of life-history innovations, identified from behavioural studies, at which we would expect genomic changes (e.g. shifts in gene transcription networks; rewiring of genes; *de novo* evolution of genomic novelty) to be important; we put forward the Vespid wasps as a key group that would facilitate a molecular dissection of the process in a major evolutionary transition. These insights are likely to be of general relevance to social evolution at other levels of biological organisation, e.g. the evolution of multi-cellularity.

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