Social insects: from selfish genes to self organisation and beyond

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Selfish gene and self-organisation approaches have revolutionised the study of social insects and have provided unparalleled insights into the highly sophisticated nature of insect social evolution. Here, we briefly review the core programs and interfaces with communication and recognition studies that characterise these fields today, and offer an interdisciplinary future perspective for the study of social insect evolutionary biology.

Introduction

Societies of ants, bees, wasps and termites (Figure 1) dominate many terrestrial ecosystems [1]. Their evolutionary and ecological success is based upon the regulation of internal conflicts (e.g. [2,3]), control of diseases (e.g. [4,5]) and individual skills and collective intelligence in resource acquisition, nest building and defence (e.g. [6,7]). Although we use similar success criteria when evaluating our own societies, these biological insights are relatively recent. There was no concept of reproductive conflict until Hamilton's inclusive fitness theory and its early elaborations by Trivers during the 1960s and 1970s [8,9]. Likewise, until the pioneering work on self organisation by Prigogine and Deneubourg and their colleagues during the 1970s [6], there were few ideas of how, in the absence of leadership, the individual capacities of small insect brains and bodies could generate such adaptive complexity.

With few exceptions, neither the insights on gene-level reproductive conflict, nor the concepts of self organisation became established in social insect research before the mid 1980s, after which these fields progressed independently from one another. To explain the historical inevitability of this segregation, we revisit at the beginning of each section a seminal symposium contribution that William D. Hamilton presented almost exactly 20 years ago. The published version [10] was to become highly influential because it evaluated the major constraints for advanced social evolution: individuality and the ensuing difficulties of communication, recognition of cheats and pressure from coevolving parasites. However, the same Hamiltonian reproductive conflict perspective that enabled these insights to develop into research programs precluded interactions with self-organisation approaches that emphasised non-reproductive aspects of social organisation that were unconstrained by reproductive conflict, for example, foraging and nest building.

First, we emphasise that selfish gene approaches not only identify issues of conflict in insect societies, but also address evolutionarily stable conflict resolution. We go on to show that self organisation in insect societies is vastly superior to the self organisation of mindless macromolecules, because self-organised feedback loops interact with brain-controlled behaviour to form complex adaptive syndromes. We then elaborate how communication and disease pressure interact with the different levels of selection that affect social evolution. We argue that joint research interests in optimisation principles and information constraints are now providing the first signs of mutual inspiration between selfish gene and self-organisation approaches, with both sides interfacing with neurobiology, communication systems and genomics. We then give our more general views on the integrated future of social insect research.

Kinship and reproductive conflicts

In the year of the first issue of TREE, Hamilton [10] wrote: ‘Organisations built from individuals differ from organisations built from cells (i.e. organisms) because being a collection of individuals normally implies relatedness of less than one’. Less-than-one relatedness inevitably leads to potential conflict over reproductive allocation and inclusive fitness theory had already provided the basic tools to analyse this [8,9]. Hamilton’s rule \((rb > c)\) asserts that a seemingly altruistic gene will spread when its benefit to the recipient in additional offspring \((b)\) multiplied by the relatedness of the recipient to the donor \((r)\) exceeds the cost of helping in foregone offspring \((c)\) [8]. The rule became the dominant theorem for the study of social evolution, particularly after it had been generalised as a selection equation with an explicit within-group and between-group term, which reconciled the kin-selection and group-selection models of social evolution as being fully equivalent (e.g. [11–13]). This implies that, although reproductive conflicts within colonies are driven by differences in relatedness, they can have colony-level costs that select against the cues or behaviours that enable the conflicts to be expressed (e.g. [14]). The proper partitioning of levels of selection has thus been essential for understanding within-colony conflicts over resource allocation for reproduction (e.g. [15]).
societies, such as *Formica* ants (e.g. [25]), and the queen in species with small colonies, such as bumblebees *Bombus terrestris* (e.g. [26], but see [27]). When established, these power asymmetries help to impose harmony and generally incur fairly low colony-level costs. This is consistent with levels of selection theory [28], that is the notion that selection simultaneously operates at different levels such as genes, individuals and groups, which implies that major evolutionary transitions are likely only after lower-level conflicts have been reduced (e.g. [14,15,29,30] and no longer jeopardise the benefits of higher-level cooperation and the establishment of super-organismic properties [1,7].

The third reproductive conflict, nepotism, is relatively more damaging for societies as it serves the selfish interests of smaller factions of close kin, provided that they can recognise each other (e.g. [21]). However, the genetic labels on which such accurate individual recognition depends tend to be removed by both individual and colony-level selection [21,31,32]. This implies that insect societies should become immune towards nepotism, unless new nepotistic lineages with distinct labels arise frequently. If nepotism is doomed to remain rare, similar to forms of interspecific social parasitism such as slave raiding (e.g. [33]), this might therefore be related to its epidemic disease-like cycling properties, in contrast to worker–queen conflicts, which can be resolved by stable power asymmetries.

Our understanding of reproductive conflicts between co-breeding queens has been enhanced by reproductive skew models (e.g. [34]). However, explicit tests of these models in social insects are still sparse (e.g. [35,36]) and partly inconclusive, because model predictions depend upon untested assumptions about kin recognition, survival during migration and the ability to coerce nest mates [37]. Other novel theories that were developed and tested concern stable dominance hierarchies (e.g. [38,39]) and reproductive conflict between farming ants and termites and their respective fungal symbionts (e.g. [40,41]). Finally, a recent focus has been reproductive conflict over caste fate, which can be expressed in social insects such as stingless bees, where brood develops in sealed mass-provisioned cells (e.g. [42,43]).

Relatedness of less than one implies that even the most advanced insect societies suffer occasionally from the expression of reproductive conflict, which is likely to preclude the evolution of super-organismic properties in resource allocation for reproduction (e.g. [2,3,14,15,32]). As we will see in the next section, this is fundamentally different in issues of resource acquisition, nest building and collective defence.

**Self organisation: an opportunity arising from socially coherent individuality**

Hamilton [10] argued that individual intelligence might be an escape route from certain constraints of social evolution. He used an exclusively human perspective to arrive at a series of insightful and yet sometimes disheartening inferences, but did not dwell on the unique opportunities available to the social insects to evolve collective intelligence (e.g. [44]). The crucial insights were
waiting in the wings as the application of self organisation to social insects had barely begun during the mid 1980s [6]. Now it is clear that complex organisation does not require complex decision rules. Thus, although insect societies might indeed be hampered by individuality relative to metazoan bodies consisting of cloned cells, this constraint appears to be alleviated by the individuals having brains (e.g. [45,46]).

Self organisation implies that patterns of colony-level organisation emerge from multiple interactions among workers based on local information, without any overview at the colony level. Self-organisation theory thus hypothesises how insect societies can be organised from the bottom up by simple reiterated feedback loops. It explains how the ensuing integrated collectives can produce complex large-scale infrastructures without administrators to tell them what to do (e.g. [6,7]). Just like division of labour, the other major factor determining how insect societies organise work, self organisation should be underpinned with principles of optimality and tradeoffs for maximising performance across environments (e.g. [47–51]). Division of labour occurs when work is partitioned among specialists who are particularly efficient because of their physiology, morphology or learned skills. Although physical castes imply that division of labour is sometimes hard wired, many other aspects are driven by demand, similar to self-organised collective behaviour (e.g. [13,52]).

Early champions of self organisation in insect societies emphasised the simplicity of the local interaction rules compared with the complexity of the large-scale structures that they produced. Certain molecules are also able to self organise [7], but the efficiency of self organisation in social insects is greatly enhanced because worker brains can evaluate and integrate noisy information from multiple cues while moving around (e.g. [45,46,53,54]). For example, honey bee Apis mellifera workers can abstract a notion of similarity of foraging cues [55] and mentally map their environment [56]. Studies of house hunting in ants and honey bees [57,58] show that ant brains of ~1/10th the size of honey bee brains have similarly sophisticated decision-making abilities. Finally, it has recently been shown that self-organising procedures can combine with leadership in cohesively moving groups such as honey bee swarms (e.g. [59,60]).

Self-organising systems appear ideally suited to self repair given that they involve constant monitoring of the local environment and rapid response to change. It also appears that social insects use layer upon layer of 'backed-up' fail-safe procedures. Honey bee communication for far-away food sources depends on many more complementary cues than information derived just from waggle-dancing workers [56]. The same is true of Pharaoh’s ants Monomorium pharaonis, which use the branching angles of their foraging networks [61], in addition to other cues and signals, for orientation. Recent neurobiological studies of Cataglyphis desert ants [46] complement these insights by demonstrating that ant spatial memory is structured in a similar way to procedures in a computer program, as proposed for honey bees [45,56]. These developments are particularly interesting because gene expression studies now enable individual brain messenger RNA profiles to be correlated with naturally plastic social insect behaviour [62].

In contrast to many of the conflict issues addressed in the previous section, self organisation typically does not involve different levels of selection because its efficiency is subject only to colony-level selection. Most studies of self organisation have concentrated on resource acquisition (reviewed in [7,63]) and few looked at resource allocation. Those that investigated interactions between workers and brood (e.g. [64]) focused on patterns in the distribution of brood, but not on the actual provisioning of larvae. It will be interesting to determine whether self organisation has any role in allocation behaviour in insect societies. It might not if, for example, its evolution is barred by conflicts such as larvae being selected selfishly to beg for resources in excess of the amount that workers are prepared to provide.

Remaining challenges owing to individuality, informational constraints and coevolving diseases

Hamilton [10] discussed two major constraints on social evolution in societies of free-moving individuals. First, lack of information might arise when mobility makes the identity of neighbours unpredictable and disrupts communication about who should do what. Second, individual mobility necessitates open societies, which weakens collective defences against infectious diseases and social parasites. These considerations have promoted substantial empirical research programs and many novel insights.

The primary mode of social insect communication is chemical (e.g. [65]) although new spectacular examples of acoustic communication and visual recognition have also been discovered (e.g. [66,67]). Batteries of diverse exocrine glands are now known and their functions have been partly elucidated (e.g. [65]). One key focal area has been the study of cuticular hydrocarbon profiles of workers and queens (e.g. [68]). The information emanating from such profiles that social insects use to discriminate between nest mates and non-nest mates resembles a blurred barcode of relatively nonvolatile compounds. The substances involved are genetically and environmentally determined and constantly mixed into a more uniform colony odour blend (gestalt) [69]. Thus, although genetically mediated individual recognition is possible in small groups of Pachycondyla ant queens [70], mutual grooming and liquid food exchange tend to erase genetic cues in larger groups of social insects [69,71]. This implies that odour mutants that would enable nepotistic discrimination might be relatively ineffective right from the start.

A recent study of Formica wood ants [32] showed that the genetic component of worker cuticular hydrocarbon profiles is just about sufficient to enable the assessment of colony kin structure, serving the collective worker interest in sex-ratio biasing, but insufficient to enable nepotistic discrimination between full sisters and half sisters. This result is consistent with ongoing selection against selfish recognizable mutants that might ‘corrupt’ cues that would normally benefit the collective interest. However, none of this applies to group-selected information that is expected to always be as informative as possible.
Such unambiguously reliable information, often signalled by pheromones [65], is an essential condition for establishing the multiple and subtle feedback loops that enable self-organising properties to evolve in foraging, nest building and defense. We therefore expect that insect societies might generally combine corporate ignorance on potentially controversial issues of reproduction [32,71] with spectacular self-organised collective intelligence for tasks that do not involve conflict.

Neurobiological studies of the perception of context-specific social cues (e.g. [45,46,72]) will be needed to make further progress in testing explicit evolutionary hypotheses. This type of study should also facilitate communication among students of reproductive conflict and self organisation about joint interests in optimality principles and informational constraints. For example, a recent modelling study [50] showed that informational constraints might be such that recruitment of foragers is not always adaptive for the colony in spite of recruits being more likely to find food than would lone foragers. This inference is strikingly similar conceptually to male production or sex-ratio biasing not always being adaptive for workers in spite of a potentially higher gain in gene copies in the next generation [14].

Although others also pioneered the conceptual understanding of selection forces imposed by coevolving social insect parasites [73], it was Hamilton’s 1987 book chapter [10] that outlined the broadest innovative perspectives. Indeed, the evolutionary study of social insect parasites became a mature and independent field within a decade [4]. Genetic variation for disease resistance has now been documented in several social insects [74–77] and the slower spread of disease in genetically more diverse colonies therefore remains one of the leading hypotheses to explain multiple queen mating and the enhanced recombination rates of derived lineages of social insects (e.g. [78–81]). Insect societies might be threatened by both generalist and coevolved specialist diseases, which require fundamentally different defences. A good example occurs in Acromyrmex leaf-cutting ants, where metapleural gland secretions are used against general soil-borne pathogens, whereas symbiotic actinomycete bacteria target a coevolved fungal disease [82,83]. Future work will need to investigate whether disease impact is fundamentally different in annual social bees and wasps versus perennial ants and termites, and whether large societies necessarily have a higher disease load than do small societies [5,84].

### The next ten years of social insect evolutionary biology

We expect that the coming decade will bring significant progress in the following five areas: (i) with larger comparative data sets, it might be possible to condense the complexity of non-relatedness factors into a few key variables representing the ‘b’ and ‘c’ in Hamilton’s rule. This should enable a more integrated understanding of the interaction between kin selection and the expression of conflict on the one hand and life-history evolution, chemical communication, disease and ecological constraints on the other; (ii) genomics will attain a more prominent role as the sequenced genome of the honey bee (with other social insects to follow) will enable the identification of major genes involved in social organisation (e.g. [85,86]); (iii) further careful field and laboratory experiments, coupled with modelling, will continue to investigate the algorithms that social insects use to express their coordinated collective behaviour; (iv) more studies focused on the perception of information should clarify the impressive abilities and specific constraints of social insect brains and link these insights to issues of reproductive conflict and self organisation; and (v) there should be new and exciting discoveries in basic natural history and biodiversity, as DNA identification of pathogenic and mutualistic symbionts that have coevolved with social insects proceeds.

Collectively, the advanced eusocial insects are as well studied as other major invertebrate model systems (Figure 2) and we expect both academic and public interest in social insect biology to increase further, because these models enable insights that cannot be obtained by studying social vertebrates. In contrast to our own primate ancestors, all lineages of advanced eusocial insects achieved their evolutionary and ecological success with little or no influence from sexual selection (but see [87,88]) and cultural evolution. The thousands of species alive today represent many different ‘evolutionarily stable social strategies’, illustrating the robustness of insect

![Figure 2. The use of social insects as model organisms. Social insects have been prominent model organisms for all fields of biology, as appears from the percentage of papers about social insects relative to two other major animal model systems Drosophila and Caenorhabditis that were published by Science (dark-blue bars) and Nature (mid-blue bars) in the period 1992–2005. Most of these 113 social insect papers were about ecology, evolution and behaviour. The search was done on 6 February 2006 using the Zoological Record (Vol. 128–141; WebSIRS; http://www.biosis.org/) by combining search entries for ‘social insect’ (? to allow singular and plural to be recognized) and for the controlled keywords ‘Vespidae’, ‘Apidae’, ‘Formicidae’ and ‘Isopeta’, so that all publications on ants, social wasps, social bees and termites were covered, but without counting a publication more than once. The search could not be extended to years before 1992, because Apoidea was not available as an entry for these early years and Apoidea would have included too many non-social bees. A search of Google™ (http://www.google.dk) entering the same keywords (in quotes) followed by the (unquoted) words ecology evolution gave the number of hits shown by the light-blue bars. Comparable scores for birds and mammals were 2.84 and 1.72 million, respectively.](http://www.sciencejournal.com)
sociality against environmental stochasticity and unpredictable interactions with competitors, predators and diseases. Insect societies have had >100 million years to realise their advanced biological innovations, which include multiple forms of division of labour, advanced building capacities, long-term food storage, waste management and hygienic practices, effective collective defence, slave-raiding and other forms of social parasitism, policing and punishment of selfish individuals, and the domestication of fungal crops and homopteran livestock [1,13,16,47,52,89]. In comparison with the large complex societies of insects, our closest relatives, the chimpanzees, are merely modest tribes of, albeit relatively intelligent, hunter-gatherers. Only humans and social insects can build and manage large-scale societies according to complex economic decision rules.

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