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Sociality and communicative complexity: insights from the other insect societies

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Recognition and communication are essential processes, when it comes to interaction of organisms with their biotic environment. As especially social interactions are coordinated by communication, it has been predicted that social evolution drives communicative complexity. However, studies comparing olfactory signals or receptor repertoires of solitary and eusocial insects found only mixed evidence for the social complexity hypothesis. We present some possible explanations and especially argue that our current knowledge of intermediate levels of sociality is insufficient to fully test the hypothesis, for which a more balanced comparative dataset would be required. We illustrate with chosen examples how complex communication within the other insect societies can be: Many messages are not unique to eusocial insects. Studying the other insect societies will provide us with a more detailed picture of the link between social and communicative complexity.

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Introduction

The beauty and surprising complexity of animal communication has always fascinated both scientists and laypeople alike. From birdsong to bee dance, interactions between individuals are almost always coordinated by communication [1]. Cooperation in groups, such as mammalian societies or the large colonies of social insects, appears to require the most intricate coordination. Social evolution has therefore been predicted to drive the complexity of recognition and communicative systems and cognitive abilities ('social complexity hypothesis', Figure 1a) [2–4]. The hypothesis has found support in diverse vertebrate taxa [2,5••]. For example in ground-dwelling sciurids, species living in more complex social systems produce a higher number of distinct alarm call [6]. However, when it comes to insects, empirical evidence for such a pattern is rather mixed.

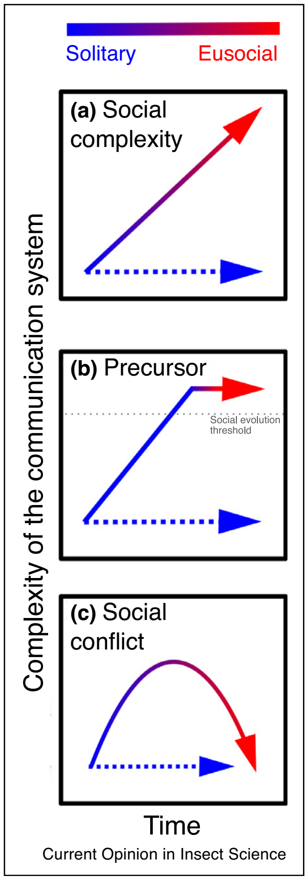
In our review, we shortly introduce insect studies that tested the 'social complexity hypothesis' and analyse potential reasons for the lack of a clear support. We highlight that studying communication in The Other Insect Societies can help us fill some of the gaps in order to better understand the relationship between communication and social evolution.

'The social complexity hypothesis': evidence from insect social evolution

There are currently a few studies available that analysed the relationship between insect social evolution and communicative complexity. In insects, the olfactory channel is the most dominant one and a variety of information is conveyed by pheromones and chemical cues. Consequently, it is not surprising that the majority of the studies focused on chemical communication. The currently best studied group of chemical compounds that play an important role in recognition and communication are cuticular hydrocarbons (CHCs), chemicals that are omnipresent on the cuticular surface of insects [7••]. They are known to contain information of, for example, sex, fertility, caste, and kin. Because coordination of groups requires various messages to be exchanged, CHC profiles have been predicted to increase in complexity with the emergence of eusociality (Figure 1a). However, a large comparative study analysing CHC profiles of 241 hymenopteran species found no difference in the number of substance classes and isomers between solitary and eusocial insects [8••]. In fact, the polyphyletic group of solitary parasitoid wasps produced some of the most complex CHC profiles across the Hymenoptera, with ants having slightly less complex CHC profiles. Bees and social wasps, however, bear surprisingly simple CHC blends, in particular when considering their social complexity.

When looking at the receiver side of communication, there is no clear-cut picture either. A study by Zhou *et al.* [9••] compared the chemoreceptor repertoire of 13 solitary and social Hymenoptera and found that the evolution of sociality does not necessarily increase the numbers of, or positive selection on, odorant receptor

Figure 1



Three major hypotheses that predict how communication systems evolve along a gradient of sociality. **(a)** According to the 'social complexity hypothesis', communicative complexity increases with social complexity. **(b)** The 'precursor hypothesis' predicts that the evolution of sociality is more likely to occur in species already equipped with a complex 'communicative repertoire'. **(c)** The 'conflict hypothesis' predicts that communicative complexity peaks at intermediate level of sociality, where conflict between group members is more likely to occur and where group members are more likely to be recognised individually. The complexity of the communication system is plotted against evolutionary time and the social complexity coded for by colour. The dotted line depicts a solitary species evolving from the same ancestor.

(OR) genes ([9,see also 10]). In fact, phylogenetic comparisons of multiple solitary and social lineages suggest that a chemoreceptor repertoire expansion may have preceded the evolution of eusociality [9••]. Interestingly, the pattern for OR gene and CHC complexity is very similar, with ants having twice as many OR genes than the social bees. Considering that the 9-exon ORs that bind to CHCs are narrowly tuned, with each OR mostly binding to only one or very few substances [11], a simple prediction is that OR and CHC complexity coevolve, with each additional CHC that is used in communication requiring an additional OR.

Another recent study compared solitary and eusocial halictid bees and used sensilla density on antennae as a proxy for communicative complexity [12]. They found that, while sensilla density is lower in secondary solitary halictid bees than in the eusocial ones, the ancestral state seems to be a solitary bee with high density; again, high sensilla density appears to have preceded the evolution of eusociality. Also studies examining the relationship of sociality and investment in insect mushroom bodies, brain centres that participate in olfactory associative learning, olfactory processing, and sensory integration, did not reveal a clear pattern. A comparative study of wasp brain morphology indicates that sociality has not increased but reduced the investment into the mushroom body [13]. However, other studies have shown that mushroom bodies of social reproductives are larger than those of solitary reproductives in a facultatively eusocial sweat bee [14], and that mushroom body development is driven by social interactions in ants [15].

What is a complex communication system?

A major challenge in testing the 'social complexity hypothesis' is to find an accurate measurement of communicative complexity. A number of traits have been used as proxies of complexity in communication systems. However, some traits such as the number of sensilla or the size of brains are not necessarily increasing the quantity of information that is communicated, but rather the quality: sensitivity, precision, and speed of information processing [16]. The large antennae of male moths, for example, have evolved to achieve a stunning sensitivity to the typically not very complex female sex pheromone, whose single message is 'I am here' [17,18]. In the same vein, larger numbers of CHCs on an insect's cuticle and a larger number of OR genes might not necessarily have evolved to communicate a larger number of messages either. In a recognition context, more CHCs and OR genes may simply allow for a more reliable discrimination between individuals through a larger number of possible different odour blend configurations, without increasing the number of messages. This could be important when individuals need to discriminate between many different individuals or multiple different groups of individuals [19].

As good physiological and morphological proxies for communicative complexity are difficult to find, we suggest ultimate analyses of the interaction between communication and social evolution to focus on the actual messages that are sent, which requires comprehensive ethological studies.

Lack of data for hypothesis testing and the benefits of studying the other insect societies

Another major problem that we currently face in testing the social complexity hypothesis is our limited knowledge of communication in insects in general. In most cases, except some well-studied models (honeybee,

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