



Understanding eusociality requires both proximate and ultimate thinking and due consideration of individual and colony-level interests

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In his recent book, ‘The evolution of social wasps’, Hunt (2007) advocates a purely proximate approach when studying the evolutionary origins of eusociality, and he proposes a research agenda for paper wasps that focuses exclusively on how sociality evolved for the good of the colony. At the same time, he dismisses ultimate levels of explanation and the consideration of individual-level interests as a “blinded view of social evolution focused exclusively on [...] inclusive fitness” (p. 164), and he devotes two chapters to analysing the supposed flaws of kin selection theory and its applications. Hunt denies any explanatory power to ultimate thinking, that is attempts to understand why sociality evolved, which he sees as being merely ‘interpretations’ (p. 193)!

We agree with Hunt that understanding the evolution and maintenance of sociality requires proximate-level studies of the underlying genetic, physiological, developmental and ecological mechanisms. But we most strongly disagree with his subordination of ultimate to proximate thinking, and his sharp criticism of kin selection theory. Rejection of ultimate thinking and individual level selection leads at best to an incomplete understanding of eusociality, and at worst to erroneous interpretations of social behaviour. The vast majority of students of social evolution acknowledge the need for a balanced approach that takes into account Tinbergen’s four questions (Krebs and Davies 1997), that is combine studies on the selective value, the proximate-level mechanisms, the ontogenetic development and the evolutionary history of social behaviours (Helanterä 2007, Korb and Heinze 2008). Understanding sociality thus requires combining, rather than opposing, proximate and ultimate levels, and it also requires considering both individual and colony-level interests.

Hunt overlooks the importance of integrating proximate mechanisms and ultimate causation. His exclusively proximate scenario for the evolution of eusociality in *Polistes*

paper wasps merely proposes that the solitary *Polistes* ancestor had two generations per year (bivoltinism). The first generation would have reproduced immediately after emergence. The second generation would have entered diapause to survive the unfavourable season (dry or cold in tropical and temperate regions, respectively), and it would have reproduced the following season. This ancestral bivoltinism would have given rise to the production of two broods in modern *Polistes*, a first brood of workers followed by a second brood of foundresses (Hunt 2007). This proximate level analysis explains some differences between first and second brood females, such as fat storage and ability to overwinter (this fat storage mechanism also occurs in the sweat bee *Halictus ligatus* (Richards and Packer 1994), and it may be common in facultative eusocial systems). However, it does not explain why most first brood females behave as workers rather than attempt to reproduce in the first place, and why this proportion varies across species or even populations within the same species. Kin selection theory does just that.

Hunt also fails to recognize that individual selection can interfere with colony level selection for eusocial organization. He considers only selection at the level of the group, but West-Eberhard (1975) and others have pointed out that members of a colony are not only ‘soma’ of a super-organism, but individuals that may pursue selfish reproductive strategies despite being related and having parallel (but not identical) collective interests. He also ignores evidence that these social conflicts can significantly reduce colony productivity in *Polistes*, where workers sometimes compete over reproduction by mutual egg eating, a costly behaviour that cannot be explained by colony level thinking (Liebig et al. 2005, numerous similar examples of social conflicts in insect societies are known e.g. Ratnieks et al. 2006, Rankin et al. 2007, Beekman and Oldroyd 2008).

Hunt's criticism of kin selection theory is unfounded. The value and contributions of kin selection to the study of social evolution have been highlighted in a recent debate (Queller 2000, Wilson and Hölldobler 2005, Fletcher et al. 2006, Foster et al. 2006a, 2006b, Strassmann and Queller 2007). Other theories can explain the evolution of cooperation between non-relatives, but only kin selection does explain the evolution of helper sterility in eusocial animals, that is species where some individuals do not reproduce and help others reproducing (social insects, some mole-rats etc, Boomsma 2007).

We agree with Hunt and others that students of social evolution sometimes neglect factors other than relatedness. However, kin selection theory itself does not (Bourke and Franks 1995, Queller 2000, Foster et al. 2006a, West et al. 2007, Strassmann and Queller 2007). On the contrary, relatedness is just one of the factors of Hamilton's famous rule: altruism may evolve if the inequality $b \times r - c > 0$ is satisfied, where r is the genetic relatedness between the altruist and the recipient of altruism, and b and c are the benefits and costs of the altruistic act to the recipient and to the altruist, respectively. Altruism may evolve when indirect fitness benefits exceed direct fitness benefits (West et al. 2007), which requires individuals to be related (i.e. relatedness greater than the background population-wide relatedness: $r > 0$) and the benefits of altruism to exceed the costs ($b > c/r$) (Hamilton 1964, Bourke and Franks 1995). Also, the scenarios for the evolution of eusociality (permanently sterile helpers) and cooperative breeding (facultative and reversible helping) are likely to be fundamentally different (Boomsma 2007). Importantly, altruism can evolve even among lowly related individuals, provided that the benefits of altruism far exceed the costs ($r > c/b$) (Poethke and Liebig 2008). b and c are determined by ecological factors, which are thus included in kin selection theory. Therefore, the current emphasis on relatedness in the literature does not reflect the relative importance of ecological factors and of relatedness (Griffin and West 2002). Both are essential. Rather, the focus on relatedness stems from the fact that measuring relatedness is often much easier than measuring ecological factors that affect the strength of selection. The importance of ecological factors has repeatedly been emphasized, and future studies will focus more on this aspect of kin selection theory (Boomsma and Franks 2006).

Proximate and ultimate level approaches are complementary (Alcock and Sherman 1994, Bourke and Franks 1995, Linksvayer and Wade 2005). Both are necessary, and attempts to promote one over the other are pointless and detrimental for the field. Kin selection is a general theory of why sociality has evolved. It encompasses individual- and colony-level selection (Hamilton 1975), which is necessary for understanding the complexity of eusociality. Models based on kin selection theory can incorporate both species-specific traits and evolutionary constraints, and the specific predictions of these models can be tested with proximate studies (Ratnieks et al. 2006). These experimental results, in turn, can help further developing the theory. Such a constructive dialogue between theoreticians and empiricists

is necessary for progressing towards understanding the evolution of sociality.

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