Kin recognition in social insects and other animals—A review of recent findings and a consideration of their relevance for the theory of kin selection

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Abstract. Kin selection is a widely invoked mechanism to explain the origin and evolution of social behaviour in animals. Proponents of the theory of kin selection place great emphasis on the correlation between asymmetries in genetic relatedness created by haplodiploidy and the multiple origins of eusociality in the order Hymenoptera. The fact that a female is more closely related genetically to her full sister than to her daughters makes it more profitable for a Hymenopteran female, in terms of inclusive fitness, to raise full sisters rather than daughters or full siblings with a female biased sex ratio rather than offspring. This is sometimes referred to as the haplodiploidy hypothesis. In reality however, genetic relatedness between workers in social insect colonies and the reproductive brood they rear is far below 0.75, the value expected for full sisters, often below 0.5 the value expected between mother and daughter and, not uncommonly, approaching zero. Such values are on account of queen turnover, multiple mating by queens or polygyny. This situation raises doubts regarding the haplodiploidy hypothesis unless workers can discriminate between full and half sisters and preferentially direct their altruism towards their full sisters only. For this to be possible however, workers should be able to recognise their full sisters inspite of growing up with and being habituated to an assortment of full sisters, half sisters and perhaps other even less related individuals. Even outside the Hymenoptera, social animals may find themselves growing up together in the company of individuals of varying degrees of relatedness. An ability to tell apart the more and less related individuals under such circumstances should favour kin selection.

Much effort is now going into assessing the abilities of animals to discriminate between kin and non kin. In every case studied carefully so far, animals appear to be capable of recognising their kin. Ants, wasps, sweat bees, honey bees, frogs, toads, mice, rats, voles, squirrels, monkeys and even humans appear to be able to recognise their kin in one circumstance or another. An ability to recognize true genetic relatedness requires genetically specified recognition labels and these must therefore be present. Recent findings of the role of the histocompatibility system provides some clues to the possible nature of recognition labels. An ability to recognise full sisters for example, inspite of being habituated to full and half sisters requires not merely genetically specified labels but also recognition templates which are based on the characteristics of the individual animals making the recognition and not templates based on all animals one grows up with. Some animals such as honey bees, tadpoles and ground squirrels appear to have such templates but others such as sweat bees and some mice appear not to. It is entirely possible that our inability to devise natural enough assays for recognition prevents us from understanding the full potential of the kin recognition abilities of many animal species. In any case, genetically specified labels and self based templates should greatly facilitate the evolution of social behaviour by kin selection.

Keywords. Genetic relatedness; kin recognition; kin selection; hymenoptera; haplodiploidy; evolution of social behaviour.

1. Introduction

There are two main grounds for expecting that animals must be capable of distinguishing between close genetic relatives and non or distant relatives. The first has
to do with inbreeding avoidance (or for achieving an optimum balance between inbreeding and outbreeding; see Bateson 1980). On theoretical grounds it can be shown that inbreeding leads to homozygosity of recessive lethal genes resulting in inviable offspring. In conformity with this expectation inbreeding avoidance is widely observed in most animal groups. The second has to do with models for the spread of 'altruistic' alleles by natural selection. The basic idea of current models is that animals must behave altruistically towards close genetic relatives and selfishly towards non relatives. Such 'nepotistic' behaviour has again been observed in a wide variety of animals. In spite of such strong theoretical and empirical grounds, efforts to unravel animals' abilities to recognise kin (other than parent-offspring recognition) began just over 5 years ago. In this paper I will review experimental evidence of kin recognition from different animal groups, both among insects and vertebrates. Given an ability to recognise kin, any animal can potentially use it both for mate selection and for structuring altruistic and selfish interactions. I will not specifically allude to the function of kin recognition in each case.

Whether animals can discriminate between close and distant relatives inspite of being habituated to both classes of relatives is of great theoretical interest. Such an ability is essential for the tenability of a widely discussed form of kin selection theory (the haplodiploidy hypothesis) that purports to explain the evolution of insect sociality. Even outside the Hymenoptera, an ability to discriminate between close and not so close relatives within a mixed cohort or family group will greatly facilitate the operation of kin selection. This is because such an ability can raise the effective coefficients of relatedness between donor and recipient in altruistic interactions. My intention here is not so much to exhaustively review the literature on kin selection or kin recognition but to examine the consequences of our present understanding of kin recognition and its possible mechanisms to the theory of kin selection.

2. The theory of kin selection

The concept of 'inclusive fitness' first put forward by Hamilton (1964a, b) has promised to provide a plausible mechanism for the evolution by natural selection of altruistic behaviour in general and sterile castes and 'worker behaviour' in Hymenoptera in particular. The basic idea is a very simple one and has now come to be known as the theory of kin selection. Since organisms are ephemeral combinations of genes it is the individual alleles that form the connecting link from one generation to the next. This being the case one must be concerned with the changes in frequency of alleles per se in a population and not merely with the numbers of offspring produced by the bearers of the alleles in question. An allele can increase in frequency not only by programming its bearers to produce more offspring (who are likely to carry the same alleles) but also by programming them to aid genetic relatives (who too are likely to carry the same alleles) and the latter could well be at the cost of offspring production. If an individual aids $n_i$ relatives (other than offspring) who are related to it by $r_i$ at the cost of producing $n_o$ offspring who are related to it by $r_o$ then, as long as

$$n_i r_i > n_o r_o,$$

(1)
even sterility could evolve by natural selection (this form of eq. is from Craig 1979). (Notice that this argument rests on the assumption that the offspring given up and