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Nice to kin and nasty to non-kin: revisiting Hamilton's early insights on eusociality

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When helping behaviour is costly, Hamiltonian logic implies that animals need to direct helpful acts towards kin, so that indirect fitness benefits justify the costs. We revisit inferences about nepotism and aggression in Hamilton's 1964 paper to argue that he overestimated the general significance of nepotism, but that other issues that he raised continue to suggest novel research agendas today. We now know that nepotism in eusocial insects is rare, because variation in genetic recognition cues is insufficient. A lower proportion of individuals breeding and larger clutch sizes selecting for a more uniform colony odour may explain this. Irreversible worker sterility can induce both the fiercest possible aggression and the highest likelihood of helping random distant kin, but these Hamiltonian contentions still await large-scale testing in social animals.

1. Introduction

The second part of W. D. Hamilton's seminal 1964 paper [1] is about the evolution of social behaviour and social discrimination, topics which both stimulated large research programmes. Subsequent studies on vertebrates focused on the efficiency of kin-discrimination (reviewed in [2–4]), whereas social insect researchers primarily developed questions and tools for estimating relatedness [5]. However, later decades of kin recognition research led to the general consensus that eusocial insects are very good at binary discrimination between nest-mates (kin, at least on average; reviewed in [6,7]), but that within-colony discrimination according to degree of kin is all but absent [8,9], unlike vertebrate cooperative breeders that may have graded nepotism when it benefits the indirect fitness of group members [4,10]. Even in very small insect societies, we lack evidence that discrimination happens on the basis of kinship *per se* instead of belonging to the same nest [11,12].

Rather than elaborating on empirical work over a broad spectrum of recognition topics, we revisit foundational pieces of Hamiltonian logic [1] to briefly explore their relevance today. We focus on aspects of cost (c), both for helping and for discrimination. In Hamilton's rule ($br > c$), these costs are normally expressed in a personal reproduction currency, so that c in fact equals cr_o, where r_o is (life-for-life) relatedness to own offspring (0.5 when parents are outbred). As long as all individuals can mate, this cr_o term, compared with the efficiency benefit (b) of raising non-offspring nest-mates of some average relatedness (r_n), determines whether inclusive fitness is maximized by helping or dispersing. However, workers of obligatorily eusocial insects [13] never mate to disperse and breed elsewhere as they are destined to raise younger nest-mates of relatedness r_n. So for anything else than indiscriminate altruism to nest-mates to be favoured the required Hamiltonian inequality becomes

$br_{n+} > cr_n$ rather than $br_n > cr_o$, where r_{n+} is relatedness to a specifically targeted nest-mate of higher relatedness relative to an individual of average relatedness (r_n).

2. Why it may almost never pay to be nicer to closer relatives in the eusocial domain?

In the section 'Discrimination in social situations' [1], we find Hamilton's summary statement that started most research programmes on kin recognition [2–4,6,7]:

> The selective advantage of genes which make behaviour conditional in the right sense on the discrimination of factors which correlate with the relationship of the individual concerned is therefore obvious. . . . If he could learn to recognize those of his neighbours who really were close relatives and could devote his beneficial actions to them alone an advantage to inclusive fitness would at once appear'. (p. 21)

In the 1990s, Ratnieks [14] showed that kin-discrimination within colonies would rarely be accurate enough to be profitable, but that nest-mate recognition would be more stable over evolutionary time. His modelling elaborated on Crozier's paradox [15,16], the idea that recognition cue variation will become eroded in proportion to its nepotistic use to favour carriers of the same genes, unless it is maintained by another selection force [9]. Recent work by Holman *et al.* [17] indicates that an important general force might be inbreeding avoidance via disassortative mating, which can maintain negative frequency-dependent selection for genetic odour cues in spite of kin-discrimination. However, the hallmark of eusociality is that most individuals neither mate nor reproduce. Eusociality therefore entails a transition from reproductive skew among cooperative and facultatively eusocial breeders to sterility for most colony members. Such a transition to obligate eusociality is irreversible and this is significant when evaluating the likelihood of nepotism on either side of the transition [13].

Increasing unmatedness implies that selection for mate-choice targets a decreasing proportion of individuals as reproductive division of labour increases. This is particularly so in the obligatorily eusocial Hymenoptera, where individuals either mate for life shortly after reaching sexual maturity or not at all [13,18], whereas vertebrate helpers that become breeders can mate later in life. In figure 1*a*, we have mapped the effective proportion of reproductively totipotent individuals (the fraction remaining in the white triangle: zero when eusociality is obligate and variable for cooperative and facultatively eusocial breeders) on the parameter space provided by Hamilton's rule. When the transition towards eusociality makes colony size increase, and only a single pair or few individuals breed, clutch sizes must necessarily increase and then disassortative outbreeding becomes easiest when all reproductives raised in a clutch have similar smells. This would almost inevitably induce selection for odour-mixing via trophallaxis or other mechanisms producing a unique colony Gestalt (figure 1*b*). In turn, this would make it hard for workers to identify more closely related sexuals when they provision them. Erosion of cue diversity would thus decrease the left-hand term in $b_{n+}r_{n+} > c_n r_n$, so that nepotism would not pay off.

This logic may explain why even in small halictid bee societies selection has not precluded the evolution of Gestalt odours [19]. It implies that with technology we can discriminate between patrilines within the same colony of honeybees [20], yellowjacket wasps [21], leaf-cutting ants [22] and matrilines of ponerine ants [23], even though the workers of these bee and ant species do not appear to use such differences for nepotism [8,22,23]. Finally, it is consistent with the transferability of recognition cues among *Formica* ant workers being positively correlated with their heritability [24]. Such transfers make it very difficult to discriminate between different degrees of kin within a colony, but they very efficiently mobilize the entire spectrum of available cues for obtaining a colony Gestalt that avoids inbreeding during nuptial flights.

3. When does it pay to be nasty to non-kin and nice to distant kin?

Hamilton was aware of the analogy between social insect colonies and metazoan bodies in which somatic cells readily kill themselves in defence of the germline [1]. As insect colonies are not clonal, he also realized that the extent of individual sterility should correlate with the degree of suicidal aggression. In the section 'Colonies of social insects' [1], we can read

> The correlation of these (aggressive) characters with sterilization does seem to hold very well throughout the social Hymenoptera. Queens are always timid and reluctant to use their stings compared to workers. In *Polistes*, workers, unless very young, are more aggressive than auxiliaries, and auxiliaries more than the reigning queen. Races of honeybees in which laying workers occur more frequently or appear more readily when the hive becomes queenless are generally milder than the races where they are less prevalent. Polybiine wasps, pleiometrotic and lacking pronounced caste differences, are generally somewhat less fierce than vespines. (p. 39)

To the best of our knowledge, this suggestion has hardly been elaborated upon in spite of the intriguing generalizations that it may offer. Testing for a relationship between aggression and sterility across species would require adjustment for many confounding variables, but tests within species comparing the aggression of same-age workers with and without developed ovaries would seem very interesting.

It is important to realize that some relatedness has fundamentally different consequences than no relatedness at all. In Hamilton's section 'Valuation of the welfare of relatives' [1], we read

> [. . .] the behaviour of a post-reproductive animal may be expected to be entirely altruistic, the smallest degree of relationship with the average neighbour being sufficient to favour the selection of a giving trait. (p. 21)

This refers to a solitary breeder for whom cr_o no longer exists, so that $br_n > cr_o$ is fulfilled for any $br_n > 0$, favouring indiscriminate altruism towards random neighbours in genetically viscous populations. No non-human examples appear to have been documented, which is perhaps not quite surprising as animals rarely become post-reproductive in good health. However, in the obligatorily eusocial domain, this is equivalent to $br_{n+} > cr_n$, which is easier to satisfy when $cr_n = 0$ than in the within-colony nepotism scenario where $cr_n > 0$. This would apply to a colony of obligatorily sterile workers who have lost their mother queen without the possibility of replacing her, which should make them inclined to be altruistic to any distant relatives. Consistent with this idea, orphaned army ant workers are known to merge with a neighbouring colony in spite of distinct cuticular hydrocarbon profiles, as average relatedness among random neighbouring colonies is
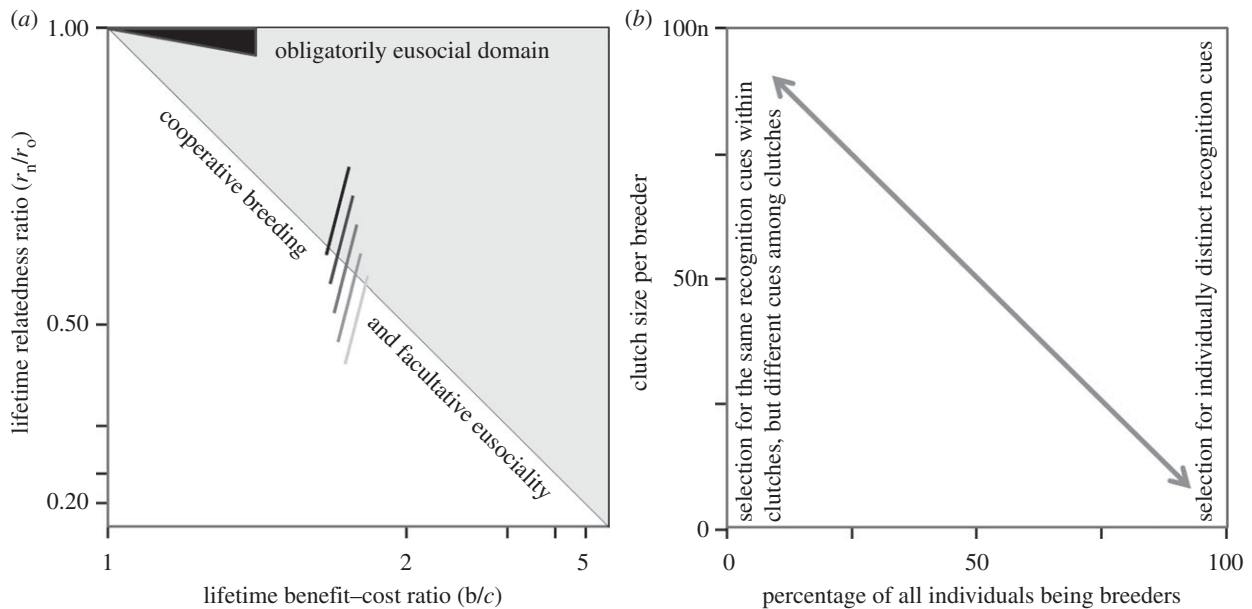
Figure 1. Unmatedness, clutch size and the maintenance of recognition–cue diversity. (a) Heuristic diagram outlining how reproductive division of labour may erode recognition–cue diversity in spite of disassortative mating [17]. The log–log plot, derived from fig. 5a in [13], has a light-grey triangle where Hamilton's rule $br_n > cr_o$ is fulfilled (c is the efficiency of personal reproduction, b is the efficiency of raising nest-mates, r_o is relatedness to offspring, r_n is relatedness to immature nest-mates other than offspring) and a white triangle where Hamilton's rule is not satisfied over the lifespan of helpers. Being in the light-grey triangle makes the pursuit of indirect fitness more favourable than direct fitness and the opposite is true when being in the white triangle. Obligatorily eusocial Hymenoptera (ants, corbiculate bees, vespine wasps) have strict lifetime monogamous ancestors [13,18] so that r_n/r_o equalled one when workers became physically differentiated (the black triangle in the top-left), but this condition is not fulfilled in cooperative and facultatively eusocial breeders where individuals may change roles from helper to breeder later in life. In terms of lifetime inclusive fitness, individuals in such populations will always hover around the diagonal as helping never becomes fixed in the obligatorily eusocial sense. We have drawn hypothetical populations of cooperative or facultatively eusocial breeders as lines in different shades of grey, all crossing the diagonal but varying from very few individuals devoting their life to helping (lightest grey line) to most individuals being permanent helpers and very few managing to become breeders later in life. The likelihood of nepotistic discrimination should then be proportional to the relative number of individuals remaining in the white triangle. (b) The smaller the proportion of individuals in a population that breed (normally very low in obligatorily eusocial species and variable in cooperative and facultatively eusocial breeders), the larger the average clutch size of mating swarm reproductives produced per breeder (here assumed to be linearly proportional to multiples of n). Towards the right selection for disassortative mating should give individuals distinct odours, but towards the left odours should become the same within clutches and different among clutches.

slightly positive because of reproduction by colony fission [25]. The 'average' is crucial here, as a generally adaptive behaviour does not preclude occasional non-adaptive mergers, such as some dwarf honeybees joining colonies of a closely related species, as long as colonies merge with the right other colonies most of the time [26].

4. Conclusion and implications

Although genetic variation allowing for kin-discrimination may be maintained in spite of Crozier's paradox [15,17], we hypothesize that the increasing unmatedness and larger clutch sizes that accompanied the loss of reproductive totipotency in the eusocial Hymenoptera shifted selection from favouring individuals with unique personal odours to clutches that entered mating swarms with the same odour (figure 1), a colony-level trait that precluded any form of eusocial nepotism. Rereading Hamilton's original paper, we conclude that his generalization of nepotism relied on the (as we now know incorrect) assumption of sufficient detectable intra-colonial variation for genetic recognition cues throughout all domains of social evolution. It now seems more likely that there is a gradient of nepotism, which is negatively correlated with reproductive division of labour, so that nepotism is most

easily maintained in advanced primate (including human) groups, less so but still frequent in other vertebrate societies [4,10], but absent in the more organismal [27] insect societies. When high levels of organismality are reached [13,27,28], nepotism likely becomes an aberration rather than a kin-selected norm, analogous to cancer in metazoan bodies [29]. If it is to be maintained in obligatorily eusocial insects, it would seem most likely in cases of moderate secondary polygyny with high queen turnover, fluctuating relatedness, and substantial worker reproduction [30].

Revisiting Hamilton's original text on helper sterility and aggression [1] reveals that obvious questions remain to be broadly investigated. For example, can aggression differences between castes be experimentally manipulated by altering the likelihood of sterility? A recent study suggests that this is the case in leaf-cutting ants [31]. Or conversely, does the likelihood of sterility decrease when relatedness incentives for personal reproduction increase? A recent study indicates that the answer is affirmative for honeybees [32]. Finally, might the occasional merging of orphaned and queen-right army ant colonies in viscous natural populations just be an example of a more common phenomenon? Similar to army ants, invasive ant workers seem unable to produce males from worker laid eggs and always appear to have genetically viscous populations when they become unicolonial [33].

It seems we still have a long way to go until we will have exhausted the inspirational observations reported in Hamilton's classic 1964 paper [1], a contribution that forever changed the way in which we understand social evolution.

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