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Special Issue: Kin Selection

Kin and nestmate recognition: the influence of W. D. Hamilton on 50 years of research

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Kin selection stands among W. D. Hamilton's most influential ideas. The purpose of this review is to assess the impact of Hamilton's ideas about kin selection on studies of social recognition. Kin selection theory predicts that animals should direct aid-giving behaviour to closely related animals, provided that a positive net benefit in inclusive fitness is achieved from the altruistic act. Kin recognition is the key proximate mechanism by which animals can sort more related from less related interactants in a population. Kin recognition also has the potential to allow fine distinctions among animals based on identity by descent. Following the publications of Hamilton's 1964 papers on kin selection, studies of kin recognition focused on four disparate behavioural contexts: identification of group membership, inbreeding avoidance, alarm calls and other forms of aid-giving, and parent–offspring interactions. Investigations of eusocial insects have focused on identification of group membership by phenotypes that are shared among all members of a colony. In birds and mammals, social structure is often based on individual recognition. Some species, particularly rodents, have the ability to make discriminations based on relatedness among animals that they have not previously met. Future studies of kin recognition should be less reliant on assumptions that all forms of societal closure are due to factors related to kin selection. These studies should acknowledge that the role of individual recognition in vertebrate societies is key to understanding the full texture of social interactions, and that individual recognition may be equally important in many other types of animals. Of particular interest will be the discovery of how information about kinship is integrated with information about individual identity.
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> It should by now be clear that, if kin selection models are a fair image of reality, closeness of relatedness is a crucial factor for determining adaptive courses of action in social situations. Thus an ideally adapted social organism would know the relatedness of every individual around it and would make its behaviour finely conditional on the relatedness perceived (Hamilton, 1987, p. 491)

Hamilton's (1964a, 1964b) ideas about kin selection naturally led to the hypothesis that animals, in order to behave consistently with kin selection theory, must be able to identify close kin and to make discriminations among members of their social group based on genetic relatedness. Kin selection theory predicts that animals will behave in ways that promote the reproductive chances of their kin. Animals should engage in this helping behaviour, even if it is costly to the aid-giving animal, provided that the reproductive benefit to the relative, times the genetic relatedness between the two animals, is greater than the reproductive cost to the aid-giver. During the 1970s kin recognition came to be considered a necessary corollary of kin selection. Wilson (1987) lists 10 frames of reference in which kin recognition can function: altruism, parent–offspring interactions, alloparenting, adoption, mate choice, schooling, grooming, alarm signalling, cannibalism and habitat selection. The richness of the literature on kin recognition is in part due to the breadth of behavioural context in which it could be useful.

The purpose of this review is to evaluate progress in our understanding of kin recognition since the publication of Hamilton's 1964 papers on kin selection. My main focus is a critical evaluation of the development of kin recognition research over the last 50 years. I first review the development of knowledge about how animals make social discriminations. This is followed by discussions of nepotism and inbreeding avoidance. Finally, I briefly weigh the impact of sensory limitations and population viscosity on interpreting the kin recognition literature. Throughout the review I highlight and evaluate current directions in this area. These

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evaluations lead to some thoughts about future directions in kin recognition research.

Kin recognition can be narrowly defined as the ability to ascertain relatedness due to identity by descent (Hamilton, 1964a, 1964b). Broader definitions of kin recognition include behaviour that reflects classification of others as members or nonmembers of a social group, provided that the social group members are likely part of the same extended family (Sherman, Hudson, & Pfennig, 1997). Assessments by animals of kinship are sometimes based on deterministic information about genetic matches, but are often centred on probabilities based on the likelihood that life history keeps family members together (Mateo, 2004). The process of kin recognition depends on the presence of cues or signals containing information about an animal's genetic identity. The study of kin recognition includes understanding the cues or signals as well as the sensing of phenotypic information by the receiver, assessment of that information, and the measurement of how behavioural responses of the receiver are changed or modified in response to the information (Breed & Buchwald, 2008; Mateo, 2004; Sherman et al., 1997).

Kin recognition is used in coordination with other types of identification information, such as species recognition (Ryan & Rand, 1993), sex identification, and assessments of age and size that are typically available to animals (Sherman et al., 1997). Identification information is often presented redundantly, so that the same message can be gained from visual, odour, auditory or other cue modalities (Sherman et al., 1997). Kin recognition should always be considered within the context of other types of identification information that an animal might employ in a given behavioural context.

Research on kin recognition was slow to take off following the publication of Hamilton's 1964 papers, but by the mid- to late 1970s researchers were actively engaged in pursuing empirical hypotheses related to kin recognition in a wide range of organisms (Sherman et al., 1997). As scientific thought and empirical knowledge about kin selection grew, a continuing interest in kin recognition helped to inform thought about how finely tuned the relationship between recognition behaviour and kinship might be. The literature on kin recognition, which has grown to be quite large, is the subject of a large number of reviews including Fletcher and Michener (1987), Blaustein, Porter, and Breed (1988), Hepper (1991, 455 pp.) and Starks (2004). Some authors, such as Dawkins (1982), have written extensive popular accounts about the broader evolutionary implications of kin selection and kin recognition. As investigators have begun to explore the sensory and neural basis for social recognition the literature on kin recognition is becoming broader than just explorations of discrimination mechanisms. Kin recognition studies have expanded in the five decades since Hamilton's (1964a, 1964b) exploration of kin selection to encompass a broad spectrum of animal taxa and to incorporate conceptual advances. In retrospect, kin recognition has proven to be a powerful concept, but the concept has also come with costs in that investigators have looked for 'kin recognition' in a variety of behavioural contexts without thinking deeply enough about other routes, such as individual recognition, for using recognition information in shaping social interactions.

The most influential early studies of kin recognition dealt with alarm calls among members of vertebrate social groups (Sherman, 1980). Because birds were not credited with the olfactory or auditory abilities necessary to make finely tuned distinctions, early work focused on mammals. Alarm calls provide a particularly good model system for studying kin selection and kin recognition, as there are potential costs to giving the call, potential benefits from hearing the call, and varying degrees of relatedness among members of the social group.

Stimulated by the same line of reasoning, a related set of studies focused on group identity and closure. Group closure is the process by which nonmembers of a group are excluded, and it usually relies on discriminating members from nonmembers. Studies of social insects took advantage of the nest defence systems of termites, ants, bees and wasps to explore cues used in the inclusion or exclusion of potential members of the social group. Key to this literature was Greenberg's (1979) study of nestmate recognition in a sweat bee, *Lasioglossum zephyrum*. Greenberg found that the degree of relatedness between a guard bee and a bee trying to gain entrance to the colony was negatively correlated with the likelihood that the guard bee would exclude the other bee. This result, although it did not demonstrate an ability to make fine kinship distinctions, established what was viewed as a key link between studies of social insect colony defence and studies of aid-giving behaviour in other animals. Greenberg's study was important as a critical acknowledgment of the potential role of kinship in nestmate identification in eusocial insects. Previous work, such as Kalmus and Ribbands's (1952) study of honeybee nestmate recognition, dealt with group identification without linking the process to kinship. Greenberg's (1979) work was also important in helping investigators studying vertebrates, such as Sherman (1980), to draw analogies between kin recognition in eusocial insects and vertebrates.

Clearly, dynamics other than kin selection that might lead to social behaviour, formation of social groups, and perhaps even group closure. Members of many types of social groups, such as animals in aggregations where the benefit comes from shared vigilance, need not be related to gain benefits from association with other animals. Kin selection and its corollary, kin recognition, need not be invoked as mechanisms in these cases. Some investigators have felt cooperation among unrelated individuals represents a challenge or difficulty for kin selection theory (Wilson, 2005), but the point that benefits from group membership can be accrued in many ways, sometimes relating to kinship and sometimes not, seems fairly obvious. Leadbeater, Carruthers, Green, Rosser, and Field (2011) provide a clear-cut example of how unrelated individuals might be drawn together by the potential for benefiting from resources held by the group. Associations among unrelated ant queens during colony foundation are fairly frequent and likely derive from the potential benefit of gaining possession of the nest (Cahan & Fewell, 2004). These examples illustrate the richness of interaction between the literature on social behaviour and the literature on recognition. In the following sections I explore how relatedness distinctions are made (Lacy & Sherman, 1983), with nestmate recognition in the eusocial insects as a unique example (Breed & Bennett, 1987), the relationship between the major histocompatibility complex (MHC) and social recognition (Penn & Potts, 1998), nepotism (Mateo, 2004), mating systems (Pusey & Wolf, 1996) and sensory limitations (Reeve, 1989), and how population viscosity might affect kin recognition (Mitteldorf & Wilson, 2000) (Table 1).

MAKING RELATEDNESS DISTINCTIONS

How might animals gain the information needed to make distinctions among other animals on the basis of degree of relatedness due to identity by descent? In natural conditions, detecting affiliation with kin is typically confounded by the fact that, in species with parental care, nearby animals are often kin. Early in the discussion about kin recognition, this led to consideration of models that postulate kin selection effects as a result of association, rather than as a behavioural choice using perceptual inputs that allow assessment of kinship. Association can lead to recognition by 'familiarity', a slippery concept that has been defined in a variety of

Table 1
Types of recognition, cue variance, source of cues, recognition mechanisms and contexts in which recognition information is used

Type of recognition	Cue variance	Genetic versus environmental cues	Mechanisms	Contexts
Learned group or type identity Nestmate recognition in eusocial insects Family closure Familial matching	Low cue variance within social group, high variance among groups At population level cues may be hypervariable	Either genetic or environmental cues	Phenotype matching Self-referencing	Group closure Inbreeding avoidance Nepotism
Individual recognition	Hypervariable cues Within-family similarity may be important	Cues more likely correlated with genotype	In some cases specialized brain regions (e.g. facial recognition in humans)	Information used in social interactions, including mate choice, cooperation and nepotism
Green beard effects	Low cue variance within social groups	Cues always genetic	Genetic association between recognition and cooperative behaviour	Cooperation

ways (Lacy & Sherman, 1983). Much of the early post-Hamilton discussion about making distinctions about identity by descent centred on the question of the outcomes of familiarity. The role of familiarity in social recognition stimulated one of the first post-Hamilton arguments to emerge in the kin recognition literature: could familiarity lead to information about kinship, or was another mechanism required (Breed & Bekoff, 1981)? Being able to ascertain whether a social relationship has already been established with another animal can have considerable value. Information may already have been learned about factors such as the other individual's value as a mate, threat to territory, and likelihood of cooperation (Strodl & Schausberger, 2013). Thus, considerable data might be gleaned from familiarity, including individual identity, independent of information about identity by descent. Historically, many field observations of animals made with the goal of ascertaining how kinship and behaviour are correlated were confounded, often hopelessly, by the entwining of familiarity with identity by descent, resulting in claims about kin recognition that could easily be explained by individual recognition or some sort of social categorization, instead of assessment of identity by descent.

Individual Recognition

The literature on the topic of individual recognition is rich and is ably reviewed by Tibbetts and Dale (2007). Individual recognition relies on substantial phenotypic variation in the cues used for recognition; cues like this are sometimes called hypervariable. The need in recognition systems for variation in cues brings about an interesting problem, sometimes called 'Crozier's paradox' (Holman, van Zweden, Linksvayer, & d'Ettorre, 2013), that directional selection on a trait will inevitably lead to reduced genetic variability. Holman et al. (2013) suggested that disassortative mating may be a widespread mechanism for maintaining variability. Breed and Buchwald (2008) argued that relaxed selection may, without any special mechanism, result in the accumulation of variability over evolutionary time. Cues associated with MHC loci are hypervariable; these are discussed in a separate section below.

Examples of recognition cues that are at least subjectively hypervariable include primate faces (Marechal, Genty, & Roeder, 2010; Platek, Krill, & Kemp, 2008), bird calls (Godard, 1991; Yorzinski, Vehrencamp, Clark, & McGowan, 2006), paper wasp cuticular colour patterns (maculations) (Tibbetts & Dale, 2007), mammalian odours (Brennan & Kendrick, 2006; Brown & MacDonald, 1985; Halpin 1980, 1986; Johnston, 2003; Mateo, 2003, 2004, 2006a, 2006b; Swaisgood, Lindburg, & Zhou, 1999), fur seal vocalizations (Insley, 2000), cockroach surface hydrocarbons (Lihoreau & Rivault, 2009) and honeybee surface hydrocarbons (Breed & Buchwald, 2008). Crows can even distinguish among human voices (Wascher, Szipl, Boeckle, & Wilkinson, 2012). Tibbetts and Dale (2007) as well as Breed and Buchwald (2008) argued that selection could favour cue diversity (and hence underlying genetic diversity) if accurate identification of individuals enhances fitness. Phenotypic diversity in cues used for individual recognition is analogous to the maintenance of immune hypervariability at MHC loci (Penn & Potts, 1998). The small colony sizes of primitively eusocial bees and wasps, which range from a very few individuals to perhaps a few hundred workers, would seem to open the door for individual recognition among workers.

As mentioned above, the first important post-Hamilton studies of nestmate recognition in social insects used a primitively eusocial species as the model system, the halictid bee, *Lasioglossum (Dialictus) zephyrum* (Greenberg, 1979). Greenberg (1979) found a correlation between nestmate recognition response and kinship, suggesting that the tools for individual recognition might be available in these bees. Soro, Ayasse, Zobel, and Paxton (2011) found that the level of phenotypic diversity in odours used by these bees for social recognition was insufficient for what they hypothesized would be needed for individual recognition. However, this was a statistical conclusion based on the investigator's assumptions about what cues the bees might use in discriminations. Dani et al. (2004) made a similar argument for eusocial wasps; they also made a statistical argument that the information available is only adequate to support nepotism in special cases. Further work will be required to determine whether these results reflect the actual perceptual and information processing abilities of these insects. In larger eusocial colonies, individual recognition of thousands, or tens of thousands or more workers would seem to be infeasible. Breed and Buchwald (2008) modelled how sensitivity to differences in compound concentrations (or the ratios of compounds) can affect the information content of cue signatures. A contemporary view of individual recognition was expressed by Pollard (2011) and Pollard and Blumstein (2011, 2012); they emphasized the value of the information gained by the receiver when the receiver can attribute a message (specifically an alarm call) to a specific sender.

As an adjunct, or perhaps as an alternative, to arguments invoking familiarity, the discussion in the 1980s turned to more direct mechanisms to obtain information about identity by descent. These mechanisms are categorized as 'green beard effects', self-referencing and phenotype matching.

Green Beard Effects

One of the interesting ideas to flow from Hamilton's work was the 'green beard' (Axelrod, Hammond, & Grafen, 2004; Dawkins, 1976; Gardner & West, 2010; Hamilton, 1964a, 1964b). Imagine that all family members carry the same distinctive phenotype, such

as a green beard. That label then allows family members to distinguish other family members from the larger population. Although green beard models were seriously discussed in the early post-Hamilton literature (Axelrod et al., 2004), they fell from favour because of the difficulty of modelling genetic systems in which the signal and perceptual systems are linked and covary. In other words, how do members of a family possess both the same signal phenotype, the green beard, and the information to 'know' that the green beard signifies membership in their family? Simple genetic thinking suggests that if a model starts with unique families, each with its own beard colour, that outbreeding will result in uniformity in phenotype among families and loss of any information that is relevant to kin recognition. Also possible are evolutionary arms races with cheaters, in which invasive phenotypes defeat the green beard system.

A recent revival of the green beard concept suggests that more sophisticated evolutionary thinking could support a green beard model for marking identities by descent (Axelrod et al., 2004; Gardner & West, 2010; Jansen & van Baalen, 2006; Nonacs, 2011; West & Gardner, 2013; West, Pen, & Griffin, 2002). Strassmann, Gilbert, & Queller (2011 and references therein) argued persuasively that green beard models apply extensively in microbes in the context of 'kind' recognition, in which matching at specific loci can lead to cooperation. The interesting result of this is that, even though 'narrow-sense' kin recognition is rare in microbes, there is considerable opportunity for cooperation via 'kind' recognition (Strassmann et al., 2011).

Self-referencing

Suppose that an animal perceives its own phenotype and uses this information to attempt to identify relatives that are identical by descent and to make distinctions among those relatives based on degree of relatedness. In a diplodiploid population, the average relatedness between full sibs is 0.50, but relatedness ranges from 0 (which would be a real oddity of genetic assortment during meiosis, but could happen) to 1 (identical twins). If an animal's recognition phenotype is highly correlated with its genetic identity (not just genes correlated with the cue, but a genome-wide correlation), then self-referencing could be a better source of precise information about true identity by descent (as opposed to identity by descent based on probability derived from a family average of phenotypes).

The theory of self-referencing has been discussed by Mateo and Johnston (2000) and Hauber and Sherman (2001), and a number of studies (e.g. Hain & Neff, 2006; Mardon & Bonadonna, 2009; Mateo, 2010) point to examples of self-referencing in mammals. Weddle, Hunt, and Sakaluk (2013) reviewed a growing body of literature that suggests that arthropods can self-reference, by using cuticular hydrocarbons in making mate choices (Neff & Sherman, 2003, 2005; Sherman, 1991). Thunken, Waltschyk, Bakker, and Kullmann (2009) demonstrated self-referencing in a cichlid fish, and Villinger and Waldman (2008) found MHC-based self-referencing in an amphibian. An interesting form of self-referencing that is genetically mediated is self-incompatibility in the mating systems of plants (Takayama & Isogai, 2005). Genetic self-incompatibility provides an interesting bridge between learned self-referencing and green beard effects, which are discussed below.

Phenotype Matching

Phenotype matching (Lacy & Sherman, 1983) relies on animals learning the phenotype of surrounding animals. The general mechanism suggests that learning occurs when the animal is young, so that the phenotypes of parents and/or siblings are used to form a template for how relatives should look or smell. Hypothetically, the average phenotype of these animals represents information that can then be used by the animal to assess its relatedness by descent with animals it meets in the future. Phenotype matching is the most frequently found mechanism for kin discrimination; studies include Amphibia (Blaustein, O'Hara, & Olson, 1984; Blaustein & Waldman, 1992; Waldman, 1991), many eusocial insects (e.g. honeybees: Breed, Diaz, & Lucero, 2004; Breed, Perry, & Bjostad, 2004; Getz, 1991), ground squirrels (Holmes, 1984, 1986a, 1986b; Holmes & Sherman, 1982), peacocks (Petrie, Krupa, & Burke, 1999) and fish (Ward, Webster, & Hart, 2007).

One criticism of phenotype matching theory is that the sample size available to most animals to build their template of their family's phenotype is small, so a considerable standard of error would be expected in estimates of relatedness. In addition the other animal, the one to be assessed, presents phenotypes that potentially have only moderate correlations with the underlying genotypes. When two predictors with high variance are coupled, the outcome will have even higher variance and it may be naïve to expect knife-edge precision in relatedness assessments via phenotype matching. Self-referencing (discussed above) eliminates one of these variance components.

GROUP MEMBERSHIP AND NESTMATE RECOGNITION IN SOCIAL INSECTS

Many animal societies are 'closed', meaning that nonmembers are excluded from the social group and from access to the group's resources. Closure can have important but disparate roles such as preventing parasites and predators from entering the group, retaining resource monopolies for the group, and ensuring that aid-giving behaviour is directed to close genetic relatives. Because there are several possible independent evolutionary causes for societal closure, studies that assume that closure has always evolved to maintain the integrity of a kin group in which inclusive fitness effects favour altruism are at least somewhat flawed in their interpretations.

The line of reasoning that group closure always evolves in the context of altruism was a common thread in studies of social insect nestmate recognition in the 1970s and 1980s (Breed & Bennett, 1987). Much of the literature about social insects that discusses kin recognition focuses on recognition of group membership, and deals with nestmate recognition rather than kin recognition in a stricter sense. Nestmate recognition is the ability to discriminate nestmates from non-nestmates. Thus, nestmate recognition is typically a simple classification, yes or no, of group membership. When all members of the group are part of the same family, then nestmate recognition is, perforce, a form of kin recognition. However, stating that nestmate recognition is transitive, via kin recognition, to kin selection is logically problematic. The belief that kin selection is the only evolutionary mechanism that favours discriminatory abilities to distinguish group members from nonmembers needs to be critically assessed.

The most common result of studies of nestmate recognition in eusocial insects was finding that group members are identified by an environmentally derived phenotype that gives all members of the group a commonly held odour. In some cases this phenotype originates at least partly from the workers (is correlated with genotype) and is transferred via nesting material to other workers in the colony (many species of *Polistes* wasp: Gamboa 1996; Gamboa, Reeve, & Holmes, 1991; honeybees, *Apis mellifera*: Breed et al., 1995; d'Ettorre et al., 2006). In other cases, odours derived from food or nesting materials may have the potential for providing the basis for the group phenotype (Liang & Silverman, 2000). However, in many

ants the colony-level signature is established by a mixture of hydrocarbons deriving from the workers themselves (Bos & d'Ettorre, 2012; Brandt, van Wilgenburg, Sulc, Shea, & Tsutsui, 2009) and is therefore reflective of the genetic background of the colony. These results support arguments that mechanisms of recognition in eusocial insects are unique or different from those found in birds and mammals. Interesting and relevant to this point is Hughes, Oldroyd, Beekman, and Ratnieks (2008) paper on ancestral monogamy in eusocial Hymenoptera. Monogamy translates into low intracolonial genetic variance, relative to population level variance. The relatively low genetic variance may favour the use of colony-level environmental cues and not provide the information needed for within-colony nepotism.

If nestmate recognition had always evolved as a result of kin selection, the underlying assertion is that the phenotypes of semisterile or sterile workers translate into genotypic contributions to the next generation. In other words, worker genotypes that yield phenotypes for recognition of group members and that behave in ways that benefit group members should increase in succeeding generations. The lack of direct worker reproduction makes this an unlikely evolutionary route. In nest defence, workers often function as an extension of the queen's phenotype. More direct evolutionary reasoning argues that colonies with sound defences against parasites and predators will survive better, and that selection acts to favour the genotypes of queens whose offspring have better abilities to discriminate and exclude natural enemies. For an extended discussion of how unicoloniality, a condition found in some ant species in which colonies extend over large geographical areas, see the review by Helanterä, Strassmann, Carrillo, and Queller (2009).

This line of reasoning was not so obvious to investigators in the 1970s (Breed & Bennett, 1987). In the intervening years there have been several surges of intense discussion concerning the level of biological organization at which selection acts (Tarpy, Gilley, & Seeley, 2004). Some of this conversation has been specifically aimed at discerning whether the queen or the workers in eusocial insect colonies are the unit of selection. This makes a tremendous difference in discerning whether behaviour fits a Hamiltonian kin selection model, which generally assumes that workers make proximate choices about working for their own direct benefit or for the benefit of a relative.

Primitively eusocial insects provide the perfect, perhaps the only, laboratory for studying nestmate recognition in social insects in a context in which kin recognition might relate directly to kin selection. Studies of highly eusocial insects can tell us much about mechanisms, but these mechanisms must be interpreted considering that evolutionary changes have occurred after the presence of a worker caste is firmly canalized. In primitively eusocial insects, workers have the morphological and physiological capability to mate and produce their own offspring. Many primitively eusocial insects have the ability to discriminate nestmates from non-nestmates, a fact that easily leads to the hypothesis that the discriminatory system could have a dual role, giving information that can be used in both the exclusion of non-nestmates and the direction of aid-giving behaviour to the most highly related individuals in the colony. Studies of *Lasioglossum* bees (Greenberg, 1979) and *Polistes* wasps (Gamboa, 1988, Tibbetts & Dale, 2007) fit this mold, while studies of ants or highly eusocial bees, such as the honeybee, deal with animals that have traversed substantial evolutionary ground since the evolution of worker sterility. In many species, eusocial insect workers retain some reproductive potential, and chemical suppression of workers provides a very different route to understanding the evolution of worker behaviour (Peeters & Liebig, 2009). Recently Van Oystaeyen et al. (2014) suggested that pheromones that suppress worker reproduction are deeply rooted in the phylogeny of the Hymenoptera; further studies will reveal whether these compounds are actually suppressive or whether they are signals used by workers to assess the presence of a queen.

The kin selection model predicts that workers in haplodiploid eusocial insect colonies should favour the production of their full sisters (to which they are related by 0.75, on average) over that of their own daughters (with which they hold a relationship of 0.50). To obtain this genetic premium, workers should aid their mother, the queen, to which they are related by 0.50. From a worker's point of view, in a colony containing both her mother and some full sisters, the aid-giving behaviour should be directed not to the individuals with which she is most closely related, but to the individual (her mother) that is most likely to produce the highly related offspring. High relatedness, an ancestral characteristic in the Hymenoptera, may help to explain why eusociality evolved so many times in this order. From a worker's perspective, the benefits of helping the queen rear more offspring may be very high relative to helping a sister reproduce in the face of smaller ovaries or policing behaviour.

MHC GENES AND RECOGNITION IN CHORDATES

Outside the social insects, Hamilton's (1964a, 1964b) papers had a significant and lasting effect on studies of mammalian social behaviour. Early in this investigative thread, work on rodents suggested that odours associated with MHC loci could be used in kin-based discriminations, brood care interactions and inbreeding avoidance (reviewed by: Beauchamp & Yamazaki, 2003; Penn & Potts, 1998). Since the pioneering work on MHC/recognition correlations in mammals, we have grown to understand that MHC differences are correlated with recognition in many chordate species; the prevalence of this phenomenon (e.g. Olsén, Grahn, M., Lohm, J., & Langefors, 1998; Villinger & Waldman, 2008; Zelano & Edwards, 2002) suggests that the use of MHC-correlated odours in social recognition may a plesiomorphic characteristic in this clade. Outside the chordates, allorecognition is genetically mediated in colonial anemones (Cadavid, Powell, Nicotra, Moreno, & Buss, 2004).

NEPOTISM

Hamilton's contribution to the conversation about nepotism (Hamilton, 1987) pointed to published examples of nepotism, but he mostly called for a more concerted effort to test the hypothesis that animals can make finely tuned discriminations based on identity by descent. Early investigations included tests of the hypothesis that alarm calls might be directed to close relatives, a clear corollary of kin selection (Sherman, 1980, 1991). Mateo (2002, 2003, 2004) very thoroughly reviewed these studies. Evidence for nepotism is found in a number of primates, such as baboons (Smith, Alberts, & Altmann, 2003). Pfennig (1999) and Pfennig, Collins, and Ziemba (1999) showed that choices of victims for cannibalism in salamanders can be driven by kinship information, with kin being avoided. Further insight into the complexities of alarm calling, particularly concerning the question of whether the call attracts attention of the predator to the caller, have been detailed in the work of Magrath and colleagues (e.g. Haff & Magrath, 2011). Queller and Strassmann (1998) and Queller (2011) emphasize the role of kin selection in the evolution of eusociality and the important potential for kin recognition to mediate nepotism.

Breed, Welch, and Cruz (1994) reviewed the literature on within-colony nepotism in honeybees; the basic finding at the time of that review was that workers did not preferentially direct their behaviour to more closely related nestmates, or promote rearing of more closely related queens. Since publication of that review two decades ago, follow-up work on honeybees and other social insects

have confirmed that experiments testing the hypothesis of within-colony nepotism yield negative results (e.g. Koyama, Takagi, Martin, Yoshida, & Takahashi, 2009; Rangel, Mattila, & Seeley, 2009). As Ratnieks and Visscher (1989) pointed out, worker policing can destroy much of the evidence for kin-biased behaviour. Negative results in tests for fine-tuned, within-colony nepotism apply to other social insects as well, such as the ant *Platythyrea punctata* (Kellner & Heinze, 2011), the ant *Ectatomma tuberculatum* (Zinck, Chaline, & Jaisson, 2009), and the termite *Nasutitermes corniger* (Atkinson, Teschendorf, & Adams, 2008). In a minority of published studies evidence for relatedness effects have been found, such as foreign queens having lower reproductive value in ants (Holzer, Chapuisat, & Keller, 2008). Given the greater likelihood of publication of positive results than of negative results in science (Fanelli, 2012), it seems remarkable that so many negative results have been published for tests of nepotism in eusocial insects; this could be because each time a negative result is obtained it surprises the investigators, or perhaps the published negative results are only the tip of a much larger iceberg.

In mammals, a typical result is that of Blumstein, Ardron, and Evans (2002), who found differences in behaviour based on having either high or low kinship among tammar wallabies, *Macropus eugenii*, that could not be explained by familiarity, sex, body size, or other factors. This type of generalized ability to make discriminations between close kin and other population members probably serves animals well in preventing inbreeding and escalated aggressive interactions between unfamiliar close relatives, but it does not suggest fine tuning of aid-giving behaviour.

Experimental designs to parse out whether animals exert active choice in associating with kin have revealed that, in general, young animals accept association equally with kin and nonkin, and that adult animals, particularly females, are often accepting of nonkin young (Breed & Buchwald, 2008). The universality of the potential for adoptions speaks to the helplessness of young animals of many species, the strength of drives for parenting, and the fact that social recognition is usually based on postnatal learning (Sherman et al., 1997). The effects of adoptions on social interactions later in life are unknown, but these are likely subtle and difficult to separate from other causes of variance in social behaviour.

In some instances females are known to reject unfamiliar young. Is this because the young animal is unknown to the adult, as an individual, or because the adult perceives that the unfamiliar young animal is not closely related? It is harder to draw a generalization on this point. Despite the importance of knowing the answer to this question, experimental tests of the effects of kin recognition cues on acceptance of young have not been the focus of many studies. Or perhaps, such studies have generated negative results and consequently remained unpublished.

MATING PREFERENCES

Social recognition in the context of mating can be divided into the use of genetic information in mate choice and the use of individual phenotypes to recognize mates. Some types of genetic information, such as MHC matches or mismatches, may be used in mate choice without specifically referencing information about identity by descent. But being able to recognize close kin can translate also into not mating with close kin. Kin recognition cues that might be used in sorting out decisions about nepotism thus are potentially also used in inbreeding avoidance. Pusey and Wolf (1996) reviewed the literature on inbreeding avoidance in vertebrates. The genetics of inbreeding avoidance are best known in house mice, *Mus domesticus*, in which major urinary protein (MUP) matches are used to avoid consanguineous matings (Sherborne et al., 2007). Human leukocyte antigen (HLA) alleles are important in human mate choice (Jacob, McClintock, Zelano, & Ober, 2002). The use of non-MHC cues, such as MUP or HLA, suggests that considerably more exploration of social recognition in inbreeding avoidance and mate choice is needed.

Bateson's (1983) model for optimal outbreeding provides an interesting basis for thought about how kin recognition information might be used in mating contexts. Thoss, Ilmonen, Musolf, and Penn (2011) showed that there is an optimal level of MHC heterozygosity for fitness in wild house mouse populations. Optimal outbreed models have been applied more often in plant-breeding schemes than in field studies of animal behaviour, but recent work (Tabadkani, Nozari, & Lihoreau, 2012) argues that inbreeding avoidance mechanisms are widespread in arthropods and that inbreeding avoidance may have provided key mechanisms in the evolution of eusociality.

Maintenance of pair bonds is another arena in which social recognition is vitally important. Because pair affiliations endure over time in many birds and mammals, individual recognition of mates is often simply assumed. Bonadonna and Nevitt (2004) studied individual recognition of mates in birds based on odours (also see a review of this topic by Zelano & Edwards, 2002).

SENSORY AND INFORMATION PROCESSING LIMITATIONS

The possession of a hypervariable cue phenotype is only one of the necessary elements for making fine discriminations based on identity by descent. The other elements needed are the sensory and neurobiological capabilities to perceive and utilize the information embodied in the cues. Reeve (1989) developed a model of thresholds for responsiveness in recognition assays based on degree of difference in cues between a pair of animals. One important point in Reeve's (1989) argument is that response threshold can be adjusted depending on ecological circumstances; the costs and benefits of making a discrimination can change, and the threshold model gives a way of measuring how short-term environmental change can affect nepotism or other social interactions mediated by kin recognition.

Few studies have explored the sensory basis for discriminations based on a threshold of similarity or whether much finer distinctions can be made (see Breed, Diaz, et al., 2004; Breed, Perry, et al., 2004 for an exploration of how concentration ratios affect discrimination in honeybees). The length of time a social identity can be remembered also may be an important limitation that has not been deeply explored (Errard, 1994; Godard, 1991). Behavioural ecologists were slow, and continue to be slow, in incorporating developments on the neurophysiological bases of making discriminations between odour mixes (Ozaki et al., 2005) and on facial discrimination into discussions of kin recognition.

VISCOUS POPULATIONS

Very much underrepresented in the literature until Mitteldorf and Wilson's (2000) analysis were considerations of how population structure could affect kin selection and kin recognition. If local populations consist of highly related animals, does this reduce the likelihood of evolution of mechanisms for discriminating kin by degree of relatedness, or does it increase the premium for such a mechanism? More recent research has greatly expanded our understanding of how population viscosity and the evolution of altruism interact. Shorey, Piertney, Stone, and Hölund (2000) showed that population structure in a primate could be documented on a very fine scale, with implications for interactions that might be mediated by kin recognition, such as nepotism. Hauert and Doebeli (2004) integrated considerations of population structure with game theory analyses, and Lion and van Baalen (2007)

expanded the theoretical foundation for integrating population viscosity into kin selection models.

SUMMARY AND CONCLUSIONS

In retrospect, the gap between the publication of Hamilton's paper in 1964 and the flurry of papers on nestmate and kin recognition in the late 1970s seems inordinately long. The fields of animal behaviour and ethology were focused on questions of proximate causes and ontogeny, and it took some time for scientists to incorporate evolutionary thinking of the sort that characterizes contemporary studies in behavioural ecology. Kin selection, optimal foraging theory and mate choice theory are examples of the movement to bring direct thinking about ultimate causes into experimental design and interpretation of results. Hamilton was far ahead of his time in leading us to think more deeply about how behavioural mechanisms and evolutionary theory fit together.

My assessment is that Hamilton's (1964a, 1964b) core arguments about kin selection are sound, but that empirical findings on the use of kin selection in nepotism are much more nuanced than investigators in the 1970s might have expected. Individual recognition and self-referencing are strong themes emerging from studies of vertebrates (Mateo, 2010; Pollard & Blumstein, 2011, 2012), while the use of colony-level environmentally mediated cue profiles is the primary theme coming from work on eusocial insects (Breed & Buchwald, 2008). An important remaining problem is understanding the evolution of mechanisms for generating, perceiving and processing the information from hypervariable cues, such as MHC-related odours, primate faces or cuticular hydrocarbons (Breed & Buchwald, 2008; Tibbetts & Dale, 2007).

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