Problems of Kin Recognition

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Behavioural ecologists have long assumed that animals discriminate between their kin and non-kin, but paid little attention to how animals recognize their relatives. Although the first papers on kin recognition mechanisms appeared barely 10 years ago, studies now appear frequently in journals of animal behaviour. Initial findings reveal that kin recognition abilities are surprisingly well-distributed throughout the animal kingdom. Yet an understanding of the evolutionary and ecological significance of these abilities demands further analyses of the components of kin recognition mechanisms and the social contexts in which they are expressed. Many controversies and unresolved issues remain, and experimental approaches to these problems promise to continue making kin recognition an important, rapidly moving discipline within behavioural ecology.

The study of social behaviour was revolutionized two decades ago by W.D. Hamilton's proposal\(^1\) that apparent altruism could arise through natural selection when animals interact with close genetic relatives. While evidence of nepotism is widespread, how animals distinguish their kin from non-kin remained largely a mystery until very recently. Experimental studies of kin recognition mechanisms have proliferated rapidly in the past few years (Fig. 1), building upon a large body of earlier research which focused on parent/offspring recognition\(^2\). Although kin recognition abilities have now been found in a diverse array of organisms, the means by which they develop and are expressed vary widely. Recognition abilities of some species appear remarkably precise: individuals not only distinguish between kin and non-kin, but may even discriminate among close and distant relatives. Kin recognition abilities are expressed in many social contexts, not only mediating cooperative or altruistic behaviour, but also influencing, for example, mate choice.\(^3\) The empirical evidence for kin recognition has been the subject of several recent reviews\(^4\). Rather than summarizing these results, we present an overview of some conceptual and methodological issues that arise from this work.

Kin recognition is an emerging discipline and, not surprisingly, it is beset with controversy. Starting with the meaning of 'kin recognition' itself. Holmes and Sherman, for example, defined it as the differential treatment of conspecifics as a function of their genetic relatedness\(^5\) (italics added)\(^6\). We suggest that to avoid confusion the term kin discrimination be used henceforth to describe kinship-correlated differential treatment of conspecifics. Kin recognition can be defined more narrowly as the processes by which individuals assess the genetic relatedness of conspecifics to themselves or others, based upon their perception of traits expressed by or associated with these individuals\(^7\). We emphasize the distinction between kin recognition and kin discrimination because recognition - a series of internal and essentially unobservable physiological events - may occur without any behavioural response. In other words, recognized kin need not be differentially treated (i.e. discriminated).

Behavioural discrimination of kin may be based on the perception and evaluation of relatives' phenotypic traits (a process we term direct kin recognition), or it may be elicited by certain contextual features that are predictably associated with kin (indirect kin recognition), or both. Animals often rely upon aspects of the environment to discriminate between kin and non-kin. When the location of a nest serves as a good predictor for finding offspring, the nestlings themselves may not be recognized - a fact made use of by cowbirds and other brood parasites\(^8\). Should kin be encountered in a variety of contexts, discrimination is likely to be based mainly on direct recognition. Here we focus on the problems inherent in studying direct kin recognition.

Detecting kin recognition abilities

Kin recognition abilities can be studied by behaviourists only when they are expressed. We infer that animals directly recognize their kin when, without relying solely on contextual cues, they behaviourally discriminate between relatives and non-relatives or among kin of different degrees of relatedness. Conspecifics may be individually identified, and categorized as relatives or non-relatives based on the extent and context of their previous social interactions. Individual recognition abilities can lead to complex systems of kin discrimination, as in some primates (see Box 1). By contrast, conspecifics belonging to different kinship classes may be differentially treated even though they may not be individually recognized. For organisms living especially large kin groups, such class discrimination may represent the predominant mode (see Box 2). Kin discrimination might be evidenced in patterns of spacing\(^9\), distribu-

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tion of beneficial or detrimental acts\textsuperscript{1,2}. Frequency of exploration or avoidance behaviours\textsuperscript{1,2}, admittance to social groups\textsuperscript{1,4}, mating preferences\textsuperscript{1}, or parental care\textsuperscript{2}.

Direct kin recognition has now been demonstrated in many vertebrate and invertebrate taxa, and discrimination is apparent in a wide range of social behaviours. Yet kin discrimination can be highly context-dependent, leading to apparently contradictory experimental results. Studies designed to determine whether male wasps (Polistes luscatus) recognize their brothers have yielded both negative\textsuperscript{15} and positive\textsuperscript{19} results in the same laboratory. Honey bee (Apis mellifera) workers either do\textsuperscript{17,18} or do not\textsuperscript{19} preferentially rear as queens those larvae most closely related to themselves. Depending on precisely how they are cross-fostered and the behavioural assay used, deer mice (Peromyscus leucopus) either do\textsuperscript{11} or do not\textsuperscript{13} discriminate between unfamiliar siblings and unfamiliar non-siblings. Laboratory studies of kin discrimination in pigtail macaques (Macaca nemestrina) reveal similar discrepancies\textsuperscript{21}, again in a single laboratory. Toad (Bufo americanus) tadpoles do not discriminate between familiar siblings and familiar non-siblings in some laboratory conditions, but orient toward unfamiliar siblings rather than familiar non-siblings in others\textsuperscript{22}.

Clearly, negative results should not be interpreted as evidence of an inability to recognize kin. Moreover, positive results, especially from laboratory studies, do not clarify the function, if any, of such abilities (see below). Rather, such results suggest that our inferences as to whether animals recognize kin are dependent on the behavioural measures chosen and on the procedures used to evaluate them. It is important not only to determine whether and how animals recognize kin, but to understand why they discriminate in some contexts rather than others.

Mechanisms of direct kin recognition

Direct kin recognition results from a concatenation of three distinct elements\textsuperscript{22} (Fig. 41). First, individuals must bear labels which reveal information about either their individual identities or the kin group to which they belong. Labels may be continuously expressed, such as morphological traits, or they may be selectively produced, such as behavioural displays or chemical, auditory or visual signals. Labels can be either predominantly environmental\textsuperscript{21} or genetic\textsuperscript{11,23} in origin, but frequently incorporate multiple components which can be teased apart through careful study\textsuperscript{24}.

Secondly, individuals must have some receptor mechanism by which they can perceive conspecifics' labels, and an internal representation, or template, that provides a model of kin traits with which perceived labels can be compared. A template may store labels encountered at an early life stage, or may be continually updated to reflect changing labels of known individuals. At present, templates are more difficult to study than labels — indeed as in studies of bird song, they remain hypothetical constructs, describing features that we assume must exist. Animals commonly acquire kinship templates by learning the traits of putative kin or their own traits. Conceivably, however, templates could also be genetically determined, or could be selectively learned according to a genetic programme.

Finally, a decision effectively must be made concerning the relatedness of a conspecific. The fit between labels and templates is evaluated by some criterion (a decision rule). The characteristics of the decision rule will be determined by the extent of label variability, within and among kin classes\textsuperscript{26,27}, the likelihood that conspecifics of each kin class will be encountered, the social context in which conspecifics meet\textsuperscript{4}, and the benefit conferred by correctly identifying kin versus the cost of mistakenly treating non-kin as kin\textsuperscript{28}.

Contexts of kin recognition

Kin recognition abilities should be favoured by natural selection when individuals interact with both kin and non-kin, or with kin of varied relatedness, and kin discrimination confers an advantage greater than its cost measured in terms of inclusive fitness. In the current literature, kin recognition abilities are often categorized according to the social contexts in which they are expressed.

Discrimination of specific individuals with which one has previously interacted can be attributed to a form of 'familiarity-based recognition', or recognition by association\textsuperscript{6}. Individuals presumably learn one another's traits in a setting where only relatives are likely to be present, later distinguishing them from non-kin in other potentially more ambiguous settings. Thus parents and young of many species typically learn each other's traits just before the young first interact with non-kin\textsuperscript{6}. Similarly, young animals may learn their siblings' traits. If the labels expressed by every member of a circumscribed kin group (e.g. within a nest, burrow or insect colony) are distinct, individual recognition may result\textsuperscript{29}. Alternatively, labels may be pooled to form a ubiquitous group label, as in desert woodlouse (Hemilepistus reaumuri)\textsuperscript{10}, or they

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**Box 1. Recognizing own and others' relatives**

Kin recognition research typically examines mechanisms by which animals recognize their own relatives. Yet in complex animal societies, animals also may recognize kinship relationships among other individuals. Cheney and Seyfarth have shown that vervet monkeys (Cercopithecus aethiops) not only recognize each other individually, but use this information to group conspecifics based on matrilineal kinship. For example, vervets were more likely to act aggressively toward an individual if they had previously fought its close kin (i.e. mother, offspring or maternal sibling). Animals more than three years old were observed to threaten a conspecific more frequently if that individual's close kin had previously fought their own close kin\textsuperscript{17} (Fig. 2).
Animals living in kin groups comprising thousands or tens of thousands of individuals, such as social insects and amphibian larvae, probably recognize close relatives based on shared traits rather than individually distinctive traits. Experiments on American toads \textit{Bufo americanus} tadpoles illustrate how the ontogeny of such recognition systems can be studied \cite{Note1}. Embryos were separated into individual petri dishes a few hours after fertilization, and larvae were reared in social isolation for several weeks. When 10 isolates belonging to two sibling groups were mixed in a laboratory test pool, the groups sorted out. Tadpoles similarly discriminated between unfamiliar full-siblings and paternal half-siblings, but not between full-siblings and maternal half-siblings, suggesting that siblings may recognize one another by their shared maternally-derived labels (Fig. 1a). Results differ when tadpoles experience socially enriched environments. Larvae reared in mixed groups with both siblings and non-siblings during the first few days after hatching subsequently failed to discriminate between these classes, but larvae reared just with their siblings did discriminate between siblings and non-siblings (Fig. 1b). Taken together, these results suggest that animals may recognize kin by comparing conspecific traits with some model or template. Reared in isolation, individuals necessarily use their own traits as a model, but individuals may also recognize conspecifics whose traits are similar to kin that they have previously encountered in contextually reliable circumstances. As tadpoles passively remain in sib groups for several days after hatching, such a mechanism would ensure subsequent kin identifications. Holmes and Sherman \cite{Note2} termed this process phenotype matching.

Increasing numbers of studies demonstrate that animals can also discriminate between unfamiliar kin and unfamiliar non-kin, or among familiar kin of different degrees of relatedness \cite{Note3}. Here, kinship identity may be inferred from the perceived overlap in traits between conspecifics, a process which has been termed 'phenotype matching' \cite{Note4}. In other species, however, the recognition of familiar individuals also involves matching phenotype \cite{Note5}. Kin discrimination may be selected even in circumstances in which familiarity provides no indication of relatedness. Polyandrous mating provides a case in point, because it often leads to the simultaneous presence of full- and half-siblings within a common brood or nest. When males provide parental care, selection may favour males that discriminate between their own young and others. Among the progeny, full-siblings might be expected to cooperate preferentially with one another. Similarly, half-siblings reared in separate burrows or nests might gain some advantage if they can recognize one another.

Kin recognition expressed in these different contexts is generally attributed to different mechanisms. Yet it is important to realize that the actual behavioral and physiological processes leading to kin discrimination may be the same. Because of a tendency for individuals to generalize the models upon which recognition is based, unknown relatives may be discriminated not because recognition necessarily confers some advantage but simply because they resemble individually known kin. Generalization of genetically determined cues has been most clearly documented in social bees (see Ref. 31). For example, the frequency with which a sweat bee guard \textit{Lasioglossum zephyrum} admits a conspecific into her nest is directly proportional to the coefficient of relatedness between them \cite{Note6}. This might be interpreted as evidence of a 'phenotype matching' mechanism, but may instead represent mistaken individual identifications of non-nestmates due to their nest similarities with nestmates.

 Genetic recognition

Experimental results sometimes reveal kin recognition abilities that appear not to be due to social experience. Attributing these effects to 'genetic' recognition systems in the absence of knowledge of the ontogeny of recognition does little to explain either the mechanisms underlying discrimination or its evolutionary basis \cite{Note7}. If kin are to be recognized through a purely genetic system, in most cases this will require matching of multiple labels encoded by alleles at many loci with a genetically-determined template that similarly reflects the overall genome. An alternative interpretation of such results is that individuals, in assessing their relatedness to conspecifics, learn their own phenotypic characters and use them as a model. In essence, comparisons are then made with a self-template, comprising labels that individuals perceive from themselves. By changing these labels early in life \cite{Note8}, indeed before individuals experience them (e.g. by transplanting embryonic tissues involved in the production of labels \cite{Note9}), it may be possible to test whether or not self-templates are learned.

Another type of genetic recognition is also possible. Hamilton \cite{Note10} suggested that alleles might exist
that (a) encode a phenotypic label, (b) enable their bearers to perceive this label, and (c) induce them to treat favourably those conspecifics that share this label. Conflined to a single locus, this would not necessarily lead to recognition of kin that share the allele by common descent. Hence, Dawkins' dubbed this process a "green beard" effect, as it would facilitate cooperation among all individuals sharing a green beard, whether they were related or not.

Although such "recognition alleles" are often discussed as determinants of innate recognition, the crux of Hamilton's argument is not that these alleles would lead to recognition in the absence of learning. Indeed, they would function in much the same manner if they caused their bearers to learn the phenotypic marker that they produce. Rather, the important issue is whether such alleles could spread, and if they do, how behavioural traits can be influenced at different levels of selection. These points are still debated, but it appears unlikely that such alleles would spread if they caused their bearers to favour non-kin that shared their copies at the expense of kin that did not.

Recognition alleles might spread, however, if they effectively led to kin discrimination. This could occur if there were high levels of allelic polymorphism, such that non-relatives shared alleles very infrequently. Such extreme polymorphism has been found to date only in loci involved in immune function. The major histocompatibility (MHC) locus of vertebrates and its possible antecedents in marine invertebrates both appear to be sufficiently variable potentially to code kinship identities. This polymorphism must be maintained by selective factors independent of those favouring nepotism, or recognition alleles would become fixed in populations. Labels encoded by histocompatibility loci influence kin-directed behaviours both in rodents and various marine invertebrates. Indeed, sea squirts (Botryllus schlosseri) in field arenas settle more closely to non-kin with which they share a histocompatibility allele than to kin bearing a different allele. Because the be-

a single allele, this finding lends credence to Hamilton's original conjecture. Given the extent of polymorphism, in nature the likelihood of a sea squirt encountering non-kin sharing a histocompatibility allele would probably be small.

Problems of interpretation
Experimental demonstrations of kin recognition abound in the recent behavioural literature. Although nepotism or "optimal outbreeding" are often presented as the probable selective advantages associated with discrimination, only rarely is the functional basis of kin recognition known (see Box 1). Here we consider some of the problems of determining why animals recognize kin.

Because recognition abilities are indirectly assessed, experiments are especially susceptible to both false negative errors (an absence of behavioural discrimination even though animals can recognize kin) and false positive errors (observing behavioural discrimination in the absence of kin recognition). As we have noted, kin discrimination is highly context-dependent. False negative errors can result if recognition abilities are assessed in an inappropriate setting. Although such negative results are often not deemed interesting enough to publish, much insight can be gained if the conditions under which animals do and do not discriminate kin are systematically compared.

If researchers are aware of the relatedness of interacting conspecifics, false positive errors may occur if inadvertent observer bias subtly influences results. Biased sampling is particularly dangerous in studies of kin discrimination because behavioural preferences for one kin class over another are often reported to be slight. Blind studies are especially difficult when phenotypic markers are used in distinguishing between various classes of kin and non-kin. When possible, relatedness should be evaluated after behavioural observations are made (e.g. by electrophoretic or DNA measures), and in all cases the degree to which studies are conducted "blind" must be specified.

Similar errors can result if the experimentally to distinguish kin groups themselves influence discrimination. Research into the consequences of multiple mating by honey bee (Apis mellifera) queens has shown that workers can discriminate between full- and half-sister

Box 3. The functional basis of kin recognition
Knowledge of the mechanisms underlying kin recognition may permit behavioural ecologists to predict more precisely the circumstances in which kin-directed behaviours are expressed and the extent to which they can augment inclusive fitness. Field studies of kin recognition are thus especially important. Nepotism, manifested in alarm calls and territory defense benefiting kin, has been particularly well documented in Belding's ground squirrels (Spermophilus beldingi). By cross-fostering pups in the field at different times prior to natal dispersal, Holmes and Sherman found that pups learn to recognize as littermates those individuals with which they shared a natal nest. Not all siblings in a nest are equally related, however; females mate multiply, and litters often consist of full and half-siblings which can be identified by electrophoretic allozyme analyses. This multiple paternity makes possible a natural "blind" experiment, as behaviours of individuals can be observed before paternity relationships are determined. Among yearling females from the same litter, full-sisters were found to be more cooperative and less agonistic than half-sisters (Fig. 7). The ability of yearlings to discriminate between unfamiliar paternal full-siblings and unfamiliar non-siblings was also reported, based on laboratory arena tests ( Fig. 8). Other laboratory tests suggest, however, that familiar individuals generally act less agonistically toward one another than do unfamiliar individuals. Hence, S. beldingi appear able to use both direct and indirect mechanisms of kin recognition. Females, especially, appear able to use their own phenotype as a model for identifying close relatives, both familiar and unfamiliar.
Fig. 5. Agonistic interactions recorded in the field among yearling female Spermophilus beblington from broods of mixed paternity. Full- and maternal half-siblings were determined by allozyme analyses of blood samples only after behavioral measurements had been made. (a) Mean proportion of fights per encounter on females’ territories between pairs of littermate sisters (full- and half-sisters combined), full-sisters, and maternal half-sisters. (b) Mean proportion of chases per trespass on females’ territory between littermate sisters, full-sisters, and maternal half-sisters. Error bars denote ± 1 st. Numbers of dyads in each category given in parentheses. From Ref. 12.

Fig. 6. Agonistic interactions of yearling female Spermophilus beblington in laboratory tests. For siblings reared together, paternal half-siblings reared apart, and non-relatives reared apart. Mean number of agonistic encounters. (relatedness x rearing group) Pairs Tested. Redrawn, with permission from Ref. 18.

Fig. 5. suggests that the use of cuticle color markers enhances odour differences among patriline and may lead to 'kin' discrimination that would not normally occur (P.C. Frumhoff, Ph.D. thesis, University of California, Davis, 1987). When phenotypic markers are used, researchers must assess and control for their effects.

Even when appropriate controls are used, laboratory studies can still be difficult to interpret if little is known about the organism's natural history or if domesticated, highly inbred lines are used, or both. Laboratory studies of such organisms can elucidate the origin of labels and templates and the ontogeny of recognition abilities; functional interpretations of these results, however, may be difficult if not impossible.

While laboratory studies provide opportunities to test discrimination among a variety of kinship classes, evidence of discrimination between classes that do not regularly co-occur in the wild usually fails to provide evolutionary insight. Experimental studies revealing kin discrimination within particular social and environmental conditions are of interest to behavioral ecologists to the extent that the conditions approach those found in nature. For example, data suggest that Cascade frog (Rana cascades) tadpoles preferentially associate with unfamiliar siblings over unfamiliar non-siblings and with maternal half-siblings over paternal half-siblings. Tadpoles are difficult to place in an ecological context because tadpoles are unlikely to encounter either unfamiliar siblings or half-siblings in nature. Because eggs typically are communally oviposited, tadpoles are usually exposed to both siblings and non-siblings, yet familiar siblings are not distinguished from familiar non-siblings in laboratory tests.

Interpreting the adaptive significance of kin recognition is difficult even if these methodological problems are resolved. Consider, for example, evidence that toad (Bufo americanus) tadpoles preferentially school with siblings rather than non-siblings in their natural habitat. Studies of the mechanisms underlying kin discrimination suggest that siblings share maternally-derived labels, which might be produced by the intestinal gut fauna that they acquire from their mothers. Grafen (pers. comm.) has suggested that, because of microfaunal variation, different siblings might develop different feeding preferences such that siblings would sort out into separate schools. If this were true, schooling with siblings rather than non-siblings may confer no particular social advantage. In fact, evidence now exists that tadpoles react in distinctly different ways to kin and non-kin, and that these interactions can influence their respective growth rates. But there is no reason a priori to conclude that kin-directed behaviors result from kin selection or selection on mate choice.

Prospects

Studies of kin recognition abilities hold promise both for understanding the proximate mechanisms of inclusive fitness maximization and for elucidating how animals perceive their social environment. During the past 20 years, research in behavioral ecology has shifted from a primarily typological approach to one in which variation among individuals has become the principal focus. Kinship is a key corollary of that variation. The development of an ecological framework for understanding how organisms attend to their relatedness to conspecifics remains a challenge for future research.

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References
