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Mechanisms of Kin Recognition

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Although kin recognition mechanisms are necessary neither for the operation of kin selection nor for optimal mate selection (e.g. inbreeding avoidance), once established, such mechanisms may accelerate the evolution of kin-directed behaviors. Aside from spatially-based recognition, in which organisms adjust their behavior principally in response to their immediate location, several behavioral mechanisms originally suggested by Hamilton recently have generated discussion and controversy. Familiar kin can be identified individually, but individual recognition mechanisms alone cannot serve to distinguish between closely and more distantly related kin, or to identify novel relatives. These kin can be identified through group recognition mechanisms that evaluate the extent of trait overlap among individuals to determine their probable genetic relatedness. Precisely whom an organism recognizes as kin using either type of mechanism may be dependent on its past social experience. Individual recognition permits discrimination of previously encountered conspecifics, whereas group recognition generally leads to discrimination of individuals sharing traits with previously encountered conspecifics. Individual and group recognition mechanisms are not mutually exclusive, and they may operate concurrently. Furthermore, they are not distinct, separable processes. Mistaken individual identifications become more likely as conspecifics show increasing phenotypic resemblance, and hence kin discrimination can result directly from individual recognition mechanisms. The extent to which kin are identified depends on a criterion rule which may fluctuate in response to social, spatial, and temporal factors. When favored by natural selection, kin recognition may be facilitated by the process of stimulus generalization, as trait matching is achieved within wider tolerance ranges. But such generalization may occur even in the absence of selection *per se*.

Recognition effected through the action of hypothetical "recognition alleles" does not constitute a logical alternative to individual or group kin recognition mechanisms. In common with those processes, recognition alleles must operate by the effective matching of phenotypes. Unlike kin recognition mechanisms, which assess similarity by generalized phenotypic comparisons, the phenotype compared by a recognition allele (or linkage group) is that it itself generates, leading to the possibility of intragenomic conflict. As suggested by Hamilton, alleles might be expected to induce their bearers to favor behaviorally conspecifics that share their copies, regardless of the overall genetic relatedness of those conspecifics. Hence, recognition alleles, if they exist, would not invariably lead to kin identifications. Moreover, such alleles need not act in a manner that necessarily excludes learning.

Through inbreeding experiments, a genetic component to the labels that elicit kin recognition has been demonstrated in some invertebrates. Genetically determined kin recognition templates, with which the labels are compared, have yet to be established. A "genetic recognition system" cannot be safely inferred when experiments fail to demonstrate experiential effects on recognition abilities. Kin recognition mechanisms can be characterized through detailed examination of the ontogenetic

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and sensory processes underlying recognition abilities, and of the ecological and social contexts in which kin-directed behaviors are expressed.

Introduction

As the field of sociobiology matures, investigators are becoming increasingly concerned with the mechanisms underlying the complex social behaviors they study. Hamilton's (1963, 1964*a*) extension of Darwin's theory of natural selection to consider the effects of interactions among genetic relatives, together with renewed interest in problems of inbreeding and outbreeding (e.g. Bateson, 1983), recently has sparked a flurry of empirical investigations on how animals behaviorally differentiate between kin and non-kin. Kin discrimination abilities have been demonstrated in a wide variety of animals, with evolutionary consequences that often are still unknown. In many cases, social discrimination appears to be facilitated by the operation of kin recognition mechanisms. Kin recognition is the perception of cues associated with individuals that permit an assessment of their genetic relatedness to one another or to oneself. Behavioral discrimination may, but need not, follow from recognition.

After formalizing genetical kinship theory, Hamilton (1964*b*, pp. 21–25) suggested various means by which differential behavior toward kin might be achieved. From his discussion, four possible mechanisms can be extracted (e.g. Holmes & Sherman, 1983): (1) When organisms exist in highly structured ("viscous") populations, kin discrimination can incidentally result from philopatry, e.g. an individual might simply alter its behaviors depending on its distance from home. (2) Even when populations are less rigidly structured, kinship might be assessed by one's familiarity with particular conspecifics, identified through a system of individual recognition. (3) More generally, discrimination of those individuals that "look alike" (or otherwise resemble each other) effectively provides a means for detecting kin if phenotypic similarities reflect genotypic similarities. (4) At the genic level, one might expect alleles to be selected to cause their bearer to recognize, and to act in a manner that benefits, conspecifics that share their copies.

While these proximate means of kin recognition have been recently reviewed and elaborated on (Alexander & Borgia, 1978; Alexander, 1979; Harvey, 1980; Hölldobler & Michener, 1980; Bekoff, 1981; Waldman, 1981, 1983; Beecher, 1982; Dawkins, 1982; Holmes & Sherman, 1982, 1983; Blaustein, 1983; Gadagkar, 1985; Sherman & Holmes, 1985; Hepper, 1986), experimental investigations of mechanisms have lagged behind. Many species are apparently capable of identifying kin with which they have not previously interacted (social insects (Greenberg, 1979); fish (Quinn & Busack, 1985); amphibians (Blaustein & O'Hara, 1981, 1982; Waldman, 1981, 1986*b*); rodents (Davis, 1982; Grau, 1982; Holmes & Sherman, 1982; Kareem & Barnard, 1982; Hayashi & Kimura, 1983; Wills *et al.*, 1983; Holmes, 1986*a*); primates (Wu *et al.*, 1980; but see Fredrickson & Sackett, 1984; Sackett & Fredrickson, 1987)). Nonetheless, for most social species, the finding that kin recognition abilities can develop in the absence of opportunities to interact with relatives implies little about the ontogeny of these abilities under natural conditions (see Buckle &

Greenberg, 1981; Waldman, 1981, 1982). Studies aimed at understanding (1) the development and expression of traits communicating information about individuals' kinship identities, and (2) the processes involved in perceiving and acting upon this information, have been conducted on only a few species (see Linsenmair, 1972; Greenberg, 1979; Buckle & Greenberg, 1981; Waldman, 1981, 1984, 1985*a*,*b*; Shellman & Gamboa, 1982; Hepper, 1983, 1987; Pfennig *et al.*, 1983*a*,*b*; Gamboa *et al.*, 1986*a*,*b*; Carlin & Hölldobler, 1986).

The paucity of data on the ontogeny of recognition cues and the behavioral preferences that they elicit in part reflects confusion regarding the relationship between these two separate components of kin recognition (which were delineated by Alexander, 1979; Beecher, 1982; Waldman, 1983, 1985*b*; Sherman & Holmes, 1985). While kin recognition systems can function only if individuals are differentially responsive to cues associated with conspecifics genetically related to themselves (or to each other), the cues and responses may be influenced by different ontogenetic processes. Yet recognition mechanisms underlying different forms of behavioral discrimination may involve similar processes of phenotypic comparison. In suggesting that discrimination abilities evidenced in varied social contexts are due to different recognition mechanisms, recent reviews on kin recognition (e.g. Holmes & Sherman, 1983; Sherman & Holmes, 1985) have drawn attention away from problems inherent in characterizing properties of the recognition mechanisms. As a result, a dichotomy between learned and innate recognition systems often has been drawn without due consideration of the mechanisms underlying discrimination. Although genetic models of phenotypic comparison have been proposed (Crozier & Dix, 1979; Getz, 1981; Lacy & Sherman, 1983), a theoretical framework for the behavioral and physiological processes involved in making kinship discriminations has been generally lacking (also see Byers & Bekoff, 1986; Hepper, 1986; Halpin & Hoffman, 1987). The purpose of this paper is to integrate genetic, mechanistic, and functional perspectives on kin recognition. My review of the empirical literature is thus necessarily selective, discussing only key papers that illuminate how various processes may interact to effect the identification of kin.

Spatially-based Recognition

Differential behavior based on one's physical location, rather than on the perception of traits expressed by one's conspecifics, represents a means of social discrimination if location constitutes an accurate cue as to genetic relatedness. Organisms that lack a dispersal phase during their life-cycle are typically surrounded by close relatives, and their social interactions then may be largely confined to these kin. When average relatedness is high and variation in relatedness is low, any cooperative acts expressed, even indiscriminately directed, should be favored by kin selection (Alexander, 1979). Even for very mobile organisms, spatially-based behavioral rules may be sufficient to enable individuals to effectively discriminate between kin and non-kin. Two general types of locational cues might be used. Behavior might be varied in accordance with one's proximity to a clearly identifiable location such as a nest or a burrow that for most species is likely to contain close kin. Mother–offspring relations provide one common instance in which the correlation between location and relatedness is likely to be high, especially during early ontogenetic stages prior to dispersal (see Holmes & Sherman, 1983; Michener, 1983). Individuals located in a nest then may be treated as kin simply because they are present there. Indiscriminate behavior toward neighboring conspecifics might also be selected among classes of individuals that share characteristic patterns of post-natal dispersal (or lack of dispersal). Home ranges or territories may then serve as markers, but these spatial cues provide a less reliable indicator of genetic relatedness than do nests or burrows.

In many mammals, males, but not females, disperse from their natal area after weaning, and often they disperse in kin groups (e.g. lions (Bertram, 1975, 1976), baboons (Packer, 1979)). Among birds, in contrast, males tend to be philopatric and females disperse (see reviews by Greenwood, 1980, 1983; Greenwood & Harvey, 1982; Waser & Jones, 1983). In these situations, cooperation directed toward spatially proximate members of the same sex might be expected even in the absence of social recognition. If the dispersing sex does not move together in kin groups, cooperation should be limited to the non-dispersing sex. Although most vertebrates do in fact appear to socially discriminate among conspecifics (see review in Colgan, 1983), patterns of cooperation reflecting differential dispersal are frequently found (Greenwood, 1983). When individuals disperse from natal areas, differential habitat selection (genetically determined or environmentally induced, e.g. by early rearing conditions) could result in a kin-structured population; kin simply need to respond in similar ways to heterogeneous aspects of their environment. Male spruce grouse have been found to disperse distances that are characteristic of their sibship (Keppie, 1980), and similar effects are apparent in other organisms (e.g. voles, Hilborn, 1975). Nest site recognition may play an important role in directing cooperative behavior among philopatric polistine wasps (e.g. West Eberhard, 1969; Klahn, 1979; Noonan, 1981; Pratte, 1982), although recent studies suggest that recognition cues expressed by individuals may derive in part from nest materials (reviewed in Gamboa *et al.*, 1986*b*). Cooperation (and reduced competition) among birds returning to natal breeding sites, presumably triggered by common responses to environmental cues, might also be favored by kin selection (Treisman, 1978, 1980; also see Greenwood *et al.*, 1979; Trainer, 1980).

Familiarity-based Recognition

When kin groups disperse and do not subsequently reaggregate predictably in time and space, the finding that organisms act differently toward kin and non-kin implies that they possess some sort of behavioral kin recognition mechanism. Most frequently, kin recognition appears to be based on recall of the extent and context of previous social interactions with conspecifics, or in other words, their degree of familiarity (Maynard Smith, 1978; Bekoff, 1981; Holmes & Sherman, 1983). In the simplest case, a female parent may lay eggs (or give birth), and then observe her offspring to learn their distinctive properties (e.g. vocalizations (Beer, 1970; Beecher *et al.*, 1981), visual characteristics (Bertram, 1979), or odors (Kühme, 1963; Myrberg, 1975; McKaye & Barlow, 1976)). Offspring similarly may learn characters of their parents, enabling them to actively solicit parental care. Parental behaviors directed toward offspring, and responses of offspring to parents, both represent mechanisms that can induce sibling association. Even in species that lack parental care, opportunities for kin to learn each other's individual traits frequently exist during early development. For example, siblings may be spatially clumped if they all hatch from the same egg mass or fledge from the same nest. Kin recognition mechanisms involving the learning of individuals' traits can only function if conspecifics encountered in particular conditions, such as these, are likely to be kin. If juvenile traits are predictive of adult traits (see Bateson, 1979), or if these traits can be tracked as they change through maturation, learned characters would provide a sufficient basis for the subsequent indentification of kin even in other life stages. Kin recognition in these contexts is dependent, minimally, on an ability to perceive differences among individuals, but recognized individuals need not share particular traits.

Discrimination of familiar individuals, those previously encountered in circumstances reliably correlated with kinship, can occur by means of an *individual* recognition mechanism (see Halpin, 1980, 1986 for examples). Because every individual may express a different set of traits, kin need not resemble one another, and an individual's genetic relatedness to others cannot necessarily be determined directly by comparing their traits. Once recognized, however, specific individuals can be categorically assigned to kin classes dependent on the circumstance in which they were previously encountered. Kin discrimination can thus be based on the very same set of traits used for individual recognition (see Porter *et al.*, 1986). That kin discrimination effectively occurs by individual identifications may not always be apparent, however, for individual recognition abilities are not expected to be behaviorally expressed in every social situation. When motivation is lacking or when such discrimination is not selectively advantageous, an individual may treat all members of a class similarly even though it perceives individual differences among them. For the same reasons, an organism may individually discriminate among a few members of a kin class but act indiscriminately with respect to the others. Degradation in individual discrimination responses might also be a consequence of memory "saturation" as social groups increase in size, especially for organisms with simple nervous systems. Then recognition effectively may be based on the detection of similarities among individuals, a potentially simpler process that is dependent on the existence of phenotypic correlates to group membership.

The theoretical distinction between recognition processes operating on individual traits and those operating on shared traits is neatly encapsulated in the concepts of heterogeneous and homogeneous groups or subgroups (Barrows *et al.*, 1975). Members of heterogeneous groups share no attribute except that they have all been experienced by the individuals grouping them. Members of homogeneous groups, on the other hand, share one or more biological characters, and thus can be considered a class. Social discrimination based on individual identifications can occur in either type of social group, whereas recognition based on shared traits can be effective only when these traits vary substantially more among (kin) classes than within classes, as when homogeneous groups exist. Barrows *et al.* (1975) argue that individual recognition is not necessarily implicated when discrimination is found in heterogeneous groups, because group members' individual traits might be collectively stored in a common memory representation. Then, if any traits expressed by an individual overlapped with those previously encountered by a second individual, the second individual might recognize the first (other matching algorithms, such as acceptance of individuals not bearing unfamiliar labels, also could effect recognition). But an organism that employed this strategy would be prone to frequently "recognize" individuals that in fact it had not previously encountered (Fig. 1). Assuming that kin are identified based on several traits (encoded, for example, by independently assorting genes) and that these traits are not rare in the population, many individuals will express particular traits though not necessarily in specific combinations. Knowledge of these combinations, or profiles, constitutes individual recognition. If populations are genetically structured in space or time so that kin are segregated in pockets, or if kin share traits in common, collective recognition is more likely (see discussion of kin recognition "templates" below). In most cases, how organisms discriminate between familiar and unfamiliar individuals remains an unanswered question (see, e.g. Hopp *et al.*, 1985), but familiar conspecifics appear most likely to be identified individually.

Non-kin, should they be encountered by juveniles (e.g. if social groups mix) during early sensitive periods, thereafter would be treated by those individuals no differently from true kin. Such mechanisms of kin identification are quite common: young birds can be experimentally cross-fostered between different parents (e.g.

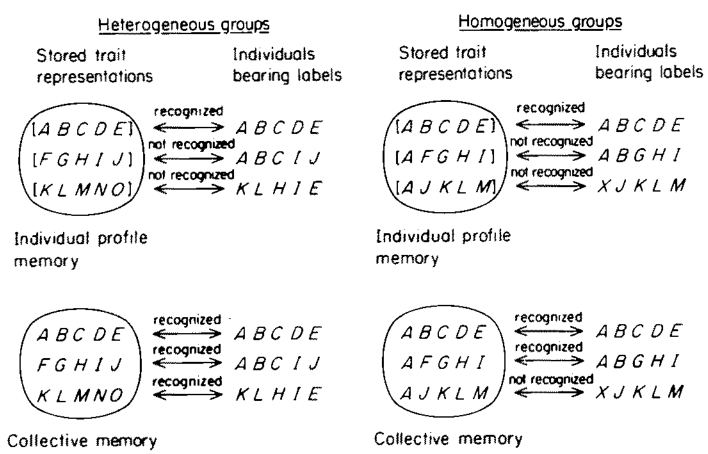

FIG. 1. Examples of how individuals would be identified based on some simple familiarity-based models of kin recognition. Once individuals (denoted by brackets) with particular labels (letters) are encountered, the labels are stored in an internal memory representation (denoted by ovals). Groups can either be heterogeneous (i.e. members do not necessarily share labels) or homogeneous (members share some labels). In identifying conspecifics it has previously encountered, an individual can recall their labels from an individual profile memory which preserves specific label combinations, or from a collective memory in which only the labels and not their associations are represented. For heterogeneous groups, familiar individuals will be recognized using either type of memory, but a collective memory may often lead to the recognition of individuals bearing familiar labels that are not group members. For homogeneous groups, in contrast, use of a collective memory will permit the identification of individuals that may not have been previously encountered but are nonetheless likely to be group members.

bank swallows, *Riparia riparia* (Hoogland & Sherman, 1976; Beecher *et al.*, 1981)), as can immature Belding's ground squirrels (*Spermophilus beldingi*) of different litters within 23 days of birth (Holmes & Sherman, 1982; Holmes, 1984). In these contexts, members of a class (i.e. putative offspring) appear to be commonly identified despite the fact that they may be expressing entirely different sets of traits. Hence, discrimination is based on traits learned from each individual rather than on those that may be shared among individuals. Indeed, interspecific cross-fostering experiments suggest that filial recognition may be mistakenly elicited not only by non-kin but also at times by heterospecifics (Lorenz, 1935). In such situations, the possibility that individuals are identified by means of the traits they share is eliminated, making individual identification of relatives the likely mechanism. When groups are not so large as to make recall of individual identities unreliable, kinship discrimination based on mechanisms that neither detect nor evaluate phenotypic resemblances among individuals may be generally quite effective. While mistakes can arise through accident, cuckoldry or deception, social discrimination systems of this type serve a variety of functions. Aside from group membership, knowledge of individual identities may facilitate social discrimination based on the age, sex, dominance status, or physiological condition of conspecifics (for reviews, see Brown, 1979; Halpin, 1986).

During the course of evolution of social behavior, an ability to differentiate among social partners on the basis of the outcome of prior interactions may be just as important as an ability to distinguish genetic relatedness (Trivers, 1971; Rothstein, 1980; Axelrod & Hamilton, 1981; Wasser, 1982). Kin-directed behaviors may be further influenced by the social status of related and unrelated conspecifics, which can be most accurately ascertained through systems of individual recognition (Barnard & Burk, 1979, 1981; Breed & Bekoff, 1981). Moreover, individual recognition of kin may more readily permit the dispensation of altruism to those relatives with high reproductive value, and such social discrimination with occasional favoritism of distantly over closely related individuals should be strongly selected for (Schulman & Rubenstein, 1983). Clearly, individual recognition abilities can serve as a foundation for many complex social systems.

From a consideration both of the behavioral consequences and the complexity of the requisite neural substrates, the recognition of individuals should be considered a more sophisticated task than the classification of individuals based on their group identities. To recognize familiar conspecifics through an individual recognition mechanism, trait profiles of every familiar individual must be stored, and then recalled in some manner when kinship assessments are made. Either serial or parallel matching algorithms might be used (Reed, 1973). Serial matching involves the sequential comparison of traits, one at at time, so that the processing time required for assessing recognition generally should be proportional to the number of traits compared. If an organism were capable of making parallel comparisons, however, many traits simultaneously could be compared, perhaps by different parts of the central nervous system, and recognition could more efficiently be assessed. To the extent that traits are compared serially (and in some cases they appear to be, even by humans; see Reed, 1973), kin recognition based on individual traits necessarily involves many more comparisons than kin recognition based on collectively represented traits. Serial processing might be especially characteristic of organisms with simple nervous systems. These organisms may be limited in their recognition abilities, matching broadly defined characters rather than specific traits. Effectively, this would result in group recognition based on shared traits. But kin identifications in organisms with more complex nervous systems, such as primates (reviewed in Gouzoules, 1984), may often be made largely through the recognition of known individuals.

Social discriminations based on individual and group recognition mechanisms are not mutually exclusive possibilities. Group recognition may occur concurrently with the recognition of individuals within kin and non-kin classes, generating increasingly sophisticated types of social organization. In a nest with multiple paternity, for example, nestmates could be identified individually and also sorted into classes based upon shared characteristics, so that full-siblings might be discriminated from half-siblings. These processes of kin recognition sometimes can be disentangled through ontogenetic studies. In the phalanger *Petaurus breviceps papuanus*, young first learn to recognize others as a member of their group, and only later develop the ability to distinguish among them individually (Schultze-Westrum, 1965). Complex classifications encompassing not only kinship, but also group membership and social status, may be based on individual recognition abilities (Cheney & Seyfarth, 1982). Young vervet monkeys recognize their own kin, and at a later age develop the ability to recognize kin of other conspecifics (Cheney & Seyfarth, 1986). But members of especially large kin groups (e.g. social insect colonies or toad clutches, which may consist of thousands or tens of thousands of individuals) probably do not regularly distinguish the individual identities of their relatives (Waldman, 1981; cf. Barrows *et al.*, 1975; see also Hölldobler & Michener, 1980; Hölldobler, 1984). Kin recognition abilities expressed by animals with these life history characteristics are more likely due to a conceptually simpler system based upon the perception and comparison of group traits.

Generalized Phenotypic Comparisons

In most cases, kin will resemble one another. To the extent that their phenotypic traits are genetically determined, it should be possible to infer the genetic relationship between individuals from their trait overlap (Crozier & Dix, 1979; Getz, 1981, 1982; Beecher, 1982; Lacy & Sherman, 1983). Traits that are environmentally influenced (e.g. by diet or nest materials; see Kalmus & Ribbands, 1952; Jutsum *et al.*, 1979; Gamboa *et al.*, 1986*a*) or are socially transferred among members of a group (e.g. odors or behavior patterns, see Eisenberg & Kleiman, 1972; Linsenmair, 1972, 1985; Gubernick, 1980, 1981; Carlin & Hölldobler, 1983, 1986) also may serve as cues indicating kinship identity if they reliably correlate with the genotypic composition of the group (see discussions in Waldman, 1983, 1984; Gamboa *et al.*, 1986*b*). Kin recognition thus may be possible through the comparison of phenotypic characters. Organisms capable of recognizing kin by this means may or may not be able to distinguish among individual members of a kin class, but they are able to assign conspecifics to particular classes (e.g. full-siblings, half-siblings, cousins, etc.) and to act accordingly. Because recognition is based on an assessment of trait overlap rather than on individual identifications of known relatives, this process enables an organism to discriminate between relatives and non-relatives even though it has not previously encountered either or has always encountered both together. Moreover, the ability to act differentially toward relatives in accordance with their relatedness to oneself or one's siblings follows directly.

Building upon Hamilton's (1964*b*) suggestion that kin recognition might be based on the detection of phenotypic similarities, Alexander (1979) proposed various models in which individuals might "compare phenotypes" of conspecifics with their own or with those of known relatives (determined through a process of "social learning"). More recently, this process has been discussed in terms of assessing "phenotypic resemblance" (Bekoff, 1981), "phenotype matching" (Waldman, 1981; Holmes & Sherman, 1982), "signature matching" (Beecher, 1982), or an "armpit effect" (Dawkins, 1982). Basically, an individual attempting to identify genetic relatives compares their phenotypes (or "labels") with some model stored in its "template" (Waldman, 1981). In principle, the template could be (1) determined directly by a genetic program, (2) selectively learned (guided by a genetically programmed tendency to learn particular phenotypes), or (3) indiscriminately learned based on phenotypes expressed by conspecifics. If learned, the template could be based on characters of (a) conspecifics to which one has been exposed during appropriate circumstances or ontogenetic stages, (b) spatially proximate conspecifics or those with which one is presently "familiar", or (c) oneself. The template may also be formed through exposure to a spatially-based environmental cue, such as a nest odor (Gamboa *et al.*, 1986*a*), if some aspect of the cue is incorporated into individuals' labels. The overlap in perceived conspecific traits with those represented in the template may be judged by acceptance or rejection paradigms to effect kin recognition: conspecifics may be accepted by an individual because they share its traits, or rejected because they possess traits it lacks (or lack traits it possesses). Recognition assessments may involve both types of comparisons (see discussions in Getz, 1982; Waldman, 1985*b*). In addition to such binary decision rules, recognition algorithms may incorporate quantitative trait comparisons (e.g. ratios of pheromone components) (Barrows *et al.*, 1975; Hölldobler & Michener, 1980; Lacy & Sherman, 1983; Waldman, 1986*a*; Hefetz *et al.*, 1986).

To the extent that kin recognition templates are socially influenced, they reflect the traits expressed by known individuals. The template formed may constitute an average representation, if based on many members of a kin class, or an exact representation, if based on oneself or a limited sample of a kin class. Because all members of a kin class need not share identical recognition labels, average templates may facilitate discrimination of a larger proportion of kin class members, especially when genetic variation among kin groups is high (Waldman, 1986*b*; also see Gamboa *et al.*, 1986*b*). Then an individual might use both average and exact templates, but in different social contexts. For example, colony cohesiveness among honeybees (*Apis mellifera*) would be facilitated if individuals were recognized by shared (genetically and/or environmentally determined) traits for nest defense and foraging, but when swarming, mating, or provisioning brood, individuals might rely solely on a self-template to discriminate between full- and half-siblings (see Getz *et al.*, 1982; Getz & Smith, 1983, 1986; Breed, 1983; Page & Erickson, 1984; Breed *et al.*, 1985; Visscher, 1986; Frumhoff & Schneider, 1987).

If its recognition template were genetically encoded, an organism might be considered to have an "innate" or "genetic" recognition system. The template would be compared with recognition labels that were also genetically determined and/or ontogenetically fixed during early development, so that subsequently they would not be labile to social or environmental influences (see Waldman, 1985*b*). A genetically determined template is not necessarily the product of special "recognition alleles" (which are discussed below). Like any other phenotypic character, a recognition template might be the product of multiple alleles, and the contributions of each allele may not be discernible. Accordingly, the template would more accurately reflect an individual's overall genome than its individual constituent alleles. Moreover, alleles represented in the template need not effect any behavioral response, nor have any specific kin-recognition function. Although the existence of this type of template has yet to be convincingly demonstrated with respect to kin recognition abilities, hybridization studies reveal that species recognition occurs by the comparison of genetically influenced cues with a genetically determined template in some taxa (crickets, *Teleogryllus commodus* and *T. oceanicus* (Hoy & Paul, 1973; Hoy *et al.*, 1977); frogs, *Hyla chrysoscelis* and *H. femoralis* (Doherty & Gerhardt, 1983, 1984)). Hybrid females orient preferentially toward vocalizations produced by hybrid males, suggesting a "genetic coupling" of mechanisms generating signal production and detection (Hoy *et al.*, 1977). Both labels and templates may be determined by some common pattern generator, but whether the neural elements responsible for this trait matching are encoded by specific alleles or more generally reflect the overall genome has not been resolved. The latter possibility seems more likely given that the pattern generator is under polygenic control (Bentley & Hoy, 1972). Indeed, trait matching might be expected even if the labels and templates result from entirely different sets of genes (Elsner & Popov, 1978).

In most studies in which the ontogeny of kin recognition has been examined, social cues have been found to be important in template formation. American toad (*B. americanus*) tadpoles can recognize their unfamiliar siblings even after having been reared in social isolation (Waldman, 1981). Nevertheless, in normal circumstances, they are more likely to base kinship discriminations upon a template that incorporates traits of conspecifics, particularly those encountered during an early sensitive period (Waldman, 1981, 1985*b*). *B. americanus* tadpoles typically are surrounded by their siblings during the first few days of life, and kin subsequently are recognized (Waldman, 1981). Whether the template acquired during early development comprises a generalized representation of all conspecifics with which they interact or is selectively biased toward traits of kin (perhaps through genetically-programmed stimulus filtering) is still unknown (Waldman, 1986*b*). The traits compared, however, appear to reflect a substantial maternal component when tadpoles are reared in social isolation (Waldman, 1981). In cross-fostering experiments, Belding's ground squirrels (*S. beldingi*) show an ability to discriminate between their siblings and foster-siblings, but they differentiate much more strongly between littermates and non-littermates, acting more cooperatively toward non-sibling littermates than toward unfamiliar siblings (Holmes & Sherman, 1982). Like *B. americanus* tadpoles, which can recognize siblings of individuals to which they have been previously exposed (Waldman, 1985*b*), female *S. beldingi* that are similarly "indirectly exposed" to each other (whether or not they are siblings) are subsequently less agonistic toward one another than are those that have never been exposed to each others' phenotypes (Holmes, 1986*b*). Kin recognition abilities such as these would not be expected if animals were directing their social interactions toward previously known *individuals*, and thus these results suggest that discrimination is effected through generalized phenotypic comparisons based on an acquired template.

Generalized phenotypic comparisons should provide a more direct and generally more accurate means for class discrimination than is possible through individual identifications. But aside from enabling organisms to discriminate between half-siblings and full-siblings, siblings and cousins, and so on, such comparisons in theory may result in other types of discrimination. First, as different classes of relatives sometimes may be mistaken for one another, occasionally individuals that lack common ancestors also will resemble one another. Individuals may rarely encounter non-relatives that are as genetically similar to themselves as are their relatives. Grafen (1985) suggests that the probability of encountering a non-relative to which one is effectively related by an r value of 0·5 is less than one in a million. However, if discrimination is based on comparisons of limited numbers of traits, the probability of making recognition errors will be much higher. Second, while members of a kin class do resemble one another, they do not all resemble each other equally. Discrimination among members of a kin class based on phenotypic resemblance may thus be possible. As a result of independent assortment at meiosis, some members of a kin class may actually share a larger proportion of their alleles than do others. In a diploid organism (ignoring crossing-over), 25% of the members of a sibling cohort will share any given pair of chromosomes, 50% will share only one homolog, and 25% will be completely dissimilar (Barash *et al.*, 1978). If kin groups are genetically highly variable, recognition of genetically more similar and less similar individuals might be possible. In agreement with the predictions of this hypothesis, Sherman (1979) found a positive correlation between diploid numbers and the extent of eusociality in social insects. Species having more numerous, shorter chromosomes should be genetically less variable and phenotypically more similar than those with fewer, longer chromosomes, and thus may be expected to evolve stronger cooperative tendencies (Sherman, 1979). How frequently phenotypic variability within kin classes is sufficient to permit discrimination is unknown, but from a mechanistic perspective, there is nothing special about the recognition processes underlying such discrimination. Recognition by generalized phenotypic comparison in principle could lead to within-class as well as between-class discrimination.

Single-locus "Genetic" Recognition Systems

Hamilton's (1964*a*) genetical kinship theory predicts that in their social interactions organisms will favor kin, i.e. individuals with which they share alleles because of their common descent. The evolution of kin recognition mechanisms, such as those already described, may represent a response to kin selection or selection for appropriate mate choice. Yet Hamilton (1964*b*) suggested that selective pressures and recognition abilities might extend even further: any allele that somehow effected an identifiable phenotype, and that also caused its bearer to specifically favor those conspecifics that shared that phenotype, might spread more quickly by natural selection than would other alleles. Dawkins (1976) popularized this concept as the "green beard" effect (but mostly as a thought experiment; see Dawkins, 1982). By this model, recognized individuals need not be kin; they simply need to share particular recognition traits. These traits are special in that their expression is attributable to a single gene (or tightly linked group of genes). When considering how such "recognition alleles" might affect social behaviors, it makes little difference whether the individuals bearing them have inherited them from common ancestors or not. Hence, in Dawkin's example, if individuals share alleles that result both in the expression of green beards and cooperative responses toward conspecifics with green beards, other phenotypic traits the individuals express are largely irrelevant.

Presumably, if one gene can evolve to produce such a complex phenotypic effect, alleles at other loci might also. The result might be an intragenomic "tug of war" as each gene attempts to influence the behavior of its bearer in its own interest. Alexander & Borgia (1978; also see Leigh, 1977) outline several possible problems with the evolution of such recognition systems. Not only would the genetic underpinnings of such a system need to be complex (as noted by Hamilton, 1964*b*), but such effects might be susceptible to other alleles that produced the phenotypic marker but not the accompanying altruistic behavior. Whether other genes would be selected to counteract the action of recognition alleles as Alexander & Borgia (1978) suggest remains problematic, and may depend on precisely how preferences are expressed and the extent to which kin lacking the allele are placed at a competitive disadvantage with respect to non-kin possessing the allele (Ridley & Grafen, 1981; Rothstein & Barash, 1983). How polymorphism would be maintained is also uncertain. If their principal effect were to direct nepotism, recognition alleles would be expected to rapidly become fixed in a population, although genetic diversity might be maintained if the alleles had additional pleiotropic effects, influencing outbreeding responses or immune function, for example (also see Scofield *et al.*, 1982; Crozier, 1986).

At present, the hypothesis that any form of behavioral discrimination could be due to the operation of a single-locus recognition system lacks empirical support. Where behavioral preferences are based on a single well-defined genetic character, such as plumage color as a determinant of mate choice in lesser snow geese (*Anser caerulescens caerulescens*), social experience plays a profound role in shaping character preferences (Cooke *et al.*, 1972, 1976). Most individuals select as a mate a conspecific of the same color as that of the family in which they have been reared (Cooke & McNally, 1975; Cooke, 1978). A frequently cited possible example of such a system is the *H-2* locus of mice (*Mus musculus*), which appears to influence not only histocompatibility and immune function, but also mate choice and associated behaviors (Yamazaki *et al.*, 1980, 1983; Boyse *et al.*, 1982, 1983; Schwende *et al.*, 1984). Indeed, Yamazaki *et al.* (1976) initially suggested a model in which tendencies of genetically dissimilar mice to associate with one another could be attributed to "two linked genes in the *H-2* region, one for the signal and one for the receptor" (p. 1333). More recent evidence suggests, however, that although the signal may be imparted by alleles in the *H-2* region, in part through their effects on the hematopoietic system (Yamazaki *et al.*, 1985), mating preferences are strongly influenced by social experience. Male progeny cross-fostered at birth to parents genetically dissimilar from themselves subsequently choose to mate with females differing from their parents' rather than their own *H-2* type (Yamazaki *et al.*, 1987). Nonetheless, the extreme genetic polymorphism at this locus (Klein, 1979) suggests that odors encoded by *H-2* alleles usually differ between families, potentially making them highly effective kin recognition labels. Further study of this system should clarify the relationship between the genetic substrates of signal production and detection.

A functional link between histocompatibility and kin recognition has been more firmly established in marine invertebrates. In recent years, the population structure of sponges, coral, sea anemones, hydroids, bryozoans, and ascidians has been experimentally investigated through the use of "self-recognition" bioassays in which genetic identity is inferred if colonies fuse (reviewed in Neigel & Avise, 1983; also see Grosberg *et al.*, 1985). In laboratory conditions, Keough (1984) found that larvae of the bryozoan *Bugula neritina* settled with siblings in clumped spatial distributions, whereas unrelated groups settied at random. In field experiments, larvae of the tunicate *Botryllus schlosseri* show similar patterns of preferential sibling recruitment (Grosberg & Quinn, 1986). Such differential settlement might be attributable to a kin recognition mechanism. Kin discrimination may serve several functions for these organisms. Genetic studies of *Botryllus* reveal that colony fusion is controlled by a single gene locus, and that colonies fuse only if they share one allele at this locus (Scofield *et al.*, 1982). Moreover, as suggested also in the mice studies, the locus may facilitate outbreeding, preventing fertilization of gametes sharing alleles (Scofield *et al.*, 1982). Thus, although genetically similar colonies tend to aggregate and fuse, barriers appear to have evolved to prevent sexual reproduction among them. Both these tendencies are controlled by the fusibility locus. Using inbred lines of *B. schlosseri*, Grosberg & Quinn (1986) determined that larvae sharing an allele with previously established colonies, whether they were siblings or not, settled closer to those colonies than did larvae with a different allele. The fusibility locus is characterized by polymorphism comparable to that present at vertebrate MHC loci (such as *H-2*). The extent of allelic polymorphism at the fusibility locus ensures that siblings, but not non-siblings, will usually share an allele.

"Kin" recognition in tunicate larvae thus appears to occur by the matching of histocompatibility types rather than of general phenotypic characters. Intriguing as these results are, whether the alleles directly effect the behavioral preference, or simply code for the phenotypic character recognized, has not yet been established. In general, the influence of social experience on self-recognition abilities in marine invertebrates has not been investigated (Stoddart *et al.*, 1985). While sea anemones (*Anthopleura xanthogrammica*) discriminate between neighbors and non-neighbors, habituation to neighbors, even if non-kin, appears likely with time (Sebens, 1984).

Although Grosberg & Quinn (1986) do not describe how larvae were held prior to their experimental tests, in each case 20 siblings were introduced together, suggesting that social effects could have influenced settlement behavior. Even should further study confirm some ontogenetic variability in the expression of this behavior, it may make little difference from an evolutionary perspective if individuals normally discriminate among conspecifics according to single-locus differences. The functional relationship between the expression of recognition labels and templates still needs to be examined, however.

Familiarity-based Recognition Occurs by Phenotype Matching

Recent discussions have contrasted mechanisms of kin recognition based on conspecifics' familiarity (or "association", Holmes & Sherman, 1983; Sherman & Holmes, 1985) with those that effectively compare phenotypic characters among individuals. That these represent discrete, alternative mechanisms seems to have become generally accepted (e.g. see Lewin, 1984), and in certain situations, a distinction can be experimentally demonstrated (e.g. Porter *et al.*, 1983; Holmes, 1986*b*). These mechanisms are contrasted more by ecological and contextual considerations than by physiological ones. Recognition of previously encountered individuals is attributed to familiarity. Phenotype matching, by contrast, is said to occur in situations in which animals recognize unfamiliar kin on first encounter, or when they can discriminate among equally familiar individuals of varied genetic relationship (Holmes & Sherman, 1983). The ability to recognize similarities among individuals within classes may seem more relevant to the expression of kin-directed behaviors than the ability to recognize differences among individuals. Yet when studying kin recognition by this classification scheme, we run the risk of overlooking basic similarities in the ontogenetic processes underlying these recognition abilities.

In either case, an organism attempting to identify its relatives must match conspecifics' traits with those it expects of kin, either previously learned in appropriate social contexts or internally derived (acquired from self-observation or directly determined in a genetically programmed template). Kin are recognized because they express traits that are either identical to, or overlapping with, those of previously encountered individuals. Even when recognition is based on comparisons with one's own traits, this process will most often reflect a learned familiarization of oneself. The apple maggot fly (*Rhagoletis pomonella*) secretes a pheromone regulating oviposition, but a fly cannot recognize the pheromone it has secreted in the absence of previous experience of it (Roitberg & Prokopy, 1981). Young chicks reared in isolation may learn their own body color, even if experimentally altered, and approach conspecifics with a similar phenotypic expression (Salzen & Cornell, 1968). If an organism were reared in social isolation, somehow deprived of all self-exposure, then any kin recognition it subsequently demonstrated might be described as phenotype matching without prior familiarity of kinship cues. Alternatively, if individuals were somatically changed, for example by transplanting embryonic tissues, so that their phenotype no longer corresponded to their genotype (Yamazaki *et al.*, 1985) and still recognized their true genetic kin, recognition might be considered to be based solely on a genetically determined template (although this interpretation, too, would be problematic, as the tissues altered might be directly or indirectly involved in the perception of labels). In normal circumstances, familiarity with conspecific cues undoubtedly affects subsequent social discrimination, whether through recognition of individuals or members of kin classes.

Kin identifications based on behavioral mechanisms necessarily involve some matching process. Kin recognition by means of a *familiarity-based system* (by previous association) implies recognition of specific individuals, in principle through precise matching of the traits they express with stored profiles of traits recalled from previous encounters. While individuals occasionally may be recognized after a single encounter, individual recognition more frequently constitutes a probabilistic process, dependent on the frequency of prior social interactions, the time lag since the last encounter, and the number of characters used (Breed & Bekoff, 1981). Kin recognition through comparison of *generalized phenotypic characters* (phenotype matching) implies recognition of members of a kin class based on a probabilistic determination of their trait overlap with known relatives. Perceived traits are compared with those represented in a model (template), often determined in past social interactions. In both cases, kinship assessments are usually based on probabilistic comparisons with expectations generated through previous experience (Fig. 2(a), (b)).

Although data are few, we have no reason to believe that these forms of kin recognition are the products of discrete neural processes. While the recognition template thought to integrate and compare sensory information with stored features characterizing kin remains a theoretical construct, modern neurobiological techniques make possible investigations of the neural mechanisms of kin recognition. Studies on the maternal recognition system of rats illustrate how these questions can be addressed. In common with many organisms that have been shown to recognize kin, a rat's early olfactory experience plays a substantial role in determining its subsequent behavioral responses to conspecifics (Leon, 1983). Examination of the olfactory bulb reveals possible physiological correlates to this behavioral development, as individuals show increased neural activity after exposure to familiar odors (Coopersmith & Leon, 1984). The acquisition of the presumed olfactory template is dependent on experience in particular circumstances; in the rat, odors must be experienced in tandem with tactile stimulation, as if actually provided by the mother (Sullivan & Leon, 1986). Single-unit recordings in the mitral cells reveal that familiar odors elicit fewer excitatory and increased numbers of inhibitory responses than do unfamiliar odors (Wilson *et al.*, 1987), suggesting that template formation may involve physical changes in these cells. Early behavioral preferences, and changes in the neural substrate, are retained into adulthood (Coopersmith & Leon, 1986). Exposure to odors under varied circumstances may affect different areas of the nervous system (Coopersmith *et al.*, 1986). Using paradigms such as these, eventually it should be possible to characterize recognition mechanisms based on their neural properties.

Unless the neural apparatus mediating familiarity-based recognition mechanisms and that involved in making generalized phenotypic comparisons are found to be

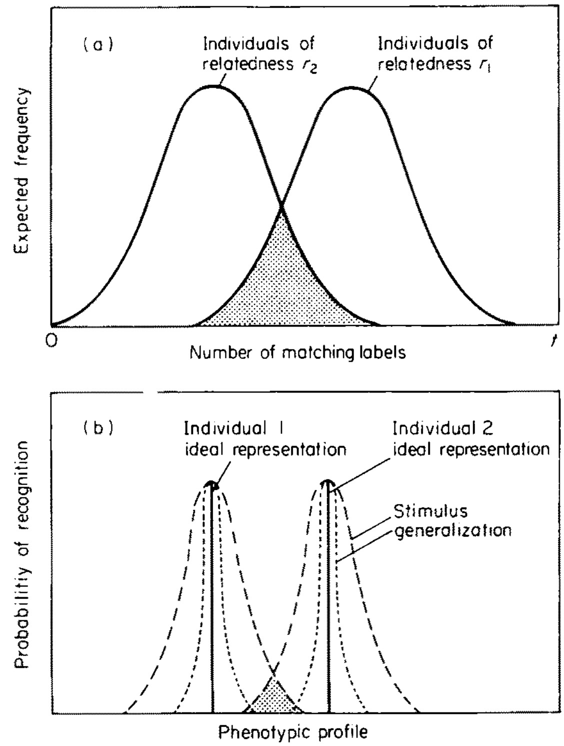

FIG. 2. Probability distributions associated with recognition of relatives not known from other social cues (a) and of individuals known from previous social interactions (b). (a) When recognition is based on genetically determined labels, different sib groups are expected to share some proportion of their labels (shaded area) depending on their genetic relatedness (r), the number of labels compared (t), and the extent of genetic variability within sibships. The precision of a kin recognition system, i.e. the probability of mistaking an individual for a member of a different kin class than the one to which it belongs, is a function of the overlap range. (After Getz, 1981; Lacy & Sherman, 1983). (b) The recognition of a previously encountered individual requires the recall from memory of its phenotypic profile, or set of labels that uniquely identifies it. Ideally, recognition should occur if perceived traits exactly match this phenotypic profile (dark vertical lines). Because of some inprecision in the neural processes underlying recognition, however, stimulus generalization may occur, resulting in the recognition of individuals having profiles somewhat different from those initially perceived (dashed curves). This generalization may facilitate individual identifications when phenotypic profiles change in time, but may also result in the mistaken recognition of individuals not previously encountered. The probability of recognition error (shaded area) increases with progressive stimulus generalization.

different, distinctions between these mechanisms are unlikely to be clear-cut in practice. Organisms that are capable of individual discrimination are expected also to have the neural capacity to assess the extent of phenotypic similarity among individuals. Moreover, while kin can be distinguished from non-kin through individual identifications, individual recognition is unlikely to be error-free. As group sizes increase, stored representations of individuals may become generalized (cf. stimulus generalization, see Staddon, 1983; Rumelhart *et al.*, 1986). To accommodate increased numbers of phenotypes, the template may extract only selected features, or may store them internally in stylized fashion rather than as exact representations (also see Reed, 1973). Effectively, criterion rules for identification will then be characterized by wider tolerance ranges, so that unknown individuals may be recognized if they resemble known individuals (Fig. 2(b)). Behavioral studies of discrimination learning (Kintsch, 1970) suggest that a novel stimulus will be mistaken for a known stimulus with a probability that corresponds to the trait overlap between them. As kin usually express similar phenotypic traits, they sometimes might be identified even on first encounter. An individual is more likely to be mistaken for its sibling than for a non-relative, especially if simultaneous comparison is not possible.

Identification of genetic relatives by phenotype matching therefore can be a direct outcome of the processes underlying individual recognition, or familiarity. Although they are not necessary for making generalized phenotypic comparisons, individual recognition abilities, once established, can serve as the groundwork for the evolution of increasingly sophisticated kin recognition systems. If favored by natural selection, tendencies to generalize recognition templates may become accentuated to facilitate the identification of unknown kin. On the other hand, even if selection does not specifically favor an organism's ability to identify unfamiliar kin or to discriminate between familiar individuals according to their relatedness, we might expect empirical studies to reveal such effects. In other words, organisms that identify kin by familiarity should show concomitant (but weaker) tendencies to identify relatives, whether they are familiar or not, simply as a consequence of the processes underlying individual or self-recognition.

Experimental results generally cited as evidence for a special phenotype matching mechanism (e.g. Holmes & Sherman, 1983) may, in some cases, be explained more parsimoniously as indirect effects of individual recognition. Consider Greenberg's (1979) study of nestmate discrimination in sweat bees, *Lasioglossum zephyrum*. Using inbred lines, Greenberg set up artificial colonies, each consisting of six sisters. He found that the frequency with which colony members permitted others passage into their nest directly increased as a function of the coefficient of relatedness, r, between the colony members and the intruder. This result suggests, as Greenberg (1979) points out, that traits used for recognition are genetically determined (also see Smith, 1983). Whether sweat bees have been selected specifically to make these graded discriminations is another matter altogether. Although the data can adequately be described by a linear regression (Greenberg, 1979), each individual is either allowed entry or not. At intermediate values of r (0·4–0·6), roughly as many individuals are allowed entry as are turned back. Hence the mechanism of kin recognition, surprisingly, is not very precise. Moreover, natural selection should not, in general, favor behavioral responses that vary in linear fashion with respect to r as we see here (Altmann, 1979; Weigel, 1981). These results might be accounted for, however, by the action of an individual recognition mechanism, if the probability that a novel individual is mistaken for its sister corresponds to the phenotypic resemblance between them. Indeed, sweat bees do learn the individual identities of their nestmates (Bell, 1974; Kukuk *et al.*, 1977), and individuals can be experimentally induced to simultaneously accept as nestmates members of two unrelated (and presumably phenotypically dissimilar) sibships (Buckle & Greenberg, 1981).

From their experiments on Belding's ground squirrel (*S. beldingi*) kin recognition, Holmes & Sherman (1982) infer that females make two types of distinctions among conspecifics, first assessing familiarity (prior association) and second assessing trait overlap (phenotype matching). In laboratory arenas, levels of agonism between yearling females and males reared together are less than those between yearlings reared apart, but superimposed upon this effect, sibling females act slightly more cooperatively than non-siblings. While individual recognition has not been established in any sciurid (see review by Michener, 1983), such abilities presumably are responsible for the familiarity effects. Because individual discrimination abilities may be subject to stimulus generalization, weak discrimination between kin and non-kin within familiarity classes would be expected, just as the laboratory test results show, even without selection for special phenotype matching abilities. Holmes and Sherman (1982) suggest that phenotype matching based on a self-template may be particularly important in enabling females to discriminate between full- and half-sisters in natural conditions (also see Getz & Smith, 1983, 1986; Holmes, 1986*a*; Visscher, 1986; Frumhoff & Schneider, 1987). Such abilities may have been selected because of factors associated with the organism's life history (e.g. polygamous or promiscuous mating that results in multiple paternity of clutches). When the potential inclusive fitness gains to individuals making these discriminations are large, the evolution of such kin recognition abilities is to be expected, especially if the same physiological substrates underlie both processes. Even in these instances, however, the discrimination tendencies observed conceivably could represent secondary effects of self-recognition abilities, for example in detecting scent markings or even vocalizations (e.g. McArthur, 1986).

The process of individual recognition in itself can result in the acceptance of novel kin of known individuals (including oneself). In effect, the same matching processes may be involved in individual and group recognition, but the criterion levels may vary. Because individual recognition based on familiarity can effectively result in kin recognition by phenotype matching with similar evolutionary consequences, these processes functionally as well as mechanistically overlap. To distinguish experimentally between the mechanisms involved may be much more difficult than to contrast the social contexts in which they are expressed. The current emphasis on uncovering examples of kin recognition abilities not attributable to experiential effects thus may be misdirected. More careful examination of the ontogeny of the response, the cues that are used, and the manner in which behavioral preferences are expressed, will prove more valuable in elucidating mechanisms underlying kin recognition.

"Genetic" Recognition Occurs by Phenotype Matching

Hamilton (1964*b*) speculated that some alleles might evolve to induce their bearers to preferentially treat conspecifics that share their copies. Extrapolating from this, Holmes & Sherman (1982) state that kin recognition might theoretically occur via "a process of direct genotypic comparison" (p. 510). Much discussion has centered around the idea that kin recognition might be brought about by the action of special "recognition alleles" of the type Hamilton was considering (e.g. Blaustein, 1983; Holmes & Sherman, 1983). Two important points appear to have been generally overlooked. First, recognition alleles, if they exist, cannot in themselves lead to *kin* recognition abilities, only to the discrimination of individuals that share particular phenotypic traits due to the action of those alleles. The individuals need not be kin (Dawkins, 1976, 1982; also see Rushton *et al.*, 1984; Mealey, 1985; Rushton & Russell, 1985). Second, organisms cannot directly compare their genotypes. Any recognition mechanism determined by alleles would necessarily be expressed as a form of phenotype matching. The traits compared might not be readily apparent—indeed they might be exceedingly subtle—but if genotypic differences among individuals have no phenotypic consequences, discrimination would be impossible. Of course any phenotypic differences compared would be those caused by the alleles in question rather than traits generally characteristic of the individuals.

Many references to "genetic recognition systems" appear in the literature (e.g. Blaustein & O'Hara, 1981; Davis, 1982; Rothstein & Barash, 1983; Grafen, 1985). This terminology, though never explicitly defined, is frequently used to refer to instances in which learning appears to play no role in influencing kin preferences. Such recognition theoretically could occur by means of generalized phenotypic comparison with a genetically determined template. In considering apparently innate kin recognition abilities, most discussions focus instead on the possible role of special recognition alleles (e.g. Blaustein, 1983; Holmes, 1986*a*). I suggest that the terms "genetic recognition" and "recognition allele" are best reserved for the specific case proposed by Hamilton in which phenotypic differences generated by alleles at particular loci (or linkage groups) are compared (also see Alexander & Borgia, 1978). His concept subsumes a common *genetic mechanism* by which traits are determined and detected but does not in itself implicate any particular behavioral *recognition mechanism* to assess phenotypic similarity. Indeed, such alleles need not act in a manner that excludes any role of learning. For example, an allele might express itself by (1) producing a marker trait, (2) causing its bearer to learn this trait, and (3) also inducing its bearer to behave altruistically toward conspecifics that share the marker. This allele would certainly fulfill Hamilton's criteria, and it is not inherently less likely to exist than the one he proposed. With this extension, Blaustein's (1983, p. 753) assertion that the difference between "phenotypic matching and recognition allele explanations ... is trivial" is obviously correct, although I suggest that this comparison is inappropriate in any case, as the explanations concern different levels of analysis.

Once we determine particular traits or labels that serve as cues for social discrimination, experimental analyses of the relative importance of these traits, in relation to overall phenotypic expression, as determinants of social behavior should be possible. Grosberg & Quinn's (1986) study on settlement patterns in *B. schlosseri* larvae provides a first step in this direction, and in this case, histocompatibility type rather than genetic relationship *per se* determines behavioral responses. Further genetic studies, using modern molecular techniques to characterize allelic interactions, may enable us to more generally probe how recognition systems are affected by possible intragenomic conflict. Until then, we cannot safely infer that apparently innate kin recognition abilities revealed in laboratory experiments may be attributable to the action of special recognition alleles, as argued by Blaustein (1983). Rather than addressing the physiological mechanisms by which social discriminations are made, the distinction between recognition effected by specific alleles and that ascertained by making generalized phenotypic comparisons concerns the levels of selection to which traits (and social behaviors) respond. If alleles at many loci independently exert their influence on their bearer's behavior, their summed effect might be equivalent to that generated by generalized phenotypic comparisons.

The temptation to denote a kin recognition system as purely genetic if laboratory experiments fail to demonstrate an environmental component must be resisted. Some workers appear to have become so enamored with "genetic" recognition terminology that they seemingly have lost sight of the functional significance of their results. For example, although many studies have shown that *Rana cascadae* (like *B. americanus*) larvae can discriminate between unfamiliar siblings and unfamiliar non-siblings, in laboratory experiments they uniformly fail to discriminate between familiar siblings and familiar non-siblings (O'Hara & Blaustein, 1981). In breeding ponds, *R. cascadae* deposit their egg masses in communal clumps. Larvae of different broods hatch synchronously, disperse limited distances, and consequently interact extensively with one another (see discussion in Waldman, 1984). Hence, in natural conditions, *R. cascadae* tadpoles are unlikely to encounter totally unfamiliar individuals, instead associating with individuals to which they have been exposed since early larval stages. In citing the ability of individuals to distinguish between unfamiliar siblings and unfamiliar non-siblings as possible evidence for a genetic recognition system, Blaustein & O'Hara (1981) ignore the fact that this paired choice situation is unlikely ever to occur in natural circumstances. Waldman (1981) obtained essentially the same results on *B. americanus*, and yet interpreted his results as evidence of an experiential component to the ontogeny of kin recognition. Although both species discriminate between unfamiliar kin and unfamiliar non-kin, and neither discriminate between familiar kin and familiar non-kin, terminology used by the authors strongly influences subsequent reporting and interpretation of the results (e.g. Gadagkar, 1985). While the kin recognition mechanisms of these two species differ in important respects (reviewed in Waldman, 1986*a*), the fact that the genetic recognition system proposed by Blaustein & O'Hara (1981) seems *not* to be expressed in laboratory simulations of natural conditions suggests that the results, though intriguing, may have little bearing on the behavior of tadpoles in the wild (Waldman, 1984; see response by O'Hara & Blaustein, 1985). Possibly such abilities arise from other physiological processes and are only epiphenomenal with respect to their influences on behavior.

Spatial/Temporal Factors May Affect Criterion Rules

The study of kin recognition in animals presents behaviorists with one acute difficulty. Until the neural processes underlying kin discrimination responses are identified and appropriate recording techniques are devised, recognition abilities can only be inferred when they are behaviorally expressed. The organism's physiological state and its motivation to behave differentially toward kin thus are inexorably confounded with its ability to perceive differences between kin and non-kin. Failure to discriminate between kin and non-kin may indicate either than an individual is incapable of recognizing its relatives, or that it can recognize kin but "chooses" not to discriminate (contradictory results can thus be generated even with similar procedures; see, e.g. Ryan *et al.*, 1984; Shellman-Reeve & Gamboa, 1985). Response tendencies,while they may be affected by many factors, are likely to be determined in large part by physical and social aspects of the environment, and by the physiological condition of one's relatives and oneself (Schulman & Rubenstein, 1983). I discussed earlier the possibility that honeybees (*A. mellifera*) might discriminate between full- and half-siblings in some contexts but not others. Similarly, amphibian larvae may aggregate in large mixed kinship groups at times, perhaps when circumstances favor the formation of "selfish herds" (Hamilton, 1971), but break up into smaller groups composed just of kin at other times to share food resources, to maximize growth rates, or to cooperate in other ways (Waldman, 1982).

Contextual cues, in time and space, may be important not only ontogenetically in the development of discrimination preferences (as illustrated by Sullivan & Leon, 1986), but also more proximately in setting specific criterion rules for assessing recognition. While few animal species live in such highly structured populations that they can rely solely on spatial proximity as a measure of genetic relatedness, overlap in temporal and spatial distribution can still provide one basis for kin discrimination which can be used together with other available cues. Familiarity and spatial distribution are covarying factors, as identification of individuals will be facilitated with repeated encounters in specific contexts. Aside from this, recognition might be more reliably or more efficiently assessed in some circumstances by individuals that use contextual cues together with generalized phenotypic comparisons. We would then expect that kin would be more readily identified in certain contexts (time of day, locality) than in others, and that organisms might effectively switch between mechanisms of kin recognition in response to these variables. The characterization of species-specific kin recognition mechanisms may be exceedingly difficult, because populations may respond to varied cues in different ecological contexts. Interspecific comparisons are even more problematic when little information is available concerning the ecology of source populations (e.g. Porter *et al.*, 1983).

Field observations on the alarm calling behavior of Belding's ground squirrels (*S. beldingi*) are consistent with a spatially-based kin recognition system. While reproductive females call more frequently after spotting a predatory mammal than do nonreproductive females, reproductive but nonresident females ("temporary invaders") call approximately as frequently as nonreproductive resident females (Sherman, 1977, 1980). Females call if they are near their home and are in reproductive condition but fail to call otherwise. Males call even less, but as they disperse from their natal area at an early age, they are rarely near relatives (Sherman, 1977). Because female reproductive residents call whether or not their family members are actually present at the time (Sherman, 1977), spatial distribution may suffice as an effective kin recognition mechanism to elicit calling behavior (see Shields, 1980 for discussion on how reproductive condition might affect alarm calling). Discrimination among kin based on other mechanisms is also evident in field observations: while genetic relatedness cannot be precisely inferred from nest burrow proximity, closely related individuals are favored over more distantly related individuals in a variety of social interactions (Sherman, 1980, 1981). Like the half-sibling recognition previously discussed, these behavioral discriminations may be based on generalized phenotypic comparisons possibly using one's own traits as a model. Upon detecting a predator, however, female residents need not make these comparisons, and given time constraints more specific forms of discrimination may be dangerously inefficient. Since alarm vocalizations are likely to warn all nearby individuals, kin and non-kin alike, a simpler spatially-based behavioral rule may be more effective in this circumstance.

Social context represents a cue which may be involved in kin recognition, whatever other mechanisms are additionally employed. A conspecific encountered in circumstances that are characteristic of kin is thereby more likely to be perceived as a relative. For example, a known individual encountered near its home (nest, burrow, territory, pond) will probably be recognized more frequently than it would be if it were encountered in a novel habitat where it would be unexpected. To compensate for this, criterion rules for recognition should generally become more precise as the social context in which a conspecific is encountered becomes more improbable. Because male Belding's ground squirrels do not disperse together, they might be less likely to recognize brothers should they encounter them, even if they previously had identified them in the context of the natal nest. Such sex-bias in recognition abilities has been demonstrated in laboratory studies (Holmes & Sherman, 1982, Holmes 1986*b*). Demographic models of discrimination abilities (Sherman, 1980, 1981) may govern changes in criterion rules. Evidence of context-dependent switches in kin recognition mechanisms has not been sought, but certainly their existence is a real possibility.

Conclusion

Given the importance of genetical kinship theory (Hamilton, 1964*a,b*) to our understanding of the evolution of social behavior, the current surge of research on mechanisms used by animals in discriminating between kin and non-kin—and among kin of varied genetic relatedness—is long overdue. With the advent of this work, a variety of mechanisms have been described and a host of terms proposed to describe these mechanisms. To empirically distinguish among competing hypotheses, laboratory experiments have been designed to uncover recognition abilities, in some cases without due regard to functional considerations in natural conditions. Here I have attempted to point out the conceptual differences and similarities among the mechanisms that have been discussed. Kin recognition can be accomplished through various means, but we should not expect to find that organisms necessarily rely on one mechanism to the exclusion of others, because in fact such mechanisms may be highly interrelated. Rather than representing discrete processes, the various mechanisms that have been proposed may be considered as points along a continuum of possible means to identify kin. While all forms of discrimination are likely to be modulated by the social context in which individuals encounter one another, kin

TABLE 1

Hierarchial framework for the consideration of properties of kin recognition mechanisms

Level of recognition	Referent	Recognized individuals
Allelic recognition	Individual bearing allele a encoding label A	Conspecific bearing allele a encoding label A
Individual recognition	Individual bearing labels $A_1, A_2, \ldots, A_n$	Referent
Group recognition		
1. Heterogeneous groups	Individual bearing labels $A_1, A_2, \ldots, A_n$	Referent (= individual recognition)
2. Homogeneous groups	Individual or individuals bearing labels $A_1, A_2, \ldots, A_n$	Conspecific bearing some proportion of labels, $A_1, A_2, \ldots, A_n$ (proportion may reflect r)
	Individual or individuals bearing label C	Conspecific bearing label C

Kin recognition mechanisms can involve phenotype matching at several different levels, from single traits (which might be encoded by particular alleles), to multiple traits expressed by previously encountered individuals, to single or multiple traits expressed by individuals that permit an assessment of their group membership. At each level, an individual compares the phenotype of a referent (the individual itself, another known individual or individuals, or some internal representation or template derived from experience with these individuals) with the perceived phenotype (label or labels) of the conspecific to be recognized. Allelic recognition leads to identification of individuals bearing the same label A encoded by the same allele a. Conspecifics identified by individual recognition have been previously encountered, and matches with stored profiles should generally be close if not exact. Determination of group membership results from individual recognition if group members share no common labels (i.e. are heterogeneous), but can be based on generalized phenotypic comparisons if group members share some labels (i.e. are homogeneous). If group members share variable numbers of labels (A_1 through A_n), as when the labels are genetically determined, recognition may be based on the extent of label overlap. If all members of a group share a label (C), as can occur when labels are environmentally influenced, socially spread, and/or applied to members of the group by a dominant or maternal individual, recognition may be based on exact matches. These processes, while conceptually separable, may operate concurrently and together effect kin recognition.

recognition can occur at several different levels, and the processes effecting this recognition can operate concurrently (Table 1).

A major emphasis of much ongoing research is the discovery of kin discrimination responses that cannot be attributed to common social experience, from which a genetic component to kin recognition is often inferred. While such results are intriguing, neither kin recognition (as a proximate mechanism) nor kin selection (as an evolutionary process) require such effects. Any character expressed by an individual that is consistently correlated with its genetic identity can incidentally serve as a kinship label to which its conspecifics may be selected to respond. A broad range of characters might serve this function: morphological traits, behavioral repertoires, social signals, territorial or nest positions, temporal activity patterns, excreted metabolic by-products, or even cues imparted by symbiotic organisms such as secretions of microbial gut fauna. To elucidate these cues and the mechanisms by which they are evaluated represent the principle challenges facing those studying the mechanisms underlying kin-directed behaviors.

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