

Recognition systems and biological organization: The perception component of social recognition

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Recognition of conspecifics is necessary for differential treatment of individuals in a variety of social contexts, such as territory establishment and defense, dominance hierarchies, reciprocal altruism, mate choice, parent–offspring interactions and nepotistic contexts, to name a few. Here I first review various categories of perceptual mechanisms of social discrimination, focusing largely on the extensive literature on the perception component of kin recognition, although the ideas presented here can and have been used for analyses of recognition at many levels of social organization. I then discuss a range of recognition mechanisms observed in a model species, Belding’s ground squirrels, and how socio-ecological factors influence the development and expression of each mechanism. Finally, I address several theoretical and empirical controversies in the kin-recognition literature which pertain to the perceptual component of recognition, as well as areas in need of additional investigation.

Introduction

An understanding of recognition systems can be important for explaining interspecific variation in population cycles, nepotistic patterns, dispersal and inbreeding avoidance (Charnov & Finerty 1980, Blaustein *et al.* 1987, Hepper 1991a, Pusey & Wolf 1996, Sherman *et al.* 1997), particularly in group-living species with on-going social interactions. Recognition abilities would be expected when animals interact repeatedly over time and when discrimination among multiple familiar individuals is beneficial, such as with nepotism, reciprocal altruism and dominance hierarchies (Hamilton 1964, Trivers 1971). I define social recognition as a cognitive process (without implying any level

of cognitive processing or awareness) whereby animals become familiar with conspecifics and later remember them and treat them accordingly, based on the nature of those previous interactions. Recognition can also be based on cues of those individuals, on inanimate objects, or on other proxies for identity such as spatial location. While social recognition of individuals is not required for kin selection, mate choice, tolerance of neighbors or parental care, it can facilitate appropriate behavior in these contexts and favor behaviors directed toward particular individuals. From a functional perspective, the benefits of social recognition are clear, yet the processes underlying it can be quite complex.

Kin recognition is an internal process of assessing genetic relatedness that can be inferred

through kin discrimination, the observable, differential treatment of conspecifics based on cues that correlate with relatedness. Recognition at most levels of social organization (but not all; *see* “Context-based recognition”, below) involves three components: the expression of unique phenotypic cues, or labels (also referred to as the ‘production’ component), the perception of these labels and their degree of correspondence with a “recognition template”, and the action taken by the animal (the ‘evaluator’) as a function of the perceived similarity between its template and an encountered phenotype (or ‘cue-bearer’; Beecher 1982, Holmes & Sherman 1982, Reeve 1989, Gamboa *et al.* 1991, Sherman *et al.* 1997, Liebert & Starks 2004, Tsutsui 2004). Expression and perception components comprise the mechanism of recognition, both of which are necessary for discrimination of conspecifics before the action component can be expressed, resulting in differential treatment of conspecifics (e.g., nepotism, mate choice, avoidance, cooperation). However, social discrimination — of kin, neighbors, mates, allies, competitors, etc. — is not an inevitable result of social recognition.

Thus recognition labels and perceptual abilities provide proximate or mechanistic explanations for social recognition, whereas the action component provides a functional or adaptive explanation for recognition because it involves behaviors with fitness costs or benefits (such as agonism or avoidance of inbreeding). However, it is important to note that natural selection (and perhaps sexual selection) can operate independently on each component of recognition, such that if kin labels and perceptual abilities have not both evolved, differential treatment of individuals cannot be selected regardless of how favorable it might be (Hamilton 1964; *see also* Holmes & Mateo 2006).

Mechanisms of kin recognition

The evolution of kin-selected behaviors of course requires the evolution of mechanisms that make recognition of kin possible (Hamilton 1964; *see* Table 1). Several mechanisms for the perception component of recognition have been described, although there is disagreement about whether

all are actually mechanisms for recognizing kin (as versus perceptual abilities serving some other purpose), and whether distinctions between mechanisms are largely conceptual rather than biologically relevant, as described below. Before proceeding, I note that these mechanisms are not mutually exclusive or necessarily exhaustive, and that an individual can use several mechanisms depending on the recognition context.

Context-based recognition

Similar to Barnard’s (1990) “discrimination by non-conspecific cues”, I group together several modes of discrimination which are based on contextual cues rather than cues borne by individuals themselves. Previously I have focused on spatial cues alone (Mateo 2002, 2003), but recent studies suggest a need for an expansion of this category.

First, animals may be recognized indirectly based on spatial cues, with individuals encountered in a particular area (e.g., nest or burrow) treated as kin regardless of true relatedness (e.g., mother–offspring recognition via natal burrows; Holmes & Sherman 1982). During the last two decades this mechanism has received scant empirical attention, in part because some (e.g., Barnard 1990; reviewed in Tang-Martinez 2001) have suggested it is not a true, direct form of kin recognition, since animals are responding to locations rather than phenotypes of individuals. However, spatial cues may correlate reliably with relatedness, as when females lay their eggs or give birth in a nest to which other individuals do not have access, and when communal nesting and brood parasitism do not occur. Thus when parents return to the nest, they by default invest exclusively in their own offspring. Likewise, those young will only encounter their parents in that location, and so treating any adult found there as kin would be accurate. For example, bank swallow (*Riparia riparia*) parents use a spatially based mechanism to recognize their young confined to the nest and later switch to a familiarity-based mechanism (described below) just before young fledge (Beecher *et al.* 1981). Male black-tailed prairie dogs (*Cynomys ludovicianus*) appear to treat young-of-the-year

differentially depending on whether young are encountered in an area where the male copulated (Hoogland 1995).

Before young leave the nest and begin interacting with other conspecifics, spatially based recognition is an accurate and adaptive mecha-

Table 1. Perceptual mechanisms of social recognition.

| Mechanism | | Contexts | Type of cues | Advantages | Disadvantages |
|---------------------|----------------------------------|--|--|---|--|
| Context-based | Spatial cues | Kin (and only kin) are reliably encountered in a particular area | Location (nest, burrow, territory) | Family cues do not need to be learned | Risk of mis-identifying non-kin encountered in familiar location as kin |
| | Mating access | Social partner has no opportunity to mate with others | Evaluator's memory of exclusive mating with target's parent | Directed parental investment in offspring even if young do not produce kin labels | Cuckolded parent may invest in non-kin |
| | Cohort sharing | Young in a cohort sired by one or a few adults | Age of evaluator and target | Paternal half-siblings recognized without need for production or perception of kin labels | Recognition mistakes if many males successfully sire young |
| Recognition alleles | | Precise recognition without learning family traits | Cue-bearer's phenotypic traits | 3 components of recognition can evolve together | Risk of treating non-kin with shared trait as kin |
| Prior association | | Short-lived, little overlap of generations, few social interactions; little fitness benefit for recognizing unfamiliar kin | Cue-bearer's phenotypic traits matched against exemplars in evaluator's template | Can recognize familiar kin regardless of location | May not be able to discriminate among familiar individuals; cannot recognize previously unfamiliar kin |
| Phenotype matching | | Fitness benefits for recognizing classes of unfamiliar kin; multiple mating by males creates unfamiliar paternal half-siblings | Cue-bearer's phenotypic traits matched to prototype derived from referents in evaluator's template | Can recognize previously unfamiliar kin | Liberal matching algorithm may lead to acceptance of non-kin or rejection of kin |
| | Self-referent phenotype matching | Multiple mating creates unequally related but equally familiar siblings; precise estimates of relatedness are needed | Cue-bearer's phenotypic traits matched to evaluator's own cues | Can discriminate among full and half-siblings; can recognize kin if template is 'lost' | Linkage disequilibrium could cause aid to be given to non-kin |

nism for parent–offspring recognition, as long as other females (or researchers) do not add non-kin to the nest. The disagreement as to whether this is a true form of kin recognition (*see* also below) stems, in part, from confounding the process of recognition with the outcome of such recognition. If selection favors discrimination of conspecifics based on genetic relatedness, and all individuals in an area are reliably kin, then the rule-of-thumb ‘treat anyone in area X as kin’ will also be favored (*see* also Hamilton 1964: p. 22). That is, spatially based recognition is the most parsimonious process for recognizing kin in this context, while other mechanisms would be favored when individuals in an area are not all related, yet both scenarios lead to the same outcome: preferential treatment of kin or discrimination against non-kin.

A second contextual cue that can reliably correlate with kinship is mating effort. For example, male dunnocks (*Prunella modularis*) adjust their parental investment in nestlings according to how much time they spent exclusively with a female during the mating period. Although the males may not be discriminating between their young in the nest and those of other males, time in proximity to a female is a good proxy for a male’s relatedness to the clutch and thus he can adjust his total investment in the clutch (Davies *et al.* 1992). Similarly, if the male partner in a tree-swallow (*Tachycineta bicolor*) pair is experimentally removed during the female’s fertile period, replacement males will invest in the offspring in the nest. If the partner is removed during incubation, replacement males do not invest in the young and even commit infanticide, as there is no chance that they were the sire of any of the young (Robertson 1990, Whittingham *et al.* 1993). Recognition of offspring in these cases is based on contextual cues which correlate with relatedness — using degree of paternal certainty as a rule of thumb — rather than traits of kin themselves. This mating-effort mechanism of discrimination will be favored if it reliably leads to preferential treatment of kin, or in avoidance of or aggression toward non-kin (Holmes & Mateo 2006, *see* also Neff & Sherman 2002).

A third contextual cue I refer to as “cohort sharing” can help young animals to recognize their paternal half siblings (and perhaps other classes of unfamiliar kin), and for adults to iden-

tify likely paternal half siblings and perhaps even to assess likely paternity. If breeding in a social group is seasonal and is dominated by one or a few males, then most young born into a cohort are likely to be offspring of that male(s). For cohort sharing to be a reliable mechanism for recognition, the timing of births must be episodic enough for distinctions between separate cohorts to be clear to all in the group. From the breeding male’s perspective, he could use either mating effort or cohort sharing to identify his putative offspring. Cohort sharing could explain the differential treatment of paternal half siblings and non-kin observed in savannah baboons (*Papio cynocephalus*) and rhesus macaques (*Macaca mulatta*; Altmann 1979, Widdig *et al.* 2001, Smith *et al.* 2003; called social familiarity and age proximity by these authors). This mechanism would not lead to accurate recognition of kin groups if many males achieve reproductive success, and thus may only be favored when kin discrimination has low costs, such as in grooming dyads, play-partner preferences, or foraging proximity, rather than in mate-choice, nepotistic or coalition contexts.

Recognition-allele mechanism

Second, recognition could be mediated by “recognition alleles” which cause expression of a phenotypic cue, recognition of that cue in others, and preferential treatment of individuals bearing the cue (Hamilton 1964, Dawkins 1976, Holmes & Sherman 1982). For example, altruism in social amoebas (*Dictyostelium discoideum*) is mediated by the *csA* gene which guides molecular recognition, cell adhesion and cooperative aggregations (Queller *et al.* 2003). An allele in fire ants (*Solenopsis invicta*) causes workers bearing that allele to kill queens which do not bear that allele, with discrimination occurring through olfactory cues (Keller & Ross 1998). This recognition mechanism has not been the focus of much research because, conceptually, it is expected to result in cooperation with non-kin that happen to express that cue, and so such single-allele cue-based cooperation is unlikely to spread (Dawkins’ 1976 “green-beard” effect; *see* also Blaustein 1983). For example, planktonic

larval ascidians (*Botryllus schlosseri*) settle near and eventually fuse with kin more than non-kin, and these kin-biased aggregations are beneficial because colonies composed of kin grow and reproduce faster than aggregations of distant or non-kin. Larval settlement patterns are influenced by cellular recognition, with larvae fusing with another individual if they share a histocompatibility allele but rejecting those with a different allele, even if those larvae are kin (Grosberg & Quinn 1986). Thus in this system the expression, perception and action components all appear to be influenced by histocompatibility alleles.

The vertebrate major histocompatibility complex, a large and highly polymorphic set of genes involved in immune functioning, influences the production of kinship-correlated odors (reviewed in Penn & Potts 1998). In addition, olfactory-receptor genes are found in the MHC (although it is unclear presently whether these genes are functional; Younger *et al.* 2001), thus suggesting the MHC as candidate recognition alleles. To date there is no evidence that the MHC also causes preferential treatment of individuals with similar MHCs, so although the MHC influences the production of genetically distinct odors, these odors were likely co-opted for kin-recognition purposes independently. (If the MHC genes do influence odor perception as well as expression, this would fit Hepper's (1991b) criteria for recognition genes and Crozier's (1987) criteria for "genetic kin discrimination", which assume that other genes regulate any response that might result from recognition.) Most research on kin recognition, both theoretical and empirical, has focused on prior-association and phenotype-matching mechanisms, so I will not discuss the recognition-allele mechanism further.

Prior-association mechanism

Third, recognition may be based on familiarity via prior association, when animals learn the phenotypes of individuals during early development (e.g., siblings and parents), and later discriminate these familiar relatives from unfamiliar animals. This learning can occur through a number of processes, such as habituation, imprinting or associative learning, although the actual type of

learning involved in social recognition is usually unknown. With prior association, animals can recognize familiar individuals, but not unfamiliar kin such as paternal half-siblings or cousins. For example, animals may learn the traits of their parent(s) and same-aged siblings, as well as their older or younger siblings if dispersal is delayed, and recognize these individuals later regardless of where they are encountered. Prior association can be established or learned in the nest itself or in the family's territory, if territory use is largely exclusive and non-kin are not encountered there. If development is precocial and young mix with non-kin shortly after hatching or birth, learning should occur rapidly, to restrict establishment of familiarity with kin only (e.g., Gottlieb 1981, Gubernick 1981, Poindron & Lévy 1990).

Prior association, or familiarization, is a proxy for relatedness and as such is sufficient for accurate kin recognition when relatives reliably interact in the absence of non-kin during early learning, such as at nest sites or in exclusive home ranges (and therefore differs from a cohort-sharing mechanism). Through direct association, individuals learn and become familiar with their early associates (typically relatives) and can later recognize them as kin even if encountered in a different spatial location. Recognition can also be mediated through prior association with a third individual, as when siblings born at different times both interact with their parent (Holmes & Sherman 1982) or when a parent's behavior toward young promotes similar behavior by its older offspring (e.g., helpers at the nest; Richardson *et al.* 2003). Prior association is commonly implicated in parent-offspring recognition, when litter, brood or clutch size is > 1 or when young remain with their natal group. This mechanism is also favored when discrimination among equally familiar individuals (e.g., full and half maternal siblings) or equally unfamiliar individuals (kin and non-kin) is not advantageous, such as when animals are short-lived with little overlap of generations or when there are few opportunities for social interactions with other kin. However, prior association will lead to recognition mistakes if non-kin are encountered during the learning phase (e.g., communal nesters), or if close kin are not encountered until some time later (e.g., young born in different years).

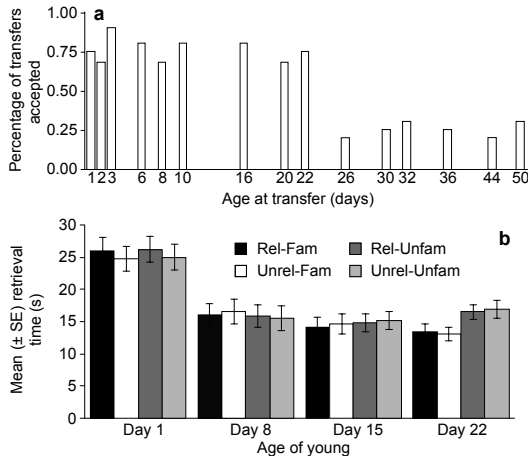


Fig. 1. — **a:** Proportion of young *S. beldingi* accepted by unrelated adult females in a field cross-fostering experiment. Free-living *S. beldingi* mothers readily retrieved into their natal burrow unrelated young placed at their burrow entrance, but only until their own young reached about 25 days of age, which coincides with when mothers' own young emerge aboveground from their natal burrow. From Holmes and Sherman (1982). — **b:** Latency (mean \pm SE) to retrieve pups by captive adult female *S. beldingi*. Mothers discriminate among their young and those of other females just prior to the age of natal emergence. Rel = related; Unrel = unrelated; Fam = familiar; Unfam = unfamiliar. From Holmes (1984).

Phenotype-matching mechanism

Fourth, through an extension of prior association, animals can learn their own phenotypes or those of their familiar kin, and later they can compare or match the phenotypes of *unknown* animals to this learned recognition template (“phenotype matching”; also referred to as comparing phenotypes and signature matching; Alexander 1979, Holmes & Sherman 1982, Beecher 1988). Phenotype matching requires a correlation between phenotypic and genotypic similarity so that individuals with traits that most closely match an animal's template are its closest kin. Both prior association and phenotype matching involve a comparison between templates and unfamiliar or familiar phenotypes, but as noted above prior association leads to recognition only of previously encountered familiar individuals, whereas phenotype matching permits discrimination among unfamiliar kin and non-

kin (Beecher 1982, Holmes & Sherman 1982, Reeve 1989). That is, unfamiliar kin are “recognized” as belonging to a particular kin class. This recognition occurs through generalization from recognition templates, with the degree of match between an encountered phenotype and an individual's template indicating the degree of relatedness between the two animals.

Phenotype matching is favored when kin are encountered after early development because it allows discrimination among individuals without prior association, by comparing their cues to a learned recognition template. This mechanism would be expected when there is multiple mating by males (for recognition of paternal half-siblings), communal nesting (so females can discriminate against familiar but unrelated young), natal or breeding dispersal (for males to recognize their older brothers or fathers), overlap of generations, particularly in long-lived species (Bekoff 1981, Holmes & Sherman 1982) or when there is no parental care (e.g., Göth & Evans 2004). Phenotype matching would also be favored in cases of intra- or inter-specific parasitism (see Göth & Hauber 2004). Finally, comparison of unfamiliar conspecifics' cues to own cues (self-referent phenotype matching) might be especially important when females mate multiply so that young can discriminate among their maternal full and half siblings (Mateo & Johnston 2000a; see also below).

An example of multiple mechanisms expressed within one species

Species can utilize several different recognition mechanisms, depending on the social context. For example, Belding's ground squirrel mothers (*Spermophilus beldingi*) use spatial cues to discriminate among young, caring for any pup in their underground nest, until just before young leave the nest (Fig. 1a). After emergence from the nest, spatial cues no longer reliably correlate with relatedness, as young may now mix with other litters. However, at this age offspring are beginning to produce unique recognition odors and mothers can use a prior-association mechanism for discriminating among own and unfamiliar young (Fig. 1b; Holmes & Sherman

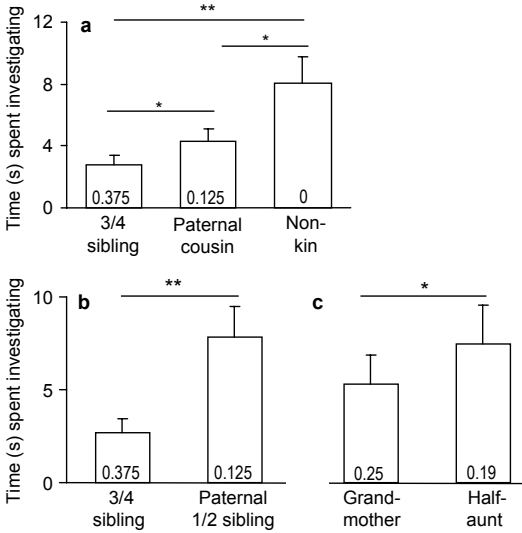


Fig. 2. Duration of investigation (mean + SE) of *S. beldingi* odors collected from subjects' unfamiliar relatives during preference tasks. — **a:** Investigation of oral-gland odors of unfamiliar kin, collected from subjects' 3/4 sibling (offspring of two sisters mated with the same male), cousin (offspring of the subjects' mother's brother) and non-kin. — **b:** Investigation of oral odors collected from subjects' grandmother and aunt. — **c:** Investigation of dorsal-gland odors collected from subjects' half aunt (mother's half sister) and non-kin. Numbers inside bars are estimated coefficients of relatedness between subjects and odor donors. Horizontal bars and asterisks represent significant differences in investigation of odors ($* p < 0.05$, $** p < 0.01$) based on repeated-measures ANOVA or paired *t*-test. An increase in investigation as relatedness of the odor donor to the subject decreases indicates that odors of distant kin are perceived as less familiar to subjects than odors of close kin. Significant differences in investigation of odors from various kin classes indicate discrimination of those odors, and thus that the subject can recognize the difference between, for example, its distant and non-kin. From Mateo (2002).

1982, Holmes 1984; J. M. Mateo, unpubl. data). Juveniles and adults can also use phenotype matching to discriminate among unfamiliar individuals based on genetic relatedness (Fig. 2; e.g., Holmes 1986a, 1986b, Mateo 2002). This recognition ability influences social behaviors, including nasal investigations (allowing perception of kin-distinct oral-gland odors; Mateo 2002) and play-partner preferences (thought to influence the development of adult kin preferences; Holmes 1994). Discrimination among unfamiliar kin and non-kin, as evidenced by differential

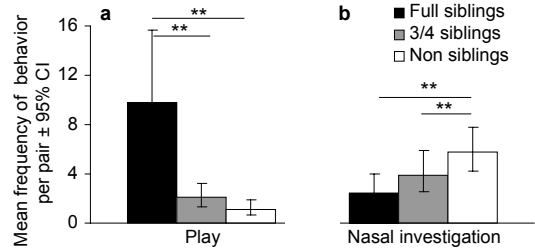


Fig. 3. Mean frequencies (+ 95% CI) of (a) play and (b) nasal investigations between pairs of juveniles as a function of relatedness (3/4 siblings are offspring of two sisters who mated with the same male). Horizontal bars and asterisks represent differences in behavior frequencies ($* p < 0.05$, $** p < 0.01$) based on Poisson regression analyses. Mean frequencies are adjusted statistically by the regression model for effects of sex of each juvenile in a pair and the weight difference between juveniles in each pair. From Mateo (2003).

nasal investigation, therefore leads to preferential social interactions with kin (Fig. 3; Holmes 1997, Mateo 2003).

S. beldingi can also discriminate among non-kin, such as territory neighbors or potential mates, using phenotype matching to recognize unfamiliar relatives of non-kin (Mateo 2002), and prior association to discriminate among individual non-kin (J. M. Mateo, unpubl. data). However, this recognition of non-kin seems to disappear during hibernation, as animals who could distinguish between the odors of familiar and unfamiliar non-kin at the end of the summer no longer show such an ability after overwintering (Fig. 4a; Mateo & Johnston 2000b). Torpor does not impair the retention of recognition of littermates (Fig. 4b), indicating that recognition of unrelated conspecifics is lost but that some level of kin recognition is maintained across hibernation. Yet if animals forget the odors of familiar, unrelated *S. beldingi*, they may also forget the odors of their littermates. That is, the recognition templates as a whole may be lost during hibernation, in which case animals must use their own odors via self-referent phenotype matching to recognize kin each spring (see also Holmes 1986b and below). Thus *S. beldingi* use a variety of perceptual mechanisms to recognize their social partners, and during their lifetimes the perceptual component, in particular recognition templates, change and need to be continually updated.

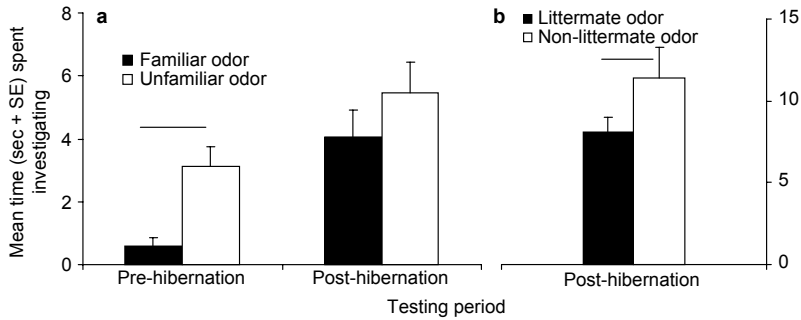


Fig. 4. Tests of odor discrimination before and after hibernation. — **a:** Duration of investigation (s + SE) of oral-gland odors of familiar and unfamiliar juveniles by Belding's ground squirrels prior to hibernation (left) and after hibernation (right). — **b:** Duration of investigation (s + SE) of odors of previously familiar littermates and non-littermates after hibernation. Horizontal bars represent differences in responses to the two odor types ($p < 0.01$). Redrawn from Mateo and Johnston (2000b).

Direct and indirect recognition

The recognition mechanisms discussed above have been categorized by some as direct and indirect. Waldman (1987) asserted that site-specific spatial recognition is "indirect" recognition because non-phenotypic cues serve as the basis for discrimination, whereas prior association, phenotype matching and recognition alleles result in "direct" recognition because discrimination is based on bearers' traits such as odors, plumage or vocalizations (*see* also Table 1). Barnard (1990) differentiated between direct and indirect cobeearer discrimination; in the former, alleles recognize copies of themselves in conspecifics, whereas in the latter, alleles use kinship as an indirect means of identifying who is likely to share copies of themselves. In a slightly different vein, Porter (1988) distinguished between direct familiarization, when recognition requires previous interactions with the animal to be identified, and indirect familiarization, which does not require prior experience with the animal to be identified (but does require direct familiarity with shared relatives).

Tang-Martinez (2001) contended that spatially based recognition actually represents errors, as kin encountered away from the home area would be treated as non-kin. Yet this mechanism will only be favored by selection when relatives reliably interact in a particular area, and not in other areas (or when preferential treatment of kin in those other areas is not favored), and thus these "errors" would be extremely uncom-

mon. Further, Tang-Martinez (2001) suggested that discrimination resulting from spatially based cues is not kin recognition, and therefore it should not be considered a recognition mechanism. Unfortunately, recognition is an unobservable, internal cognitive or neural process, and we know too little about this general process to determine whether animals actually do or do not recognize their kin when encountered in various locations. However, as I discussed above, if individuals encountered in a particular location are treated as kin, and if those individuals routinely are kin, then selection will favor a spatially based mechanism of recognition and discrimination.

The distinctions between direct and indirect recognition described above, as proposed by Blaustein (1983), Waldman (1987), Porter (1988), Barnard (1990), Hepper (1991b) and Tang-Martinez (2001), are in fact differences in expression components rather than perception components. These researchers categorize the four common recognition mechanisms based on cues to recognition, confounding the expression and perception components. Since the process of recognition and the cues for it evolve separately, as long as cues (contextual or phenotypic) vary with relatedness, any of the above perceptual mechanisms can be used for kin-recognition purposes. Thus the distinction between direct and indirect cues for recognition may be heuristic for understanding the expression component, but less so for the perception component.

Distinction among recognition mechanisms

In a recent review of recognition mechanisms, Tang-Martinez (2001) proposed that there is only one recognition mechanism — learning as a result of familiarity — with only the cues that are used for recognition differing among recognition processes. She further suggested that prior association and phenotype matching are involved in all recognition situations. That is, prior association involves learning familial phenotypes and later matching encountered phenotypes to those learned cues. And phenotype matching requires prior association with kin during some period of development during which familial cues are learned, so that later encountered phenotypes can be matched to the learned template. This is how most kin-recognition researchers have historically characterized the mechanisms, yet Tang-Martinez (2001) suggested the only difference between the two processes is that prior association involves learning of *individually* distinct cues from kin whereas phenotype matching involves learning of *kin- or family-*distinct cues, which all members of a kin class share apparently without individual variation. The reason for such a distinction is unclear, particularly since the same cues are often used for both kin recognition and individual recognition (e.g., Brown *et al.* 1990, Rendall *et al.* 1996, Todrank *et al.* 1998, Mateo 2002; J. M. Mateo, unpubl. data). Furthermore the two mechanisms, as originally proposed, mediate very different recognition outcomes. As noted above, with phenotype matching animals can recognize their familiar kin (e.g., individuals such as parents or siblings encountered when recognition templates are learned) as well as previously unfamiliar kin, allowing for discrimination of kin and non-kin, as well as categories of kin (e.g., half-sibling, cousins, and second cousins). The two mechanisms likely have different processes too, in particular how the phenotypes learned during early development are stored in memory or in a template (*see* “Recognition templates”, below).

Prior association and phenotype matching not only have distinct outcomes in terms of which kin can be recognized, but also likely have distinct physiological and perceptual processes.

In their historical development and as currently conceived, both mechanisms assume that learning occurs exclusively when kin are present, usually during early development, which is often the case in burrows or nests where single litters, broods or clutches are reared. However, the prior-association and phenotype-matching mechanisms use different perceptual processes to match conspecifics to recognition templates, with the former involving an exact match to the template and the latter generalizing from the template as a gestalt representation of kin. In addition, referents, or the familiar phenotypes learned early in development against which encountered phenotypes are matched, are likely encoded in templates differentially as well, with prior association “storing” referents as individual exemplars (e.g., mother, father, and each separate sibling) and phenotype matching likely using the referents to form prototypes (e.g., a family-wide cue). As discussed in Holmes and Mateo (2006), I use “prototype” as cognitive psychologists use it to refer to a set of features that are most commonly present in all members which belong to a particular category (Smith & Medin 1981, Estes 1994, Hampton 1995). Prototypes develop when animals experience individual instances within a category (e.g., a family’s odors) and abstract the common attributes of those instances, storing them as a generic representation of the common attributes of the category as a whole. With exemplars, animals experience individual instances within a category and store those individual instances rather than abstracting the commonalities among them. In sum, although both prior association and phenotype matching originate from learning the cues of close kin during early development, how those cues are matched against conspecifics’ cues and whether unfamiliar kin can be recognized differ.

Finally, Waldman (1987) and Porter (1988) suggested that prior association by default involves matching of phenotypes; that is, the familiar individual’s traits are compared or matched to an animal’s recognition template. While this is technically true (*see* next section), such an argument obscures the important distinction between these two recognition mechanisms. The perceptual matching algorithms fundamentally differ, with prior association allowing only

exact matches, whereas phenotype matching permits graded matches to the templates, and thus recognition of individuals of varying kin classes. In sum, I view these two recognition processes as proximately and functionally different mechanisms, although their outcomes — differential treatment of conspecifics according to genetic relatedness — can be similar.

Self-referent phenotype matching

Self-referent phenotype matching — the ability of animals to learn and use their own phenotypes as referents for recognition of relatives (termed the “armpit effect” by Dawkins 1982) — would be the most accurate way of assessing relatedness, as an animal’s own cues better reflect its genotype than those of its close kin. Self-matching should be favored in species with multiple paternity or maternity to discriminate among full and half siblings or when individuals commonly encounter older (or younger) siblings after dispersal (Holmes & Sherman 1982, Sherman 1991). It would also be favored when there is a risk of learning from non-kin, such as in brood parasitic or communal nesting situations, as animals would not have to learn the cues of familiar individuals but instead could rely solely or largely on its own cues. I have proposed elsewhere (Mateo & Johnston 2000a) that self-referent phenotype matching would be especially useful in nepotistic situations, when animals need to identify their closest kin, whereas in mate-choice or nest-defense contexts use of additional referents, such as parents and siblings, would be sufficient to avoid close inbreeding or to prevent entry of non-kin into the nest (see Hauber & Sherman 2001). The likelihood of a self-matching mechanism in nepotistic (compared with mating) contexts is controversial. Alexander (1990) argued against the evolution of self-matching in nepotism because alleles underlying such recognition would be “genetic outlaws”, benefiting themselves at a cost to the remainder of the genome, and thus would be suppressed by unlinked alleles not involved in the recognition process. Others (Dawkins 1982, Hamilton 1987, Sherman 1991) have countered that if alleles involved in both generating and perceiving recognition cues are spread through-

out the genome, then all alleles, including those not involved in recognition, would benefit from recognizing corresponding alleles in conspecifics.

To demonstrate self-matching for kin recognition, animals must be raised so that they do not experience kin cues other than their own during development. An ability to use their own cues as a referent for recognition would be demonstrated if they can later discriminate among unfamiliar kin and non-kin. However, it is critical that animals be reared without exposure to any kin cues except their own, otherwise one would not be able to rule out the possibility that their siblings’ or parents’ cues were learned (cf. Heth *et al.* 1998, see Mateo & Holmes 2004 for details).

Holmes and Sherman (1982) and Blaustein (1983) noted the difficulty in differentiating between self-matching and recognition alleles as the mechanism underlying a particular recognition event. First, our current knowledge does not allow us to determine whether alleles involved in the expression and perception of recognition cues also code for behaviors based on that recognition, which would be necessary to conclude recognition alleles as they are currently conceptualized. Second, to demonstrate self-matching one would have to manipulate an animal’s recognition cues during template formation, or prevent it from learning its own cues, as it is assumed this mechanism involves learning whereas recognition alleles do not (e.g., Hauber *et al.* 2000). Blaustein also acknowledged that, in general, phenotype matching is a more parsimonious mechanism given the theoretical arguments against recognition alleles, but added that, empirically, current data are consistent with both mechanisms.

Contextual and developmental changes in the perception component

Different recognition mechanisms may be used in different social contexts. For example, an adult may use spatial cues to identify its dependent young, prior association to avoid escalating agonistic interactions with an aggressive neighbor, and phenotype matching to cooperate with a cousin. Later, when its young become

more independent and begin to move about the environment, it may start to use prior association to distinguish between its young and those of another adult. For some animals, this ability to switch among recognition mechanisms may have a developmental component. Because recognition templates develop from early associations with familiar kin (and/or with self), prior-association-based recognition abilities are expected to precede phenotype-matching recognition abilities. For example, young Belding's ground squirrels discriminate among the cues of familiar and unfamiliar adults as early as 15-d of age, yet do not appear able to recognize unfamiliar kin via phenotype matching until 30 d (J. M. Mateo unpubl. data). This developmental pattern makes adaptive sense, as young ground squirrels do not encounter unfamiliar kin or non-kin until they leave their natal burrow, at about 27-d of age. It is important to recall that an animal may have the ability to recognize particular kin, yet not express that ability. For example, among communally nesting and nursing species, a young animal may know which female is its mother and yet nurse indiscriminately. If there is no cost of nursing from unrelated or distantly related females, then selection will not favor expression of recognition; that is, preferential nursing from its mother (*see* also Roulin 2002).

As characterized above, templates are formed during early development, when individuals interact exclusively or almost exclusively with kin such as parents and siblings. Such learning need not be confined to early development, however. It is possible, and often advantageous, to incorporate new kin like older siblings or grand-offspring into recognition templates. Non-kin may also be learned, such as mates or territorial neighbors. Thus, learning of familiar individuals could continue throughout the lifespan, with social-recognition templates continually updated as needed, so that the prior-association mechanism can be used to recognize individual familiar kin and non-kin. Updated templates can also permit expanded phenotype matching, although the extent to which this would be favored is unclear because there is a risk of incorporating non-kin into the template and thus a failure to distinguish among kin and non-kin accurately. However, there may be circumstances when

inclusion of kin and non-kin in recognition templates is advantageous. North American beavers establish monogamous pairbonds and defend territories along waterways. Natal dispersal also occurs along these waterways, so it is likely that an unfamiliar younger sibling will pass through an older sibling's territory. Not only can beavers use phenotype matching to recognize these siblings, but their mates can as well, exhibiting discrimination among its partner's relatives (Sun & Müller-Schwarze 1997). Mice and ground squirrels can also use phenotype matching to discriminate among non-kin (e.g., unfamiliar siblings of an familiar but unrelated rearingmate, or unfamiliar kin of an unrelated odor donor; Holmes 1986b, Porter 1988, Aldhous 1989, Mateo 2002). Phenotype matching among non-kin, encountered after early development, may facilitate social relationships within a colony, formation of winter groups of communally nesting rodents, and recruitment of dispersing individuals into new groups (e.g., Holekamp 1983, Wolff 1985, Hare 1992). One should bear in mind, however, that incorporation of non-kin into recognition templates may hinder accurate discrimination among classes of kin, unless some perceptual mechanism or decision algorithm keeps kin and non-kin phenotypes separate in the template.

Is phenotype matching true recognition of kin?

Some researchers (e.g., Waldman 1987, Alexander 1990) have argued that "recognition" of unfamiliar kin via phenotype matching is in fact an error, as animals mistakenly identify a stranger, whose cues match those in the template, as a particular familiar related individual (called "imperfect social learning" by Alexander). In other words, a paternal half-sibling would be treated as kin because the identifying animal mistakes it for its familiar maternal half-sibling. Waldman goes on to suggest that such mistakes would lead to graded responses to unfamiliar kin, as more distantly related kin would match the template less well than close kin, and would be treated accordingly. Yet this behavior is precisely what Hamilton's rule would predict (assuming equal costs and benefits) if these unfamiliar kin were

recognized correctly. Functionally, it does not matter whether kin are recognized correctly or mistaken for other kin, since the outcome of recognition would be favored regardless of its process, as long as individuals are treated according to coefficients of relationship.

Areas for future study

Recognition templates

The word “template” has been used to refer to animals’ memories of familiar kin, presumably learned at some early point in development, yet the meaning of the word is unclear. Do templates exist in neural structures, like face-recognition cells or song-nuclei circuits (e.g., Perrett *et al.* 1988, Margoliash 2002)? Or is “template” simply a heuristic for conceptualizing recognition abilities? One can examine whether templates consist of exemplars (e.g., specific memories of individuals’ phenotypes) or prototypes (a single amalgam or gestalt of several individuals’ phenotypes), as described above. Many species can discriminate among specific kin, such as sibling A and sibling B (e.g., Rendall *et al.* 1996, Todrank *et al.* 1998, Mateo 2002; J. M. Mateo, unpubl. data), suggesting that templates contain some specific representation of these individuals. Yet when an unfamiliar relative is encountered, such as a paternal half-sibling, do animals refer to these separate representations for recognition (necessitating multiple comparisons between each representation and the stranger’s phenotype), or do they utilize a gestalt template comprised of those representations (requiring just one global comparison)? Although the answers to such questions would further our understanding of the proximate bases of recognition, functionally, the outcome would be the same regardless of whether exemplars or prototypes are used, particularly if the referents in a template are weighted according to their relatedness to the animal (e.g., full-siblings’ traits are emphasized more than half-siblings’ traits in either template scenario). Since some animals can both recognize individual kin (via prior association) and “recognize” unfamiliar kin (via phenotype matching), templates may be both exemplar- and

prototype-based, depending on the recognition context (*see* also Breed & Bennett 1987). That is, individual representations may be used to discriminate between a mother and an older sibling or between two co-foundresses, whereas gestalt representations would be utilized when interacting with unfamiliar kin and non kin.

When animals attempt to identify strangers by way of phenotype matching, which referents should they use for comparison? Multiple individuals’ cues may be “stored” in a recognition template, such as those of siblings, parent(s), and even the animal itself, but one of the most notable gaps in our knowledge of recognition mechanisms is which of these referents are utilized and in which contexts (*see* also Mateo & Holmes 2004). That is, when an unfamiliar bee attempts to enter a nest, does the guard bee compare the stranger’s cues with those of the queen, itself, or its fellow workers? If multiple referents are used, are they weighted equally, or are some given more importance than others? As another example, if extra-pair copulations are common, young might weight their parents’ cues or their own cues more than those of their siblings, some of which may have been sired by a different male, and therefore would be less accurate referents for relatedness.

Further, different referents could be used in different situations. Cross-fostering studies in which halves of litters are transferred between mothers have shown that young incorporate into their templates cues of the adult female, of their genetic siblings, and of their foster siblings. In discrimination tasks fostered animals can recognize their familiar nestmates, and can recognize unfamiliar relatives of their genetic and of their foster siblings (reviewed in Mateo & Holmes 2004). Although cross-fostering creates an unnatural situation, it can have biological relevance, particularly when a clutch, brood or litter is multiply sired. By attending to differences in recognition cues produced by its full siblings and its half siblings, an animal can treat full siblings preferentially, or it might be able to differentially recognize its unfamiliar maternal and paternal kin, especially cues of their siblings are weighted differentially. I note that such weighting might require, firstly, preferential weighting of its own cues, since these would be shared with its full

siblings more than with its half siblings (*see* also Mateo & Johnston 2000a for an empirical example of weighting).

Neural correlates of perception

What do the empirical results of recognition studies tell us about the perception component? Across taxa, unfamiliar stimuli are usually attended to longer than familiar stimuli (Johnston 1981, Halpin 1986, Stoddard 1996). For example, animals tend to antennate, smell or look at unfamiliar individuals or most distantly related kin longer and/or more often than familiar individuals or close kin (e.g., Getz & Smith 1986, Dahbi & Lenoir 1998, Bull & Cooper 1999, Fadao *et al.* 2000, Mateo 2002). Although there are exceptions to this tendency, such investigatory behaviors suggest that it takes longer to identify or recognize unfamiliar individuals than familiar ones, as if additional time is needed for unknown cues to be compared or matched to templates to make an identification. A recent study indicates that this may be an inaccurate conclusion, at least in some rodents. Uchida and Mainen (2003) showed that psychophysical discrimination of simple odors by trained rats occurs in about 200 ms, regardless of the similarity of the odor stimuli and thus the difficulty of the task. It appears then that fine-tuned perceptual discrimination of odors does not require additional neural processing time (although how quickly behavioral discrimination will be evident is unclear). If these findings apply to other species as well, then how should we interpret differential investigation times? Although speculative, perhaps an unknown phenotype is quickly perceived and characterized (e.g., in the olfactory bulb or antennal lobe), but additional investigation is required to match it to the recognition template and accurately determine the degree of relatedness between the two individuals. Alternatively, prolonged investigation may serve to make unfamiliar stimuli familiar. Indeed, discrimination, and investigation duration, may be quicker for identifying individuals via exemplar-based template matching than for recognizing unfamiliar kin via prototype-based template matching. Familiar individuals would match the

template, producing a threshold response (match or not match), whereas unfamiliar individuals would have to be evaluated against the gestalt family cues, with some decision algorithm used to produce a graded response according to relatedness.

Dissociation of recognition components

Recall that the components of recognition evolve separately, and that the action component — preferential treatment of kin, aggressive behaviors toward non-kin, or mate choice — can only evolve if the expression and perception components of the recognition process have already evolved. Thus when kin-biased behaviors are expected, but not observed, it could be due to a failure of the expression, perception, or action components, and each possibility should be explored empirically. As an example, consider the problems faced by male birds which are unsure of their relatedness to nestlings in the nest shared with their social partner. Several studies have failed to find preferential investment in chicks sired by the male (*see* Kempenaers & Sheldon 1996), from which some have concluded that Hamilton's rule ($rB > C$) is not satisfied. That is, the risk of not caring for their own chicks outweighs the potential benefits of discriminating against chicks sired by another male and thus the action component (rejection of non-kin) has not evolved. However, it is possible that chicks do not produce kin labels (concealing information about their true father; Beecher 1991, Johnstone 1997, but *see* Bonadonna *et al.* 2003 for possible olfactory cues to social recognition and Price 1999 for possible auditory cues) or that males do not have the ability to make use of kin labels to recognize their own chicks (Beecher 1988, Kempenaers & Sheldon 1996, *see also* Hatchwell *et al.* 2001). Until such studies are done, it remains unclear which of the three recognition components have or have not evolved when kin-differential behaviors are expected but not observed.

An additional corollary of this potential dissociation of recognition components is that an absence of behavioral discrimination or of differential treatment of conspecifics cannot be interpreted as a lack of recognition ability. Ani-

mals may have the ability to recognize classes of kin and non-kin, yet do not exhibit preferential treatment or avoidance of those classes in all social contexts. In those contexts, Hamilton's rule may not favor discrimination despite accurate recognition of kin (Gamboa *et al.* 1991). For example, asocial golden-mantled ground squirrels (*S. lateralis*) exhibit no kin-directed behaviors as adults, such as cooperative territory defense or nepotistic alarm calls, unlike sympatric Belding's ground squirrels (*S. beldingi*; Sherman 1981, Michener 1983). Yet both species are able to discriminate quite accurately among classes of relatedness, indicating that the expression and perception components have evolved in both species, but the action component involving nepotistic behaviors has been elaborated only in *S. beldingi*. It is possible that *S. lateralis* use their kin-recognition abilities in some other context, such as mate choice (Mateo 2002).

Another paradoxical example of an apparent lack of differential nepotism is found in social insects. In colonies with multiple matriline (more than one queen, and thus more than one sire) or a single queen with multiple patriline, one might expect workers to tend to full sisters more so than half sisters, given the potentially significant influence it would have on their mother's reproductive success (and the workers' indirect fitness). Yet empirical studies have consistently failed to demonstrate unequivocally differential treatment of larvae or workers based on within-colony differences in relatedness (e.g., Breed *et al.* 1994, Keller 1997, Strassmann *et al.* 2000, Tarpay *et al.* 2004). Recognition cues — in the form of cuticular lipids — are acquired by all colony members from the nest, yet if individuals' cues retain some distinctiveness (for example because of when or where in the nest they developed), then they could theoretically use themselves as referents for discriminating within the colony (Carlin 1989, Keller 1997). Chemical analyses of hornet and paper-wasp lipids indicate they are variable enough to facilitate discrimination among matriline within a nest, but are unlikely to permit accurate discrimination in nests composed of different patriline (Dani *et al.* 2004). Thus current data suggest that the lack of expressed within-colony discrimination by some social insects could be due to constraints in

the expression component, and perhaps the perception and action components as well.

Conclusions

The perceptual component of social recognition has a long theoretical and empirical history. From amphibians to rodents and fish to social insects, animals use a variety of recognition mechanisms to discriminate among classes of conspecifics, such as kin, neighbors, colony members and mates. These mechanisms vary not only among species but also among recognition contexts. Future research should extend our current knowledge of the perceptual mechanisms involved in recognition, to understand the neural processes involved in discrimination, the development of recognition templates, the algorithms used to determine identity, and how decision rules are used to act (or not act) upon the resulting recognition.

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