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# Cooperation and Conflict in the Light of Kin Recognition Systems

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## Abstract and Keywords

Genetic relatedness is central to the problems of social evolution. Whenever individuals interact nonrandomly with respect to genotype, their actions may have indirect fitness consequences. Although population structure affects the frequency of interactions among relatives, kin recognition systems can help optimize behavior to the advantage of the actor's genetic posterity. Here, we review the functional and mechanistic foundations of kin recognition systems and demonstrate their effects on cooperation and conflict in a number of different species, devoting special attention to the case of *Homo sapiens*. We conclude by developing several testable hypotheses about the impact of kin recognition on social behavior.

Keywords: Kin recognition, social evolution, inclusive fitness theory, phenotype matching, green-beards

The Argentine ant, *Linepithema humile*, is a bit peculiar. Upon encountering a conspecific from an unfamiliar colony, individuals sometimes react violently. But, this behavior is contingent on the genetic diversity of the colony from which the ants are drawn, and can thus be asymmetrical: Individuals reared in genetically homogeneous colonies are typically aggressive toward foreign conspecifics, whereas those from heterogeneous colonies tend to be indifferent toward foreigners (Tsutsui, Suarez, & Grosberg, 2003). This dislike of "alien" phenotypes smacks of xenophobia (Starks, 2003). It also seems awfully human.

An appreciation for the evolved design of kin recognition systems sheds light on this phenomenon of formicine discrimination, among myriad other aspects of organismal sociality. Given the wide scope of the kin recognition literature, we cannot discuss the majority of the published works (including much of that which regards mate choice), but excellent reviews may be found in this volume (Chapter 13, by Hepper) and elsewhere

(e.g., Fletcher & Michener, 1987; Hepper, 1991; Sherman, Reeve, & Pfennig, 1997; Waldman, 1988; volume 41, issue 6 of *Annales Zoologici Fennici*). Our aim in this review, rather, is to demonstrate the utility of kin recognition in solving the functional problems of cooperation and conflict, and the predictable consequences that result from its deployment in social contexts. Naturally, our analysis begins with social evolution theory.

# Social Evolution Theory

W.D. Hamilton (1964, 1971b) provided the theoretical foundations for the study of kin recognition in his seminal work on social evolution. From the standpoint of evolutionary biology, an action performed by one or more individuals (the average actor) is said to be social when it has effects on the fitness of others (the average recipient).[1] We apply (p. 346) the term *cooperation* to the two kinds of action that increase the recipient's fitness: mutually beneficial behavior (actions that increase both the actor's and recipient's fitness) and altruism (actions that increase the recipient's fitness but decrease the actor's). Conversely, we apply the term *conflict* to the two kinds of action that reduce the recipient's fitness: selfishness (actions that decrease the recipient's fitness but increase the actor's) and spite (actions that decrease both the actor's and recipient's fitness). For reasons discussed at length elsewhere (West, Griffin, & Gardner, 2007), the fitness metric used here refers to the net consequences of the action on reproductive success—that is, summed over the lifetime of the organism—relative to the mean fitness of the population, rather than to other members of the same social group.

There are three general mathematical approaches to social evolution theory, each partitioning the fitness effects of a social action in different ways. Inclusive fitness treatments consider the effects of the action from the perspective of the actor (Hamilton, 1963, 1964, 1970; Taylor, Wild, & Gardner, 2007), whereas direct fitness/neighbor-modulated fitness/kin selection treatments consider the effects of the action from the perspective of the recipient (Frank, 1998; Taylor & Frank, 1996; Taylor, Wild, & Gardner, 2007). Finally, group or multilevel selection treatments decompose the effects of the action on fitness within and between groups (Grafen, 1984; Hamilton, 1975; Queller, 1992). All three methods are formally equivalent, but the inclusive fitness approach is perhaps the most intuitive, and so we make use of it here.

A social action will be favored when the sum of its direct ($d$) and indirect ($i$) fitness consequences are greater than the mean population fitness (set to 0 in a population of constant size), $d + i > 0$. Direct fitness is simply the increment or decrement in reproduction of the actor as a consequence of having performed the action. It is a proxy for the reproductive success of the focal allele via the actor's descendant line, and it is equivalent to the classical Darwinian notion of fitness. Conversely, indirect fitness is a proxy for the increment or decrement in reproduction of identical copies of the focal allele via individuals other than the actor or the actor's descendants; allele copies are typically housed in the bodies of collateral kin. As such, $i$ can be partitioned into two components: the effect of the social action on the direct fitness of the recipient, $x$, weighted by the relatedness of the recipient to the actor, $r$, a measure of the probability that the actor and recipient share copies of the focal allele. Thus, the rule $d + rx > 0$, known as Hamilton's rule, specifies the ecological ($d$, $x$) and genetic ($r$) conditions under which natural selection favors any social action.[2]

Simple as it is, social evolution theory often engenders confusion, especially the concept of genetic relatedness. As relatedness is very much the focus of this chapter (and book), we clarify the concept below.

## Genetic Relatedness

Genetic relatedness is usefully conceived of as a “genetic exchange rate” (Frank, 1998), as if the actor values the recipient’s genetic currency against its own (Hamilton, 1964). The value of the recipient’s reproduction to the actor lies in the former’s likelihood of carrying identical copies of an allele influencing the actor’s social behavior. From the actor’s perspective, the more likely the two are to share copies of a focal allele, the greater the recipient’s worth; conversely, the less likely the two share copies of the focal allele, the more expendable—undesirable, even—the recipient becomes. The issue at hand is how this likelihood is to be measured.

Since Hamilton’s first works on social evolution (Hamilton, 1963, 1964), the concept of genetic relatedness has been appreciably modified (e.g., Frank, 1998; Grafen, 1985; Hamilton, 1970; Michod & Hamilton, 1980; Queller, 1994). Contemporary measures take into account the *chance* probability of bearing a copy of the focal allele, which is to say the likelihood of an individual, plucked at random from the population at large, bearing a copy. This is because a social action will cause no evolutionary change when the affected recipient bears the allele at chance levels. For instance, if the population mean frequency of the allele is $\bar{p} = 0.5$, then adding or subtracting offspring from average recipient $n$ with a frequency of bearing the allele of 0.5 (i.e., chance) will result in no subsequent change in the representation of the allele; it will remain $\bar{p} = 0.5$. This result holds true at any allele frequency in the population, and so $r = 0$ for all pairs of individuals who hold copies of the focal allele at frequencies that do not deviate from chance.

(p. 347) Limited dispersal, or population “viscosity,” characterizes many breeding systems, and it has the effect of increasing the genetic relatedness of neighbors. However, it also tends to increase the competition among neighbors for limited reproductive vacancies, such that the benefits of associating with kin are cancelled by their downstream competitive effects (Queller, 1994; Taylor, 1992a,b). This and other aspects of population structure lead us to formulate a general measure of the relatedness of actor $m$ to recipient $n$ as:

$$r = \frac{p_n - \bar{p}}{p_m - \bar{p}}$$

where $p_m$ and $p_n$ are the average frequencies of the focal allele of the actor and the recipient, respectively, and $\bar{p}$ is the average frequency of the focal allele in the actor’s and recipient’s competitive pool or “economic neighborhood” (Queller, 1994). We are most often interested in the direct and indirect effects of actions performed by individuals bearing the focal allele, so $p_m$ will equal 1 in the typical analysis. Because recipients may be either more or less likely than chance to bear the focal allele, $r$ can take on both positive and negative values. When $r > 0$, the recipient is more likely than chance to share the focal allele borne by the actor, and so the two are said to be positively related. Conversely, when $r < 0$, the actor and recipient are negatively related, because the recipient is less likely than chance to bear the focal allele borne by the actor. In other

words, the actor and recipient will tend to bear *rival* alleles. Genetical evolution is the result of a change in the relative frequency of the allele in the population, so an action that decreases the reproduction of negative relatives is one that decreases the representation of rival genotypes, thereby increasing the relative representation of the focal allele. It has long been understood that positive relatedness is essential to the evolution of altruism (Foster, Wenseleers, & Ratnieks, 2006a; Hamilton 1963, 1964;). Likewise, negative relatedness is a requisite condition for the evolution of spite: As it entails costs to both actor and recipient ($d < 0$ and $x < 0$), $r$ must also be $< 0$ to satisfy Hamilton's rule (Gardner & West, 2004; Hamilton, 1970).

The mathematics of relatedness may seem tangential to the problems of kin recognition, but they highlight an important aspect of its measurement: Relatedness is a relative concept. As gene frequencies in the relevant population change, so too does the relatedness of a particular pair of individuals (Gardner & West, 2004; West et al., 2007). Below, we will show how one particular mechanism of kin recognition—phenotype matching—is ably designed to make the relative judgments expected by the modern metrics of genetic relatedness.

# Kin Recognition Systems

The ability to recognize kin is not required for an action to have indirect fitness consequences. Organisms may affect the reproduction of their relatives whenever population structure causes nonrandom assortment among kin, as in viscous populations (Hamilton, 1964), without any information about the relatedness of their neighbors. For instance, under certain competitive regimes, the pathogenic bacterium *Pseudomonas aeruginosa* evolves increasing degrees of cooperation when its neighbors are positively related (Diggle, Griffin, Campbell, & West, 2007; Griffin, West, & Buckling, 2004). Conversely, under different regimes, *P. aeruginosa* evolves to engage in conflict with negatively related neighbors (Inglis, Gardner, Cornelis, & Buckling, 2009). The effects of demography on social evolution are varied (see e.g., Frank, 1998; Queller, 1994; Taylor 1992a,b; Taylor, Day, & Wild, 2007; Wild, Gardner, & West, 2009); nonetheless, the point is that kin recognition is not strictly required to affect indirect fitness. Under certain conditions of population structure, a rule of "help thy neighbor" will suffice to benefit positive relatives.

And yet, kin recognition systems have been discovered many times over. Among species that interact in mixtures of more and less closely related individuals, discriminative responses toward relatives afford indirect fitness benefits, creating selection pressure on the design of kin recognition mechanisms. Design "options" abound for such systems—the informational inputs, computational algorithms, and consequent behavioral outputs may vary over time, place, and lineage—but all are selected to work to the same basic

end: to optimize the expenditure of resources in nepotistic fashion, as if maximizing the genetic posterity of the focal allele through direct and indirect channels of reproduction.

*Kin recognition* has several connotations. It is often operationalized as the differential treatment of genetic relatives (*kin discrimination*), but is more appropriately defined as the collection of de facto sensory and perceptual mechanisms that function to assess the relatedness of a social partner, irrespective of the behavioral response. Of course, kin recognition systems must be in the service of action, or they would be irrelevant to selection, so confusion (p. 348) between these two meanings is not entirely problematic. The danger to be avoided, rather, is in drawing the conclusion that kin recognition is absent because of a lack of evidence of discrimination, even though discrimination is not always to be expected (Holmes, 2004; Liebert & Starks, 2004; Mateo, 2004; Waldman, 1988).

The ability to recognize kin can entail rather sophisticated mental "architecture," but in many cases it will be quite simple. Indeed, its implementation is at times positively brainless: There is recent evidence that the annual plant *Cakile edentula* recognizes kin, retarding root structure growth—and thereby reducing competition—when planted beside maternal siblings (Dudley & File, 2007). Likewise, sperm of the polyandrous deer mouse *Peromyscus maniculatus* help one another as a function of relatedness (Fisher & Hoekstra, 2010). Even malaria parasites seem capable of feats of kin discrimination (Reece, Drew, & Gardner, 2008). What mechanisms might underlie such nepotism?

## Indirect Kin Recognition

The mechanisms of kin recognition may be *direct*, whereby individuals themselves are recognized as particular kin members (e.g., sibling 1 vs. sibling 2, etc.) or as belonging to a kin "class" (e.g., siblings vs. cousins), or they may be *indirect*, whereby individuals are not themselves recognized as kin, but are instead distinguished as a function of circumstance. Each has its virtues—indirect mechanisms are relatively inexpensive, direct mechanisms are more versatile—but each also entails a unique set of problems, and so their use is predicted to be favored by different ecologies (Waldman, 1988).

In many cases, context is intimately tied to genetic relatedness. Relatives are often reared together, tended to by the same individuals, and at least partly segregated from nonrelatives. As such, kinship can be assigned as a function of the context in which individuals may find themselves, and it is in these circumstances that we expect to find indirect kin recognition mechanisms at work. A simple indirect mechanism relies on location, treating individuals in one space, such as the nest, as kin and those located elsewhere as nonkin. Any organism that cares for juveniles (related and unrelated alike) placed in its nest, but not elsewhere, is effectively using location data to impute kinship. Such rules can be sensible: When recognition errors of acceptance (perceiving a nonrelative as kin) based on spatial information are rare—offspring are not ambulatory, for example, and so cannot accidentally wind up in the wrong nest—more complex

mechanisms are a costly extravagance. Predictably, then, gulls with isolated nests, such as cliff-nesting kittiwakes (*Rissa tridactyla*), will accept unrelated conspe-cific young when artificially placed in their nests, whereas other, communally nesting gulls are less inclined to do so (Cullen, 1957). It is notable, however, that this difference between cliff-nesting and communally nesting gulls may lie not in the parents' offspring-recognition abilities per se, but in their adoption of decision rules to disregard this information in favor of indirect recognition (Storey, Anderson, Porter, & MacCharles, 1992).

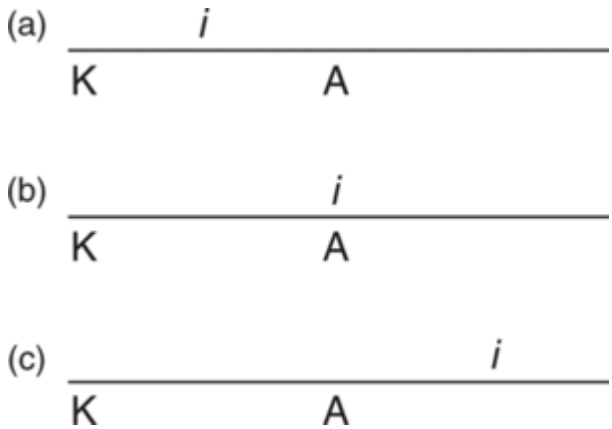
Spatial cues ought often to be mitigated by developmental timing. As offspring of many species mature, they will tend to become more mobile, so age will correlate with the likelihood of committing a recognition error. Holmes and Sherman (1982) demonstrated a temporal sequence of acceptance and rejection of juveniles at the burrow by adult Belding's ground squirrels (*Spermophilus beldingi*) roughly corresponding to the age of offspring weaning. Adult females would accept juveniles, regardless of genetic relatedness, until about the age at which the juveniles emerge from the burrow on their own accord. Prior to this age, juveniles rarely mix with nonrelatives. After this age, however, when the risk of encountering nonrelatives in the burrow increases, adult females appear to make use of other mechanisms that reduce the likelihood of making an identification error.

## Direct Kin Recognition

Context-based kin recognition systems may be inexpensive to develop and employ, but they entail increasing costs in terms of recognition errors as spatial aggregation becomes less predictive of relatedness. Once individuals begin to run a nontrivial risk of encountering nonrelatives (in previously reliable locations or elsewhere), it might pay to learn the phenotypes of various rearing associates—who, in many species, are typically parents, offspring, and siblings—instead of their locations. Early context can enable such direct kin recognition, as prior association with conspecifics in particular spatiotem-poral contexts allows an individual to encode the phenotypes of its kin before it encounters nonrelatives (Mateo, 2004). Thus, individual or class recognition can be co-opted for the purpose of recognizing kin. Animals as diverse as rhesus macaques (*Macaca mulatta*; Rendall, Rodman, & Emond, 1996) and golden hamsters (*Mesocricetus auratus*; Todrank, (p. 349) Heth, & Johnston, 1998) can recognize and distinguish kin on an individual basis, for instance, but *Homo sapiens* provides the most familiar example. Children who have been reared together and tended to by the same mother grow to individually recognize and treat each other as siblings, even when they have explicit knowledge that might be expected to obviate such familial sentiments (Lieberman, Tooby, & Cosmides, 2007).

Direct kin recognition mechanisms, however, are not limited to distinctions between familiar and unfamiliar individuals. Organisms may be reared among unequally related conspecifics (as in broods of mixed paternity), and they may frequently encounter genetically related strangers. Both circum-stances can lead to the evolution of specialized mechanisms for the detection and evaluation of cues or *labels* associated with kinship that

distinguish among familiar rearing associates and extend to interactions with unfamiliars. Rather than evaluating conspecifics on information regarding individual identity, organisms may search for labels indicative of genotype. In a process known as *phenotype matching*, individuals compare the labels expressed by conspecifics to internal, multidimensional representations (*templates*) of a variety of *referents*. A kin template is formed when the referents for the template are members of a particular kin class, and an average template is formed when its referents are members of the local population. An evaluator can compute the differences between these two templates to define the dimensions on which individuals are to be judged. When two unfamiliar individuals meet, for instance, they may effectively locate each other's phenotype along these dimensions: A phenotype that is more similar to the kin template than is the average template will be perceived as positively related, whereas a phenotype that is less similar to the kin template than is the average template will be perceived as negatively related (Fig. 20.1). The distance between the kin and average templates is expected to be a function of both the variance in and prevalence of label polymorphism to which the evaluator is exposed (Krupp, 2010).




*Click to view larger*

*Fig. 20.1* Phenotype matching in one dimension. In a phenotype matching system, one or more dimensions are defined (*solid lines*); the phenotypic values of the prototypical kin (*K*) and average (*A*) templates are represented and located along these dimensions, as well as the phenotypic values of individuals *i*. When *i* is closer to the kin template than is the average template (*a*), *i* is perceived as a positive relative ($r > 0$). When *i* is no closer to the kin template than is the average template (*b*), *i* is perceived as a nonrelative ($r = 0$). Finally, when *i* is further from the kin template than is the average template (*c*), *i* is perceived as a negative relative ($r < 0$)

Templates are generally the products of learning and may represent a weighted average of label values extracted from several individuals (other-referent phenotype matching), such as parents and siblings, values extracted from the evaluator itself (self-referent phenotype matching), or some combination of the two. As sex and age are typically uncorrelated with relatedness, kin templates are expected to overlook phenotypic differences associated with these variables.[3] They may also be fixed at particular points in development, or they may be continuously updated, allowing for a more dynamic assessment of relatedness as the average population phenotype (and, presumably, genotype) changes with time and place.

When label polymorphism is directly attributable to genetic variability, recognition may not require learning (although it is often difficult to rule out). Rather, gene products may recognize copies in other bodies, although it has been difficult to demonstrate the existence of such “recognition alleles.” In a sense, however, recognition alleles and individual recognition—any kind of direct kin recognition, really—represent special cases of phenotype matching, as the evaluator is in all cases matching the phenotypic labels expressed by an individual to an internal template. In the former case, the label is genetically determined and the template is (possibly) unlearned, whereas in the latter case the label and template are individual-specific. This is not to suggest that the differences among the various mechanisms of direct kin recognition ought to be overlooked in favor of their commonalities, but there is considerable overlap (p. 350) in the form and function of these various systems (see also Waldman, 1987).

At times, label polymorphism is caused by genetic differences among individuals. However, mere association between label and genetic diversity is often sufficient to support direct kin recognition. Common descent is the most frequent cause of genetic similarity, so the relatedness of two individuals at a given locus will tend to be correlated with relatedness across the whole genome. This makes genetic relatedness and kinship largely overlapping concepts (Grafen, 1985); thus, cues of kinship will reliably predict the relatedness of the interacting parties.[4] So, although genetic variation must be correlated with label polymorphism, it does not need to cause the polymorphism. For example, long-tailed tits (*Aegithalos caudatus*) produce nest-specific contact calls, known as a “churr” call; individuals distinguish the churr calls of their kin from those of nonkin (Sharp, McGowan, Wood, & Hatchwell, 2005). When young are cross-fostered into the nests of nonrelatives, they learn the churr call of their foster parents, so that the correlation in sound qualities of the call among unrelated foster siblings reared together is not significantly different from that of related siblings reared together, whereas both groups produce calls significantly more similar to their nestmates than do related siblings reared apart (Sharp et al., 2005). In principle, any feature of an organism (including culturally acquired accoutrements) could be used as a label of kinship, so long as it was reliably correlated with genetic relatedness and perceptible to conspecifics.

# Kin Recognition in the Context of Cooperation and Conflict

A vast number of empirical demonstrations show that kinship is associated with cooperation and conflict. Yet, it is not always clear that recognition systems are the cause of any apparent nepotism, as population structure may produce similar patterns of association without appeal to discriminative abilities. Moreover, interactions among kin may not necessarily bring about indirect fitness benefits (Griffin & West, 2002), even though they are commonly expected. Nevertheless, careful studies of kin recognition,

having flourished in the wake of social evolution theory, provide numerous examples of the effects of kin recognition on social behavior.

Kin recognition research typically investigates proximate and ultimate aspects of the three “components” of recognition systems (Reeve, 1989): (a) the *expression* component, corresponding to the mechanisms that produce the label (Tsutsui, 2004); (b) the *perception* component, corresponding to the mechanisms that interpret the label, generate the template, and test the match between the two (Mateo, 2004); and (c) the *action* component, corresponding to the mechanisms that produce the discriminatory behavioral outputs (Liebert & Starks, 2004). This work often involves divorcing genetic relatedness from any postulated kinship cue. If organisms discriminate conspecifics as a function of some cue that was associated with genetic relatedness in ancestral environments, then disturbing the relationship between genealogical kinship and cues thereof can result in recognition errors diagnostic of kin recognition systems. Effectively, the method by which researchers (or nature) can successfully create “fictive” kin reveals the design, if any, of the recognition system.

For example, indirect kin recognition mechanisms make the de facto “assumption” that individuals located in one particular place and time (juveniles in the nest, for instance) are close kin, and brood parasites have been quite successful at exploiting such mechanisms. Brood parasites impose significant costs on their hosts, so the regularity by which hosts accept and rear parasitic offspring remains an enduring puzzle (reviewed in Davies, 2000). Davies and Brooke (1989b) have nicely demonstrated that several host species of the common cuckoo (*Cuculus canorus*) fail to discriminate between parasitic chicks and their own progeny in the nest. Moreover, such ready acceptance of foreign chicks is not likely to be the result of a cuckoo trick, as host species also accept chicks of nonparasitic species. Current host species (as well as nonparasitized, but suitable, host species) do reject cuckoo *eggs* based on their appearance (Davies & Brooke, 1989a). As young, naïve hosts are more likely to accept cuckoo eggs than older, experienced hosts, host species likely learn to recognize their own eggs (Davies, 2000; Lotem, Nakamura, & Zahavi, 1992). So, host species use an indirect recognition mechanism at the chick stage, but reduce the initial risks of parasitism at the egg stage, using direct recognition when the risk of recognition errors by indirect means is elevated.

(p. 351) Unlike the common cuckoo, the American coot (*Fulica americana*) parasitizes conspecific nests. Intraspecific brood parasitism such as this should make recognition of the host’s eggs and hatchlings particularly difficult, as the objects being discri-minated will undoubtedly be quite similar. Yet, American coots are able to distinguish their own eggs from those of conspecifics based on direct recognition mechanisms. They appear to evaluate egg color, rejecting those noticeably different from their own by burial or by relegating them to lesser incubation positions (Lyon, 2003). Furthermore, because the first eggs to hatch are almost always the host’s own, they can recognize their young by phenotype matching, the first hatchlings being used as the referents (Shizuka & Lyon,

2010). As a result, juvenile parasites of this species have a significantly increased mortality risk, likely due to harm delivered by their host parents (Shizuka & Lyon).

At times, the very same recognition mechanisms can lead to both cooperative and competitive behaviors, as evidenced by the sea squirt *Botryllus schlosseri*. This marine invertebrate forms cooperative networks of colonies by fusion of blood vasculature with conspecifics. Individuals fuse strictly with clones or close relatives, and conflict is evident after contact between conspecific nonrelatives. Such interactions lead to a cytotoxic response that causes significant damage to the contacted tissues, followed by the formation of a necrotic barrier between individuals (Scofield & Nagashima, 1983). The recognition label controlling the acceptance/rejection response appears to be the product of a single, highly variable histocompatibility locus analogous to the vertebrate major histocompatibility complex (MHC) (Grosberg & Quinn, 1986). Thus, the very alleles used in immune defense also serve as labels of kinship.

It is not surprising that genes involved in immunity are sometimes involved in kin recognition. Selection will generally work against variation in traits whose primary function is to advertise kinship, because those recipients with common labels will find more opportunities to cooperate and fewer instances to compete with others (having a higher probability of encountering social partners with the same label), thus driving the most common label to fixation (Crozier, 1986, 1987; Grosberg & Quinn, 1989; Rousset & Roze, 2007). Selection will, however, tend to maintain label diversity when other, countervailing pressures favor allelic variation (Crozier, 1987; Gardner & West, 2007; Rousset & Roze, 2007). Loci coding for immune response are often highly variable because they are subject to antagonistic coevolution by parasites, so they tend to make good labels for kin recognition systems.

The same logic extends to kin recognition in parasites. The eusocial parasitic wasp *Copidosoma floridanum* is enveloped in an extraembryonic membrane during larval development inside the host. Giron and Strand (2004) propose that antagonistic coevolution between *C. floridanum* and its host has maintained polymorphism in the extraembryonic membrane, which has been subsequently exploited by the parasite as a kin recognition label. Having shown that the membrane conceals the parasite from the host's immune system, they also find that it serves as a kinship cue: Precocial soldier larvae discriminatively attack reproductive larvae enveloped in the membranes of nonrelatives, but spare larvae enveloped in the membranes of their genetically identical sisters. This is true even when the reproductive larvae have been experimentally excised from their own membranes and transferred to the membranes of other individuals—identical sisters enveloped in the membranes of nonrelatives, or unrelated females enveloped in the membranes of identical sisters, for instance.

When a kin label cannot be easily divorced from its bearer, unlike the situation of *C. floridanum*, researchers may instead rely on cross-fostering techniques, whereby responses of individuals reared with their genetic relatives are compared to those of individuals reared with unrelated "foster" families (for a review, see Mateo & Holmes,

2004). Such studies can be revealing, as a seminal kin recognition experiment by Buckle and Greenberg (1981) demonstrates. Sweat bees (*Lasioglossum zephyrum*) guard the entrances of their nests, generally allowing access only to resident conspecifics. Using cross-fostering, Buckle and Greenberg created colonies of six young bees, half from one colony (A) and the other half from a second colony (B), and demonstrated that guards of the original colonies admitted greater access to their unfamiliar relatives than to unfamiliar nonrelatives from the experimental colony (i.e., colony A guards accepted cross-fostered individuals derived from colony A at higher rates than cross-fostered individuals derived from colony B). The researchers also cross-fostered young bees singly into the nests of five nonrelatives—so that one bee from colony A was reared with five bees from colony B. In this experiment, the unique bee accepted the unfamiliar sisters of its unrelated nestmates but rejected its own, unfamiliar, related sisters, providing evidence for other-referent (p. 352) phenotype matching; in the case of *L. zephyrum*, as in many species, the referents for template composition are the individual's nestmates.

Other-referent phenotype matching appears to be a fairly common phenomenon, whereas self--referent phenotype matching has only rarely been confirmed. Peacocks (*Pavo cristatus*) are a lekking species, and males will often assemble in small groups to attract females. This sort of congregation behavior can be conceived of as a form of cooperative courtship, so it seems predictable that males sharing a lek tend to be positive relatives (Petrie, Krupa, & Burke, 1999; see also Krakauer, 2005; Shorey, Piertney, Stone, & Hoglund, 2000). What is surprising, however, is that the males are able to assort as a function of relatedness even when they have been cross-fostered and reared with nonrelatives (Petrie et al., 1999). Having few or no relatives upon which to base a kin template, this result suggests that male peacocks use self-referent phenotype matching to choose their lekking partners, although further research is needed to confirm this hypothesis. Self-referent phenotype matching is also strongly suspected in golden hamsters (*Mesocricetus auratus*; Heth, Todrank, & Johnston, 1998; Mateo and Johnston, 2000), brown-headed cowbirds (*Molothrus ater*; Hauber, Sherman, & Paprika, 2000), white-bearded manakins (*Manacus manacus*; Shorey et al., 2000), and chacma baboons (*Papio cynocephalus*; Alberts, 1999), among other species. Moreover, where paternity is relatively uncertain, self-referent phenotype matching may be involved in father–offspring recognition. In the future, we are likely to discover numerous other species that make use of self-referent mechanisms, as techniques to make a convincing demonstration have become further refined (see Hauber & Sherman, 2001; Mateo & Holmes, 2004).

Among the most spectacular mechanisms of kin recognition mediating social behavior concern those originally suggested by Hamilton (1964) and elaborated by Dawkins (1976, 1982): the *green-beards*. In order to convey the idea that altruistic behavior is in the furtherance of the focal allele (rather than the whole genome), Hamilton argued that an allele that expressed a label of its identity and acted altruistically toward those also bearing this label (in accordance with the rule $d + rx > 0$) would have a selective advantage over its rivals. Dawkins gave the example of individuals growing beards that are colored according to the identity of the allele they bear, whereby green-bearded individuals discriminatively cooperated with other green-beards (and likewise for any

other color of beard); hence, “green-beard.” Green-beard recognition is typically thought of as unlearned, but this is not a necessary condition, as the allele may simply encode a mechanism that learns its own label (Waldman, 1987). Moreover, green-beards are commonly envisioned as genetic enablers of altruistic behavior, but they can also lead to selfish, spiteful, or mutually beneficial behavior (Gardner & West, 2010; West & Gardner, 2010).

For various reasons, few thought that green-beards existed in nature, but several convincing examples have been found. One instance regards the violent “uprising” of red fire ant workers (*Solenopsis invicta*) against their queens (Keller & Ross, 1998). At the Gp-9 locus, individuals will tend to either bear two copies of the *B* allele or one of each of the *B* and *b* alleles, as workers and queens bearing two *b* alleles typically fall victim to a premature death. Homozygous (*BB*) queens rarely survive, however, as they are usually torn limb from limb by heterozygous (*Bb*) workers. When workers are rubbed against the cuticle of homozygous (*BB*) queens, other workers attack them, but workers rubbed against heterozygous (*Bb*) queens are spared, suggesting that the kin label is specified by an odor. All of this indicates that the *b* allele, or other, closely linked alleles encode a label, an algorithm that leads the labels of others to be compared to a template, and a violent reaction when there is a mismatch between the two.

Other examples are rosier by comparison. Haig (1996) has argued that green-beards may be ubiquitous but hidden in certain kinds of interactions, like those at the interface between mother and fetal placenta, which involve alleles coding for homo-philic cell adhesion molecules; such molecules simultaneously express allele identity and show greater affinity to identical copies of themselves. Thus, the coordination of multiple cells —the very definition of multicellularity—may often be the consequence of a green-beard mechanism. In much the same way, individual cells of the slime mold *Dictyostelium discoideum* (a social amoeba) congregate and adhere preferentially to those bearing identical copies of a focal allele at the csA locus when they are starved, forming a mobile slug that differentiates into a stalk (~20% of the cells) and a fruiting body (Queller, Ponte, Bozzaro, & Strassmann, 2003; Strassman, Zhu, & Queller, 2000). Because cells in the stalk die in its formation, they do not reproduce and are thus sacrificed, altruistically, for the reproductive spores in the (p. 353) fruiting body. *D. discoideum* cells can discriminate as a function of kinship (Ostrowski et al., 2008), but readily form chimeras of multiple clonal lineages, some of which exploit others (Strassman et al., 2000). Cells of the related *D. purpureum*, however, do preferentially associate with close kin, avoiding chimeric assemblies (Mehdiabadi et al., 2006).

A strain of budding yeast, closely related to that which is commonly found in beer, also seems to make use of a green-beard to facilitate cooperative behavior, but in this case the consequences appear to be mutually beneficial (Smukalla et al., 2008). Expression of the gene *FLO1* in *Saccharomyces cerevisiae* leads to flocculation, wherein cells bind to one another, creating an agglomeration, or “floc,” of cells. Flocculation appears to protect the cells interior to the floc from a variety of environmental stressors—a yeast’s version of a “selfish herd” (Hamilton, 1971a). Those *S. cerevisiae* cells that do not express *FLO1* are

excluded from joining flocs, so there is something like a green-beard mechanism at work here. It is unclear, however, whether cells recognize and show increased affinity to identical copies of the *FLO1* gene—that is, whether they discriminate potential floc partners as a function of beard "color"—or adhere to any *FLO1*-expressing cell, forming chimeras much like *D. discoideum*.

A final example of green-beard–influenced sociality regards cooperative mate guarding in the evocatively named side-blotched lizard (*Uta stansburiana*; Sinervo & Clobert, 2003). Male blue morphs of this lizard (*bb* genotype at the OBY locus) tend to aggregate with other blue males. This behavior appears to be to their reproductive advantage, as aggregated blue males have increased fitness relative to solitary blue males, presumably because cooperating blue morphs prevent yellow sneaker males (*by* and *yy* genotypes) from accessing their mates. Conversely, territory-usurping orange morphs (*oo*, *bo*, and *yo* genotypes) are significantly less likely to aggregate with one another, also to apparent reproductive advantage, arguably because this reduces competition among individuals bearing the *o* allele. The aggregation of blue males and disaggregation of orange males is independent of kinship (Sinervo & Clobert, 2003). There is, however, strong linkage disequilibrium between the genes at the OBY locus and much of the remainder of the *U. stansburiana* genome, so that a polygenic green-beard complex is the likely mechanism underlying certain key aspects of side-blotched lizard social organization.

We could go on, but we would rather devote the remaining pages to an especially tricky model species: *Homo sapiens*. We hope the reader shares our interest in this species.

# Kin Recognition and the Human Condition

*Homo sapiens* has lived among genetic relatives throughout its entire evolutionary history. The family is the primary locus of human social organization and, until recently, humans could migrate only so far as their legs would carry them, so that the dispersion of genotypes over large distances has only happened slowly. Even today, considerable genetic structuring of human populations persists (e.g., Lao et al., 2008; Novembre et al., 2008). Nevertheless, interactions between individuals would have involved both close and distant relatives, and so kin recognition mechanisms may have been employed in human affairs. Indeed, the ubiquity of (often complex) terminological systems that delineate various categories of more proximal and distal kin points to the possibility that kin recognition is fundamental to human sociality. Studies of real-world behavior routinely uncover nepotistic discrimination in human action (e.g., Bowles & Posel, 2005; Chagnon, 1988; Daly & Wilson, 1980, 1988a,b; Hames, 1987), but, with rare exception, the recognition mechanisms involved have been given little attention. Below, we catalogue some of the findings concerning the influence of kin recognition on human sociality, much of which has been published only in the last decade.

## Individual Recognition

In ancestral environments, children reared in the same household would almost certainly have been at least half, if not full, siblings. Selection may thus have favored an associative mechanism in childhood that attributes kinship to caretakers and other juvenile household members, particularly those who shared the residence for a lengthy period of time. Such a psychology might manifest itself as nepotism when competition includes nonrelatives, and it might also regulate sexual aversion toward close kin, because extreme inbreeding can have deleterious consequences. The latter notion underlies the Westermarck hypothesis, that incest aversion is the product of close association among individuals during childhood (Westermarck, 1894).

Three lines of inquiry implicate childhood coresidence in sexual aversion. First, unrelated children reared together in the same peer group on Israeli kibbutzim are extremely unlikely to marry or to have sexual relations with each other, seeking out mates from other peer groups, kibbutzim, or elsewhere (p. 354) (Shepher, 1971; Talmon, 1964). Second, Taiwanese “minor” marriages—whereby a young girl was adopted into the household of, and raised alongside, her unrelated future husband—have yielded significantly higher divorce rates and fewer offspring than the “major” marriages of two adults who had little to no association prior to the wedding day (Wolf, 1993). Third, surveys of American undergraduates show that coresidence duration with opposite-sex individuals significantly predicts aversion to sexual behavior among opposite-sex siblings (Lieberman, Tooby, & Cosmides, 2007).

The Taiwanese marriage and American survey data also supply evidence that the kin recognition mechanisms involved in sexual aversion to siblings make use of parent–child association. Humans, like many other animals, are typically reared by at least one of their genetic parents, usually their mother. Witnessing one’s mother rear subsequent individuals, then, informs the senior offspring that the junior is likely to be a sibling. Lieberman et al. (2007) argue that this cue is sufficient to infer kinship, reducing the utility of childhood coresidence duration as a predictor of sibling relatedness for senior offspring, and their results bear this out: Coresidence duration is only a significant predictor of sexual aversion among opposite-sex siblings for individuals who had no access to mother–neonate association cues (i.e., the younger sibling of a given pair), whereas siblings who could make use of mother–neonate association are generally averse to opposite-sex sibling incest, irrespective of coresidence duration. Similarly, sexual aversion varies as a function of coresidence duration in Taiwanese minor marriages for the younger of the two parties, but remains high for the elder spouse (Lieberman, 2009).

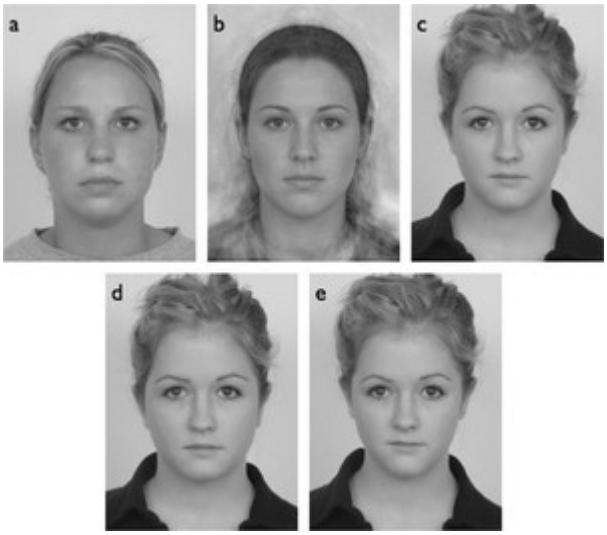
The effects of coresidence duration and mother–neonate association are not restricted to sexual aversion. Lieberman et al. (2007) find the same general pattern of results—mother–neonate association as a predictor in general, and coresidence duration as a predictor only in the absence of mother–neonate association cues—holds for sibling-directed cooperation. Thus, the very mechanisms that foment distaste for siblings in

sexual contexts likely foster affection for these same individuals in nonsexual contexts. An experiment by DeBruine (2005), discussed below, nicely demonstrates the same context-dependent effect among strangers.

## Phenotype Matching

Studying kin recognition systems in humans poses significant challenges. Data from the "field" are enlightening and important, but will too often be confounded by uncontrolled variables that obscure the details of the mechanisms involved. For obvious reasons, researchers do not cross-foster infants to expose the inner workings of human kin recognition, so a controlled method of investigation is not readily apparent. Certain labels of kinship, however, can be manipulated.

Recall that labels must be correlated with genotypes to make a useful kinship cue. As in many other organisms, there is a positive association between phenotypic and genetic similarity in humans. For instance, simple anthropometric measures and linguistic differences are correlated with genetic relatedness in the Yanomamö of Venezuela and Brazil (Spielman, 1973; Spielman, Migliazza, & Neel, 1974), and people typically perform above chance when judging the relatedness of unknown individuals to one another based on photographic (Kaminski, Dridi, Graff, & Gentaz, 2009; reviewed in DeBruine, Jones, Little, & Perrett, 2008) and olfactory stimuli (Porter, Cernoch, & Balogh, 1985)—an interesting quality in a highly social organism. Indeed, the method by which we judge relatedness is almost completely confounded with our assessment of the similarity between the individuals being judged, whereas age and sex seem to account for only a small fraction of the variance in relatedness judgments, as would be expected for a kin recognition mechanism (DeBruine, Smith, Jones, Roberts, Petrie, & Spector, 2009; Maloney & Dal Martello, 2006). With this in mind, technological innovations now make it possible to experimentally manipulate a postulated label of kinship—facial resemblance—to investigate phenotype matching mechanisms. In these studies, images of participants' own faces are used to digitally alter the appearance of a set of faces, unfamiliar to the participants, to generate realistic, self-resembling stimuli (Fig. 20.2). Participants' responses to self--resembling faces, relative to control faces, are then used as indices of cooperative and sexual inclinations toward kin (for a review of the methods and findings, see DeBruine et al., 2008).




Click to view larger

*Fig. 20.2* Example of self- and antiself-resembling transformed images. In this example, 50% of the difference in shape between the participant's face (*a*) and an average face of the same sex and ethnicity (*b*) have been applied to a third, "base" face (*c*). When the differences are added to the base face, the result is a self-resembling transform (*d*) showing increased resemblance between the base face and the participant's face. When the differences are subtracted from the base face, the result is an antiself-resembling transform (*e*) showing decreased resemblance between the base face and the participant's face

In an experimental task assessing monetary transfers between pairs of individuals, DeBruine (2002) found that participants were more trusting of self-resembling partners than controls. Furthermore, in a test of theoretical predictions that cooperation in "tragedy of the commons" contexts—wherein there is a conflict between individual and collective interests—is enhanced by genetic relatedness, Krupp, DeBruine, and Barclay (2008) found group cooperation (as measured by monetary transfers to (p. 355) the group) increased as a function of the number of self-resembling members of the group. Both studies restricted interactions to same-sex faces but, as above, there is an interesting prediction to be made with regard to opposite-sex faces.

All else being equal, individuals are expected to be more helpful toward kin. They are not, however, expected to find kin sexually attractive, especially in short-term contexts in which the genetic costs are not mitigated by the potential benefits of having a cooperative mate. For instance, several studies have shown associations between mate preferences and genetic similarity at the MHC, many of them demonstrating aversion toward MHC-similar individuals (reviewed in Havlicek & Roberts, 2009). To test the predictions that self-resemblance breeds trust but not sexual attractiveness, DeBruine (2005) assessed participants' preferences toward opposite-sex, self-resembling faces and found that, whereas self-resembling faces were perceived as more trustworthy than control faces, they were also perceived as less sexually attractive to participants in short-term contexts. This context-dependent effect provides strong support for the hypothesis that humans use facial resemblance as a label of kinship, and against the notion that the effects of self--resemblance are mere by-products of some general preference for familiarity. The hypothesis is further bolstered by differential responses to self--

resemblance in male versus female faces (DeBruine, 2004a) and at different phases of the menstrual cycle (DeBruine, Jones, & Perrett, 2005).

(p. 356) Although the typical manipulation of facial resemblance makes the resulting stimuli more *self*-resembling, it is unlikely that humans had much experience with their own facial appearance before the advent of mirrors and photographs. Thus, effects of self-resemblance are likely due to the overlap between one's own phenotype and that of the kin template built on closely related referents, such as parents and siblings. It is remarkable, then, that a recent study of twins provides evidence of self--referent phenotype matching in humans. Bressan and Zucchi (2009) gauged participants' preferences for images of self-resembling faces over control faces that resembled their (monozygotic or dizygotic) same-sex twin, showing that participants favored the self-resembling faces in two different cooperative contexts.

Although fascinating, the results of Bressan and Zucchi (2009) should be interpreted with caution. It is debatable whether twins are an appropriate model for use in investigations of "typical" human kin recognition, since surviving twins were likely rare in ancestral environments. Moreover, the authors interpret their results as demonstrating that "human kin recognition is self- *rather than* family-referential" (emphasis ours), but their forced-choice design cannot test whether self-referent phenotype matching operates in exclusion of, or in conjunction with, other-referent phenotype matching. As the authors imply elsewhere in the article, it can only show that self-referent cues are used *over and above* other-referent cues and, in any case, the only other-referent comparison was one's twin, so that other family members (such as one's mother or father) cannot be excluded as making up a portion of the kin template. Indeed, numerous studies show considerable overlap between parental traits and offspring preferences; individuals' preferences for a mate's hair and eye color, for instance, are better explained by their opposite-sex parent's hair and eye color than by their own colors (Little, Penton-Voak, Burt, & Perrett, 2003; see also Bereczkei, Gyuris, Koves, & Bernath, 2002; Bereczkei, Gyuris, & Weisfeld, 2004; Wiszewska, Pawlowski, & Boothroyd, 2007). Nonetheless, theirs is a tantalizing result, and future research should investigate self-referent phenotype matching in humans further. A study of the kin templates of adopted individuals, although logistically difficult, seems to us a promising avenue.

Phenotype matching, whether self- or other--referent, may help to solve another important reproductive problem: whether a mate's child is also one's own. Because of internal fertilization, human females can be virtually certain of their relatedness to their offspring; males cannot be so sure. This poses a problem for men, since they often invest in their social mate's offspring. Theoretically, paternity uncertainty can be mitigated by the recognition of a reliable kinship label, but it is not entirely clear whether it is in the interests of offspring to signal or conceal their relatedness to putative fathers. Early work offered evidence that babies appeared more similar to their fathers than to their mothers, but methodologically superior studies have repeatedly failed to find this effect (reviewed in DeBruine et al., 2008). Despite this, men might still place more value on their putative offspring's appearance as a kinship label than women. Predictably, then, mothers seem

more interested than fathers in noting resemblances between the father and his ostensible offspring (Daly & Wilson, 1982; McLain, Setters, Moulton, & Pratt, 2000; Regalski & Gaulin, 1993), and fathers invest in their ostensible offspring as a function of perceived resemblance (Alvergne, Faurie, & Raymond, 2009, 2010; Apicella & Marlowe, 2004). Again, experimental work initially showed that men were more influenced by facial self-resemblance than women (Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek et al., 2003, 2004), but this result has not proven robust to replication (Bressan, Bertamini, Nalli, & Zanutto, 2009; DeBruine, 2004b).

Facial resemblance is by no means the only kinship label available to humans. Some of the earliest work on human kin recognition, for instance, pertains to olfactory labels (reviewed in Porter, 1999). Human neonates can distinguish their own mother's scent from those of unfamiliar mothers, whether that scent occurred naturally or was artificially applied to the child's bassinet or its mother's breasts. Mothers are likewise able to discriminate their own child's odors from those of other children, and even to distinguish between the odors of their own children, suggesting individual recognition by odor. Third parties are also able to match the odors of unfamiliar children and mothers, implicating phenotype matching mechanisms in olfactory kin recognition. Olfactory labels associated with genetic variability, such as MHC alleles, whereas germane to mate choice (Havlicek & Roberts, 2009), are likely suspects for kin recognition labels in other contexts as well.

Culturally inherited labels, such as those based on naming practices, can present an altogether different sort of kinship cue. As implied by the term, (p. 357) family names are correlated with genetic relatedness (e.g., Sykes & Irven, 2000), and first names may also be so related (for instance, children are sometimes named after a same-sex parent or grand-parent), so they may provide a culturally acquired cue of kinship. Oates and Wilson (2002) performed a "field" study to test the hypothesis that sharing of first and family names increases cooperative behavior, measured as the frequency of responses to a solicitation of help by the experimenters, masquerading as a stranger sharing none, one, or both names with the respondent. The researchers found that sharing names increased cooperation, the largest effect being the sharing of both names, followed by the family name alone, the first name alone, and least of all sharing neither name. Moreover, rare names had larger effects on cooperation than common names, as might be expected by the notion that rare names are more diagnostic of kinship than are common names (see also Krupp, 2010).

# Conclusion

Kin recognition systems are widespread, and they play a pivotal role in social behavior. Despite volumes of research on their influence in the everyday affairs of other species, their impact is likely to have been underestimated in human social interaction (with, perhaps, the exception of mate choice decisions): Numerous models of human social evolution make much of interactions among nonrelatives (e.g., Bowles, 2006; Boyd, Gintis, Bowles, & Richerson, 2003; Gintis, 2000; Nowak & Sigmund, 1998; Trivers, 1971), but by contemporary measures of relatedness, only a handful of individuals in the population are likely to be truly *unrelated* to their neighbors. Indeed, some models tend to characterize as nonrelatives individuals who are, in fact, related by virtue of limited dispersal (Foster et al., 2006b; West et al., 2008). Below, we outline directions for future research that address questions of considerable significance to organismal sociality.

## Future Directions

We began this chapter with a discussion of *Linepithema humile*, the Argentine ant, arguing that its aggressive behavior toward alien conspecifics resembles xenophobia in humans (Starks, 2003). Recall that this antagonism is asymmetrical: Individuals drawn from genetically homogeneous colonies behaved more aggressively toward foreign conspecifics drawn from heterogeneous colonies than vice versa (Tsutsui et al., 2003). Does this asymmetrical response reflect a functional problem and, if so, how is it solved by the organism's proximate design?

Asymmetrical aggression can be understood in terms of genetic relatedness. If relatedness is measured as a function of deviation from the expected population frequency of the focal allele, then common and rare genotypes will be asymmetrically related (Krupp, 2010). All else being equal, actions will have proportionately larger consequences for rare genotypes than for common ones. Consider, for instance, two alleles in the population: $A_1$ at a frequency of 0.8, and $A_2$ at a frequency of 0.2. An action that has the consequence of bringing the frequency of $A_1$ down to 0.7 in the population—and thereby bringing $A_2$ up to 0.3—means that $A_1$ has lost 12.5% of its share of the gene pool. By contrast, the increase of $A_2$ to 0.3 represents a 50% increase in its share. Thus, an actor bearing the common allele is expected to value recipients bearing the rare allele—its rival—more negatively than the converse. As a corollary, actors bearing the rare allele are expected to value kin more positively than actors bearing the common allele.

Phenotype matching systems can readily generate asymmetrical perceptions of relatedness (Krupp, 2010). As perceptions of the kin and average templates are learned by the sampling of phenotypes in the population (the referents), the variance in label polymorphism and the frequency of particular label values will define the scale upon which the kin and average templates lie (Fig. 20.1). Individuals bearing common phenotypes will tend to develop kin and average templates that scale more closely to one another than will individuals bearing rare phenotypes, so the kinds of phenotypes that can be located between the two templates represent a narrower range of possible label values for bearers of common phenotypes than for bearers of rare phenotypes (Fig. 20.3).

Thus, a greater range of phenotypes will be perceived as positively related to bearers of rare phenotypes than to bearers of common phenotypes and, correspondingly, a greater range of phenotypes will be perceived as negatively related to bearers of common phenotypes than to bearers of rare phenotypes.

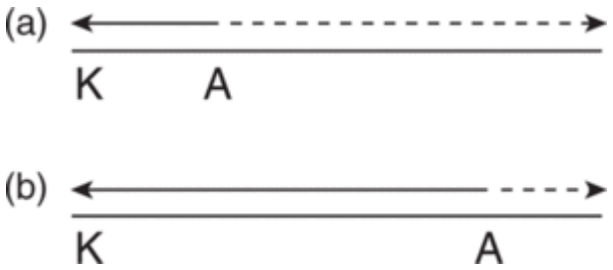



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*Fig. 20.3* The effect of label frequency on perceptions of relatedness. When individuals bear common label values (*a*), their kin (*K*) and average (*A*) templates are expected to be more similar, and thus scale more closely together than the templates of individuals bearing rare values (*b*). Consequently, a smaller range of possible phenotypes will be perceived as positively related (*solid arrows*) than negatively related (*dashed arrows*) among bearers of common label values than among bearers of rare values

In the case of *L. humile*, ants drawn from homogeneous colonies likely develop kin and average templates that are located much closer to one another than would those drawn from heterogeneous colonies, once placed on the same perceptual scale. Correspondingly, homogeneous colony-derived individuals likely "perceive" themselves to be of more (p. 358) common genetic stock than do heterogeneous colony-derived individuals. They should thus perceive ants from heterogeneous colonies as more negatively related to themselves than the converse, leading to the asymmetrical behavior reported in Tsutsui et al. (2003; see also Starks, 2003).

For similar reasons, we might expect much the same pattern among humans. Xenophobic and ethnocentric behaviors are commonplace (LeVine & Campbell, 1972; Van Den Berghe, 1981) and, like the asymmetric aggression of Argentine ants, might be an output of mental algorithms designed to assess and respond to ecological conditions (e.g., Olzak, 1992) and perceptions of relatedness (Van Den Berghe, 1981). This hypothesis can be difficult to test directly; nevertheless, laboratory analogues are possible. As discussed above, several studies have demonstrated that facial self-resemblance has effects predicted by the hypothesis that it is used as a cue of kinship. The same technology that generates self-resembling faces can be used to make "antiself-resembling" ones (e.g., Leopold, Rhodes, Müller, & Jeffery, 2005), faces that appear more dissimilar to the participant than does an average face (Fig. 20.2). It remains to be seen how participants treat such faces, but if they are perceived as negatively related, we would expect discriminatory responses that work in opposing directions to self-resembling faces.

The asymmetrical aggression seen in *L. humile* appears to change with repeated exposure to individuals drawn from neighboring colonies (Thomas, Tsutsui, & Holway, 2005; see also Sanada-Morimura, Minai, Yokoyama, Hirota, Satoh, & Obara, 2003). This kind of dynamic adjustment suggests that recognition systems can be updated with new information about the expected phenotypes of average individuals in the population. As

genetic relatedness measures the likelihood that two individuals share the focal allele relative to chance, a shift in the population mean genotype ought to be accommodated by kin recognition systems. This can be done by updating the average template through exposure to new individuals. There is evidence that humans dynamically adjust their perceptions of sex and ethnicity (Webster, Kaping, Mizokami, & Duhamel, 2004), and so it is plausible that perceptions of relatedness shift as templates germane to kin recognition are updated.

Finally, at the proximate level of description, there remain numerous questions about the ontogeny and mechanistic design of kin recognition systems. Among the most pressing are those concerning the kinds of representations contained in an animal's brain, and the mental algorithms involved in building and integrating them, as it remains unclear how individuals integrate phenotypic information to produce kin and average templates, and whether these templates are maintained over time or rapidly constructed when called upon. Moreover, it is as yet unknown whether there are critical developmental periods that constrain the updating, if any, of recognition templates. Inroads have been made in the study of the cognitive and neural architecture underlying individual recognition (e.g., Calder & Young, 2005), but the appropriate psychophysical tools have only rarely been applied to kin recognition (e.g., Dal Martello & Maloney, 2006).

In short, much work remains to be done. If research continues to advance at the current pace, however, this review may soon find itself out of date. It is our hope that this will indeed be the case.

# Acknowledgments

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(p. 363)

## Notes:

(1) This definition is slightly at odds with the literature. Typically, social actions are defined as those having fitness effects on *both* the actor and recipient (e.g., Grafen, 1985; West, Griffin, & Gardner, 2007). The common definition, however, is overly restrictive: Actions that have consequences for others are surely “social” even when they do not affect the individuals performing them.

(2) This rule is merely a restatement of the more familiar form $rb–c > 0$, where $x = b$ and $d = –c$. Unlike the standard form, the variant we present is not accompanied by any misleading connotations that $c$ represents a cost to the actor (as any $c < 0$ represents a benefit) or that $b$ represents a benefit to the recipient (as any $b < 0$ represents a cost).

(3) In point of fact, sex will correlate with kinship when it is genetically determined, and this can have behavioral consequences (e.g., Fox, Sear, Beise, Ragsdale, Voland, & Knapp,

2010). Whether kin templates are associated with relatedness at sex-determining alleles, however, is not known.

(4) Where relatedness at the focal locus and the remainder of the genome are orthogonal, “kinship” is not an entirely appropriate label. For lack of a more inclusive, well-recognized term, however, we continue to employ the term “kin recognition” in these rare instances.

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