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THE ECOLOGY OF KIN RECOGNITION

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INTRODUCTION

W. D. Hamilton's publication of genetical kinship theory (92, 93) a quarter century ago launched the modern study of social evolution. Kinship theory extends the scope of fitness to include the effects of individuals' actions on their genetic relatives. Thus, traits that offer no direct benefit or even decrease an individual's likelihood of successfully reproducing can spread if they confer a sufficiently large benefit on kin (81, 92–94, 156). Altruistic traits are not expected, however, unless kin gain more than nonkin. Mechanisms that permit individuals to recognize their kin can facilitate the evolution of social cooperation, and they may confer other selective advantages as well. Individuals that avoid mating with close relatives or "optimally outbreed" may accrue fitness benefits over conspecifics that mate randomly (12, 14, 199).

The importance of kinship in mediating social interactions has been verified through fieldwork on populations with known genealogies (e.g. 108–111, 130, 195–197). Yet the proximate means by which organisms respond to collateral kin, considered "less glamorous" by some (131), have only in the past few years begun to generate interest. Whether any organism could recognize kin in the manner that Hamilton's theory suggests was unknown just ten years ago. Research into these behavioral mechanisms is now moving rapidly forward (64, 68, 178, 198), and a theoretical framework for the consideration of kin recognition is emerging (e.g. 18, 20, 49, 74, 102, 186, 227). Knowledge of the mechanisms by which kin discrimination occurs—the extent to which different classes of relatives can be recognized, the cues upon which recognition is assessed, and the means by which social preferences develop—is important for assessing how closely behavioral tactics of individuals conform to those predicted by kinship-based models. Studies of kin recognition are most valuable, however, when framed within ecologically appropriate settings, and analyses of the contexts in which kin discrimination occurs can clarify how recognition mechanisms function.

CONTEXTS OF KIN RECOGNITION

Kin discrimination is expected in diverse social and ecological contexts which, considered ontogenetically, fall into three general categories (see 106, 198, 227). First, discrimination may occur when kin overlap predictably in time and space. Behavioral responses to conspecifics may be elicited under particular conditions, as when a parental bird feeds newly hatched young that it finds in its nest. Second, subsequent to their initial interactions in contextually reliable circumstances, individuals may be recognized in other settings. For example, after fledging from a common nest, siblings may encounter one another in novel situations away from the nest. Third, kin may meet under conditions in which they cannot identify one another based on past or present overlap in temporal and spatial cues. When brood parasitism occurs, eggs of different clutches may become mixed in a single nest (5, 33), and selection may favor parents that differentiate between their offspring and intruders. When mating is not truly monogamous (238), half-siblings may be present in the same brood, and progeny may be selected to discriminate among their broodmates based on their relatedness. Siblings that fledge from different broods of the same parents (e.g. in different years) similarly may accrue some advantage if they are able to recognize one another.

Studies of the ecology of kin discrimination suggest a basic contrast between two types of recognition mechanisms (231). If discrimination is limited to predictable contexts, kin recognition may be considered *indirect*. In other words, kin are recognized based on properties of the circumstances rather than of the individuals themselves. Evidence of discrimination of kin in varied contexts, or among classes of kin and nonkin within specific contexts, suggests that kin are recognized because they express some trait or set of traits (*direct* kin recognition). Kin may be individually identified, or recognized as members of a class, or both (91, 227). If opportunities exist during development for individuals to learn who their kin are, we presume kin discrimination occurs because they have previously associated with one another. Otherwise, discrimination likely occurs by recognition of traits shared among members of a kin class.

Although recognition mechanisms are often discussed in terms of the social and ecological contexts in which they are expressed, the same recognition mechanisms can give rise to discrimination in more than one context, and organisms may switch between mechanisms in response to the immediate circumstances (227). To classify kin recognition mechanisms based on the social context in which they operate can thus be misleading and in some cases may be incorrect. Thus, I first present selected contexts in which kin discrimination occurs, and then I consider the recognition mechanisms that facilitate discrimination.

Parental Care

The selective value of parents and their offspring recognizing one another was apparent long before Hamilton pointed out the genetic equivalence of collateral and descendent relatives. Studies of parent-offspring recognition have been reviewed elsewhere (47, 102, 210) and are too numerous to catalog here, but several interesting trends emerge from this research. Recognition mechanisms fostering parent-offspring relationships are evident throughout the animal kingdom. Woodlice (*Hemilepistus reaumuri*) recognize their young by a family-specific label they bear so they can be identified even outside their own burrow (138). Honey bees (*Apis mellifera*) recognize their own queen and can distinguish her from foreign queens based on odors that are partially genetically determined and partially acquired from the environment (29, 32). Within colonies, workers can discriminate between full-sib and half-sib larvae, preferentially rearing full-siblings as queens (164, 221). Moreover, honey bees may swarm selectively with their full-siblings prior to establishing new reproductive colonies (73a). Ants recognize and care for their brood, responding to chemical cues they secrete (42). Cockroach (*Byrsotria fumigata*) nymphs aggregate around their mother (137). Fry of cichlid fishes imprint on their parents' odors and visual characteristics, and soon after they become free-swimming, the fry orient toward their parents (11, 100). Parents similarly can recognize their own young by chemical cues and tend their schools, thus offering protection from predators (128, 150).

Parental care in birds often involves indirect recognition: young found in one's nest are treated as offspring (112, 151, and references therein). Indirect recognition is likely to be less reliable in colonially nesting species if chicks intermingle, and indeed many of these species (e.g. bank swallows, *Riparia riparia*) recognize their offspring by their individually distinctive calls (19). Brood parasites, such as cuckoos, exploit parenting efforts of other species and are successful when recognition is indirect (172). Some communal and colonial breeders (e.g. ostriches, *Struthio camelus*) recognize their own eggs and even destroy eggs laid by other females (26, 218). Aside from reducing competition among hatchlings, egg recognition could potentially facilitate later parental care if offspring can be individually identified upon hatching. Offspring are also able to recognize their parents, even in noncolonial species (e.g. bank swallows, *Hirundo rustica;* 151).

Social systems of many mammals tend to be matrilineal in character, as the female parent is the primary care provider. In rodents (e.g. gerbils, *Meriones* *unguiculatus*), discrimination of young is facilitated by salivary cues the mother applies to her offspring (28). Similarly, goat mothers label their offspring by licking them (89). Sheep dams recognize their lambs by visual and auditory cues from a distance and by smell at close range, and lambs recognize the individual calls of their mothers (175). Many ground-dwelling sciurids rear their litters in their own burrows, so social groups consist of siblings only and kin identities can be learned (155). Females of colonially nesting sciurids (black-tailed prairie dogs, *Cynomys ludovicianus*) appear to recognize their offspring only indirectly and fail to discriminate their own young from unrelated littermates (107, 111). Mexican free-tailed bats (*Tadarida brasiliensis mexicana*) also nest colonially but do selectively nurse their own young and may mark their pups with odors to facilitate recognition; pups, however, do not discriminate between their mothers and other lactating females (90). Primate infants (e.g. squirrel monkeys, *Saimiri sciureus*) recognize and orient toward their mothers by olfactory cues (120). Male vervet monkeys (*Cercopithecus aethiops*) exercise parental care as well, for example, responding to infant distress calls (98). Paternal recognition appears to be circumstantial, however, as males provide parental care to offspring of females with which they had consorted during the approximate time of conception (39, 79, 98).

Direct recognition abilities are expected in those species in which parental care may otherwise be mistakenly directed in ecological conditions typical of the parent-offspring relationship. Contrasting parental discrimination tendencies of colonially and solitarily nesting birds fit these predictions, as parents appear to recognize their offspring directly only if the likelihood of misidentification by indirect means is high. Yet studies on colonially nesting mammals do not uniformly fit this pattern. Moreover, recognition abilities of many birds and insects are sufficiently imprecise that parental care can be exploited not only by conspecifics that dump their eggs in others' nests, but also by heterospecifics whose offspring, once they become established in a nest or colony, elicit preferential parental care or act destructively toward the parents' own offspring (38, 172). Aside from cooperative breeding, other social and ecological circumstances exist in which discrimination is expected to be based on direct recognition mechanisms. Paternal care in polygynous or promiscuous mating systems provides a case in point. Few studies have systematically compared parental recognition abilities among related species in which the probability varies of encountering offspring in contextually unreliable circumstances.

Cooperation

If individuals cooperate, each stands to gain some benefit. Certainly cooperation can and does evolve in groups of nonrelatives (2, 8, 217). If individuals are genetically related, however, cooperation can be selected even if the benefits are inequitably distributed among the participants. Should a particular trait or social action not increase an individual's direct fitness (number of descendent relatives), it may still increase its indirect fitness (number of nondescendent relatives) (35). Kinship thus can enhance the advantages of sociality and possibly further accelerate its evolution. Altruism is a form of cooperation in which an individual acts in a manner that decreases its direct fitness but increases the direct fitness of a second individual. While in principle direct and indirect consequences of social interactions on fitness are separable, studies of social cooperation among kin often suggest that apparent altruism entails both types of benefits (see 34, 61).

ALLOPARENTING In many animals, offspring are regularly cared for by adults that are not their genetic parents. These "helpers at the nest" usually assist parents or siblings in rearing their brood. Often, as in the social paper wasp *Polistes fuscatus,* helping is a facultative strategy. Female wasps join together to found a colony, but a single dominant female lays most of the eggs and eats eggs laid by subordinates, leaving these cofoundresses the responsibilities of feeding and caring for her own offspring (165). Cofoundresses are almost invariably sisters, and they establish nests near their parental nest sites (125). Kin recognition in this context thus may be indirect, based on locational cues, but females can discriminate behaviorally between sisters and nonsisters placed on their nests (165). Wife-sharing between brother Tasmanian "native hens" (*Tribonyx mortierii*) provides a vertebrate analog to wasp cofoundresses; dominant males obtain most of the matings and their brothers assist in rearing the young (148). Although sterile castes of workers provide care of offspring in colonies of many social insects (243), and even in some mammals (119), helpers often are physiologically capable of reproducing. Benefits of helping have been extensively discussed (34, 61), and in some circumstances helpers gain more by caring for the young of other pairs than by immediately reproducing themselves. If they discriminate kin, helpers may also increase their inclusive fitness.

Helpers are especially common in birds and mammals, and their presence is tied to ecological constraints reflecting the availability and accessibility of breeding sites. Jackal pups frequently remain with their parents during the next breeding season (24% of silver-backed jackals, *Canis mesomelas;* 70% of golden jackals, *C. aureus*), helping to rear their younger siblings (157). In packs of dwarf mongooses (*Helogale parvula*), wild dogs (*Lycaon pictus*), and wolves (*Canis lupus*), only one dominant female usually reproduces, but her young are fed and cared for by nonbreeding members of the group, which are often genetic relatives (141). Similarly, 90% of Florida scrub jay (*Aphelocoma coerulescens*) helpers assist at least one parent by feeding and defending their brood, and only 4% of the helpers assist in rearing unrelated young

(245). Cichlid fishes (*Lamprologus, Julidochromis*) are assisted by their earlier progeny in rearing fry (214). Alloparenting in primates is also usually closely tied to kinship relations, but helpers do not provide more help to close kin than to more distant kin (77, 163, 201, 233). Although stripe-backed wren (*Campylorhyncus nuchalis*) helpers usually assist in rearing their siblings, helpers do not contribute more to rearing full-siblings than to half-siblings or nonsiblings (184). Unrelated dwarf mongoose (*Helogale parvula*) helpers appear to invest in offspring as much as do true siblings (190).

Helpers often discriminate kin by simple spatial rules (indirect recognition) and possibly by recognizing their own parents (directly). Young present in nearby nests are likely to be siblings or other collateral relatives and the probability of misdirecting aid may be so small that direct kin recognition abilities have not been selected. For communally breeding species, however, direct recognition offers distinct advantages. Comparing patterns of helping behavior in colonial and noncolonial birds, Brown (34) suggests that helpers in colonial species can recognize their kin based on cues other than simply their location in a particular nest or den. Hyena (*Hyaena brunnea*) helpers show an interesting sexual asymmetry: females provision cubs as distantly related as second cousins, while males provision half-siblings but not cousins (167). Males, unlike females, subsequently emigrate from their clan, so they may receive fewer direct benefits (e.g. reciprocity) by helping distantly related kin. Two types of helpers are found in the communally breeding pied kingfisher (*Ceryle rudis*): primary helpers which assist in rearing their siblings provide more care (guarding and feeding) than do unrelated secondary helpers (187). Young birds maintain social contact with their parents after fledging, and they may be individually recognized. Alternatively, helpers may share phenotypic traits with related young and discriminate between classes of young based on their perception of these similarities.

DEFENSE Predators that threaten social insect colonies, comprised usually of kin, are attacked and repulsed. Colony defense in ants and termites is accomplished by specialized soldier castes (243). Aphids, too, have sterile soldiers that attack colony intruders, even though in some cases they are almost certain to perish (6). Honey bee (*Apis mellifera*) workers that sting attackers commit suicide when their barbed stings remain lodged in their victims (243).

Self-sacrifice in the defense of the group may occur in other more subtle ways, as well. Fisher's (63) observations on how distastefulness might evolve as an antipredator mechanism in gregarious larvae of certain insects foreshadowed Hamilton's development of kinship theory. An individual tasted by a predator may not itself survive, but in communicating the distastefulness of its sib group to the predator, it may reduce subsequent attacks on its relatives

(21). Similar arguments have been put forth to explain the evolution of aposematic warning coloration (97, 144). Not only do gregarious aposematic larvae of insects (e.g. grasshoppers, *Romalea guttata*) reaggregate in probable sibling groups after being mixed (J. Pickering, unpublished data), in agreement with Fisher's model, but also kin association may serve as a means to advertise noxiousness in vertebrates. Toad larvae (e.g. *Bufo americanus*) are distasteful, conspicuously colored, and highly gregarious, and their schools consist largely of siblings (223). Recent analyses of allozyme variation in natural populations of several species of insects have found that individuals sampled contiguously are often closely related, but considerable variation may exist in kin structure both intra- and interspecifically (149).

In many species, individuals ordinarily interact with their close kin more than with other classes of conspecifics simply because dispersal is nonrandom. Sexually dimorphic dispersal strategies may lead to sex-biased cooperation within groups (46, 85, 183, 213). The typical mammalian pattern is that males leave their natal areas (in some species, with their brothers) while females remain, although this difference is sometimes overstated (158). When a terrestrial predator approaches nesting Belding's ground squirrels (*Spermophilus beldingi*), adult and yearling females give alarm calls more frequently and males give calls less frequently than would be expected by chance (195). Females are more likely to call if their kin are nearby; males rarely are in the vicinity of their kin, so that they would not increase their inclusive fitness by calling. Other ground-dwelling sciurids respond to predators similarly (50, 56, 193). Although by calling, *S. beldingi* females may be protecting their offspring, black-tailed prairie dogs (*Cynomys ludovicianus*) frequently call to alert nondescendent kin (109). Moreover, males as well as females call but only when close relatives are present in their home territory. *C. ludovicianus* males, unlike *S. beldingi* males, tend to disperse together with their male relatives, so that opportunities to assist kin are greater (109). Besides alarm calling, kin of these species cooperate to defend their young, chasing trespassing conspecifics and predators away from their territories. Sexual asymmetries in these behaviors follow the same trends as alarm calling (111, 195).

FORAGING Members of social insect colonies communicate to one another locations of food resources, often by laying odor trails. Odor trails sometimes have colony-specific characteristics which prevent members of different colonies from accidentally mixing (216). Honey bees (*Apis mellifera*) share information about food resources, for example, by their waggle dances, and individuals transfer food within the colony (trophallaxis) (243). Recent studies suggest that honey bees preferentially share food with full-sister over half-sister nestmates, although discrimination breaks down under conditions of environmental stress (67). In laboratory conditions, spiny mice (*Acomys cahirinus*) littermate siblings share food more extensively than do unfamiliar nonsiblings (179). Vampire bats (*Desmodus rotundus*) regurgitate blood to genetic relatives (often offspring) within roosting groups of mixed kinship composition, but they also feed nonrelatives with which they have previously associated if these individuals are in danger of starving (239). Various carnivores (e.g. lions, wolves, wild dogs, spotted and brown hyenas, jackals, coyotes, dingoes, and dholes) forage in kin groups (refs. in 141). Wild dogs (*Lycaon pictus*) regurgitate food to other members of their pack, both adults and young (143). Food-sharing among primates is relatively uncommon, although a few species collect vegetable matter to feed to their young (201). Captive vervet monkeys (*Cercopithecus aethiops sabaeus*) feed on prey together, usually with their close relatives (62). Primates sometimes communicate information about locations of plentiful food supplies to members of their groups (e.g. chimpanzees, *Pan troglodytes;* macaques, *Macaca sinica*) (208).

GROOMING Many behaviors showing a kin bias foster the maintenance of social organization by regulating the group environment, reducing the risk of disease, and reinforcing bonds between individuals. Allogrooming (grooming other individuals) is apparent in many phyletic groups from insects to birds to mammals. Honey bees (*Apis mellifera*) preferentially groom full-sisters rather than half-sisters within their colony (67). Laboratory spiny mice (*Acomys cahirinus*) huddle with their siblings (180). White-footed deer mice (*Peromyscus leucopus*) preferentially huddle with and groom nonlittermate siblings over unfamiliar nonsiblings; this suggests that recognition is not dependent on prior association alone (83). *Mus musculus* preferentially groom siblings, although they also groom other familiar individuals (121). Within day roosts, vampire bats (*Desmodus rotundus*) groom close relatives and other familiar individuals (240). Allogrooming is exceedingly common within primate troops and usually involves kin, although in many cases kin biases reflect proximity effects. Several studies suggest that individuals groom close relatives (offspring and maternal siblings) more frequently than other troop members, however (10, 76, 79, 80). This finding suggests discrimination of close kin from more distant kin within groups. Yellow baboons (*Papio cynocephalus*) and geladas (*Theropithecus gelada*) lacking close relatives within a group fail to form grooming relationships similar to those found between kin in these species (233). While grooming may have a hygienic role, for example, in removing parasites, social relationships between individuals are reinforced and strengthened by such interactions. Play behavior may serve a similar function in mammals, and juveniles frequently play with their kin (20, 76).

Competition

Organisms compete for resources, and kinship is one factor, surprisingly often ignored in ecological studies, that modulates levels of intraspecific competition. Behaviorists studying interference competition regard restraint to be functionally equivalent to cooperation. The impact of kinship on competition can be subtle, however. Recent research indicates that even organisms apparently lacking complex behaviors discriminate between kin and nonkin when they interact.

SETTLEMENT Differential responses to kin and nonkin are evidenced in many aspects of the life cycle of marine invertebrates. Sponges, if experimentally dissociated into cells and mixed, reaggregate specifically with members of their own strain or clone-type (47a), and genetically similar individuals often fuse (164, 246). Anemones tolerate clonemates as neighbors but attack nonclonemates with a nematocyst discharge (9). Colonial tunicates fuse only if they share an allele at a fusibility locus, which in the extent of its variability resembles the vertebrate major histocompatibility complex (*MHC*) (194). In *B. schlosseri,* the fusibility locus also serves as a gametic barrier to self-fertilization (194). Planktonic *B. schlosseri* larvae settle significantly closer to adult colonies of their siblings than to colonies of nonsiblings, and this may facilitate later colony fusions (88). Bryozoan larvae (e.g. *Bugula neritina*) also settle closer to siblings than to nonsiblings, although colonies are not known to fuse (124). In some colonial marine invertebrates, survivorship and reproductive output are correlated with colony size, but reproductive competition among cells (somatic cell parasitism) may lessen the advantages of colonial living unless colonies consist of closely related individuals. Furthermore, biases in settlement behavior may function to protect kin from predation (124).

GROWTH Genetic similarity among members of social groups can result in two different types of effects on levels of intraspecific competition. Kinship theory predicts that individuals in genetically homogeneous populations will cooperate. Yet because of their genetic similarity, kin may overlap more closely in their resource utilization patterns than do nonkin (147, 191a). Unless they have some means to shift their preferences for food, microhabitats, and mates, close kin may compete more intensely than nonkin. Genetically homogeneous populations may also be more easily exploited by parasites and other disease-causing organisms that face less resistance in a uniform environment (96).

Genetically variable (half-sib) stands of sweet vernal grass (*Anthoxanthum odoratum*) grow more quickly, have higher survivorship, and produce more seeds than do genetically uniform (cloned) stands (59). When populations are infested with aphids, individuals surrounded by sibling neighbors have lower survivorship than do those surrounded by nonrelatives (192). In apparent contrast, loblolly pine (*Pinus taeda*) seedlings growing in single family (maternal half-sib) plots initially experience a slight but statistically significant growth advantage over those growing in mixed (nonsib) plots (241). Susceptibility to rust infection does not differ between pure and mixed stands (241). In a glasshouse, *Phytolacca americana* seedlings planted in pots with maternal half-siblings grow larger than do those in pots with nonsiblings (242). Increased germination success and survivorship have also been noted in pure groups of two other species (*Solanum mauritanianum, Abutilon theophrasti*) (242). Whether genotypic similiarity leads to facilitative or inhibitive group effects may be determined (*a*) by the precise ecological conditions in which individuals interact and (*b*) by the extent of genetic variability within and between groups. Thus, comparisons between growth rates of cloned individuals and groups of siblings are not equivalent to those between groups of siblings and mixtures of sib groups. Kinship effects on growth need not involve a kin recognition mechanism per se. Self-incompatibility mechanisms are common in plants (189, 219), however, and this raises the possibility that close kin may be discriminated in other contexts as well. Moreover, chemical communication may serve a role in coordinating defensive reactions of plants to predators (66, 188) and in grafting (fusion of roots) between neighbors (82, 95).

Effects of kinship on growth and survivorship are also apparent in studies of animal populations. Pérez-Tomé & Toro (174) reported that *Drosophila melanogaster* larvae reared with their full-siblings produced fewer offspring than did those reared in mixed groups of half-siblings, but this result varies with changes in the experimental design (65, 145). Recent studies on intraspecific competition among larval amphibians have yielded diverse results (226). *Rana arvalis* tadpoles reared with their siblings or in water conditioned by these siblings develop more slowly than do those reared with nonsiblings, and fewer reach metamorphic climax (200). The results suggest intensified competition among genetically similar individuals. But larvae of two other anuran species, *Pseudacris triseriata* and *Bombina variegata,* actually grow more rapidly when reared in cultures just with their siblings than when reared in mixed cultures; this suggests cooperation among closely related kin (206; M. Jasiénski, unpublished data). Different species may react differently, but more likely competitive responses vary with environmental conditions. *Bufo americanus* larvae reared in pens in natural ponds just with siblings metamorphose on average at a smaller size than do those reared in mixed sib groups, but they are also more variable in size (228). In pure groups, smaller individuals may, under stressful environmental conditions, exercise competitive restraint for the benefit of their larger siblings, which are more likely to survive and reproduce. Similar effects are apparent in rigorously controlled laboratory conditions, but under favorable environmental conditions, mean growth rates of individuals reared just with siblings are enhanced with respect to those reared in mixed groups (229).

INFANTICIDE Cannibalism not only eliminates competitors but also provides food. For example, small *Bufo americanus* larvae sometimes may be cannibalized by larger siblings (223). Sib cannibalism seems to contradict kinship theory, but under many life-history conditions a larva would be selected to eat its siblings if by so doing it sped up its development just slightly (58). Cannibalism on siblings is not uncommon (176). Many social wasps devour larvae and pupae belonging to their own colony to ensure an adequate food supply for the subsequent production of reproductives, and foundresses of two species, *Polistes chinensis antennalis* and *P. jadwigae,* rob larvae and pupae from other colonies (122). Tadpoles of spadefoot toads (*Scaphiopus bombifrons* and *S. multiplicatus*) occur as two distinct phenotypes: a small, slower developing omnivorous morph and a large, rapidly developing, carnivorous morph specialized for cannibalism (177). Siblings from the same egg mass can develop into either morph depending on their diet. Intrauterine sibling cannibalism has been documented in salamanders and sharks (4, 53). Certain amphibian larvae cannibalize eggs, even siblings (202). If cannibals can recognize their close kin, they should generally avoid eating them if nonrelatives are accessible. Survivorship is higher in full-sib groups of pike (*Esox lucius*) than in mixed sibling groups because of higher levels of cannibalism in mixed groups (36). Some fish eat their eggs to supplement their food reserve during brooding, although male pupfish (*Cyprinodon macularius californiensis*) distinguish between their own eggs and those fertilized by other males and cannibalize only unrelated eggs (140). Female poeciliid fishes (*Poecilia reticulata* and *P. sphenops*) tend to avoid cannibalizing their own offspring if fry of another female are available (139).

Infanticide can facilitate access to potential mates. For example, unmated Belding's ground squirrel (*Spermophilus beldingi*) females do not feed on the carcasses of young that they kill, but usually take over the territory surrounding the victims' burrow (197). *S. beldingi* never kill young of close relatives (197). By contrast, prairie dogs (*Cynomys ludovicianus*) usually cannibalize offspring of close kin (110). Similarly, acorn woodpeckers (*Melanerpes formicivorus*) nest communally and sisters frequently remove each others' eggs and eat them, thereby reducing the vulnerability of their own eggs to brood reduction (160). Male lemmings (*Dicrostonyx groenlandicus*) kill the offspring of nonrelatives but do not attack their own young (114). Young male gerbils (*Meriones unguiculatus*) are usually indiscriminate in killing and eating conspecific pups but are inhibited from committing infanticide if they are exposed to a pregnant female (60). Gerbils are monogamous and territorial, so that any infants that a male encounters in the vicinity of a pregnant female are likely to be his own offspring. In laboratory studies of many mice and voles (*Mus, Peromyscus, Microtus, Clethrionomys*), pregnant females exposed to strange males spontaneously abort (60, 114). As the females' offspring are likely to be eaten at birth by unrelated males, termination of pregnancy may represent a female counter-strategy to infanticide by males. Male lions (*Panthera leo*) kill new cubs in prides that they have just taken over, and as in rodents, females generally become reproductively receptive more quickly, thus allowing the intruder males to breed (170). Recent immigrant male *Colobus* and *Procolobus* monkeys similarly kill unrelated infants, and this pattern is typical of the nonhuman primates (211). Mammalian studies reveal in general that males refrain from killing infants in social circumstances in which they potentially might have fathered those individuals. Only rarely does kin discrimination appear to be more precise, and then males assess their paternity by using cues of the mother rather than the infants themselves (99). For example, male mice (*Mus musculus*) kill their own offspring when they are placed in the nest of a strange female, but they tolerate offspring they have not fathered that are placed in a familiar female's nest and those that may be marked with urine odors of familiar females (114).

AGGRESSION Competition is often manifested in behavioral aggression. Even some largely sedentary marine organisms respond aggressively to nonrelatives (9). Social insects defend their colonies by a variety of means, and in some species special soldier castes appear to have evolved for this purpose (243). Discrimination of colony members is often based on odors, which may have both environmental and genetic components (32, 69, 70, 104, 154). Male cockroaches (*Shawella couloniana*) show less agonism toward siblings than nonsiblings, although females act more agonistically toward their sisters than toward nonrelatives (78). Many animals defend territories, discriminating between neighbors and strangers ("dear enemy recognition"). Although kinship relations of adjacent territory holders usually are not known, neighbors may be kin if dispersal is nonrandom. *Plethodon cinereus* salamanders recognize their own odors and those of their neighbors, and they act more submissively in enivronments marked with unfamiliar odors (118). Neighbor discrimination in another salamander, *Plethodon jordani,* is seasonally dependent: while individuals usually prefer to associate with neighbors, their preference shifts toward non-neighbors during the breeding season, possibly to avoid inbreeding (142). Bullfrogs (*Rana catesbeiana*) also discriminate between neighbors and nonneighbors, based on their vocalizations (51). Similar evidence has been found in coral reef fish (161) and numerous species of birds (87). Juvenile muskrats (*Ondatra zibethicus*) act more amicably toward neighbors than nonneighbors, and additionally discriminate between siblings and nonsiblings (41). Red-backed voles (*Clethrionomys rufocanus bedfordiae*) in experimental field populations tend to establish home ranges adjacent to their siblings, but smaller individuals disperse when competition becomes intense (123). Yellow-bellied marmots (*Marmota flaviventris*) share foraging areas with close relatives and defend these territories against outsiders even if they are distant kin (7). Home-range overlap among female kin (and concomitant tolerance of neighbors) tends to be generally greater than that among nonkin in many mammals (235).

In competing for nesting sites, female Belding's ground squirrels (*Spermophilus beldingi*) typically chase and fight nonrelatives more than relatives (195, 196). Even among littermates, full-sisters cooperate more frequently to chase away intruders and fight less frequently among themselves than do half-sisters (106). Black-tailed prairie dogs (*Cynomys ludovicianus*) interact more amicably with kin than with nonkin, but nepotism decreases when intraspecific competition for estrous females (among males) or nesting burrows (among females) increases (111). Competition among close kin can be fierce when resources are limiting. Male lions (*Panthera leo*) compete for females in estrus, and fights are no less frequent between brothers than between nonrelatives (168). By many measures, primates are more aggressive toward close kin than toward distant kin (25). Yet individuals are much more likely to come to the aid of close relatives if they are attacked, and kin more often than nonkin form alliances for mutual assistance (24, 146). Male rhesus macaques (*Macaca mulatta*) transfer into the same social groups as their older brothers, form alliances with their brothers, and tend not to interfere with their brothers' mating attempts (152). Vervet monkeys (*Cercopithecus aethiops*) not only aid their close kin preferentially (115, 133), they also act agonistically toward kin of those individuals with whom their own kin have recently fought (45). When aggression does occur among close relatives, it is frequently less severe than that among nonrelatives (25).

Mating

Kin discrimination may be important in mate choice. Breeding with close relatives can lead to "inbreeding depression": levels of homozygosity increase; potentially deleterious recessive alleles are expressed; disease resistance may be lowered (96); and genotypic variation generally decreases (44, 171). Outbreeding also may entail some risks: traveling to obtain an unrelated mate can be costly and dangerous; genetic adaptations for the local environment may be lost; and coadapted gene complexes may be dissolved (171, 232). "Optimal outbreeding", i.e. mating with a relative but one not too closely related to oneself, has been suggested as a compromise strategy (12, 14, 199, 219). Deleterious consequences of inbreeding have been well documented (209), but little evidence is available to suggest that outbreeding depression occurs normally in animals although it may occur in some plants (234). The notion that coadapted gene complexes are disrupted by outbreeding remains speculative. While local populations may be adapted to their microenvironments, the gene complexes can be relatively simple and outbreeding depression may represent a temporary phenomenon (215).

DISPERSAL Sexually dimorphic dispersal patterns serve as potential barriers to inbreeding, at least in endotherms (46, 85, 183, 213; but see 158, 169). In many mammals, females are organized in matrilineal kin groups, and males disperse, either alone or with kin. Birds show the opposite pattern; males generally remain philopatric and females disperse (there are some exceptions). Few data are available on other phyletic groups.

Even in situations in which related males and females come into contact, many studies suggest that they do not mate (185). Most male and female acorn woodpeckers (*Melanerpes formicivorus*) disperse from their natal units in separate sib groups, but those females that remain in their natal groups fail to become reproductively active if their fathers (or probable fathers) are still present (126). Although male black-tailed prairie dogs (*Cynomys ludovicianus*) usually leave their natal coteries before breeding, young females are unlikely to come into estrus in the presence of their father (108). When coteries contain both related and unrelated males, females copulate exclusively with the unrelated males (108). In chimpanzees (*Pan troglodytes*), unlike most primates, males remain in their natal area and females disperse. Males thus have the opportunity to mate with their mothers, but they never do (182). Male wild horses (*Equus caballus*) disperse farther than do females from their natal areas (22). Because harems are frequently taken over by new males, females sometimes grow up in groups with stepfathers. Before dispersing, females avoid mating with either fathers or stepfathers, although they do mate with males from other bands (23, 55). Evidence for "optimal outbreeding" in natural populations is lacking, but how one would determine optimal levels is unclear. Great tits (*Parus major*) apparently mate with kin and nonkin at random (220), although incestual pairs suffer inbreeding depression (86). Long-distance dispersal probably decreases the potential for inbreeding in indigo buntings (*Passerina cyanea*). Close relatives sometimes mate, and direct cues (e.g. songs) are not used in kin recognition (173).

DELAYED MATURATION Individuals may avoid breeding with close relatives because their physiological responses to close and distant kin differ. California voles (*Microtus californicus*) and prairie voles (*Microtus ochrogaster*), housed in sibling groups or exposed to sibling odors for extended periods, grow more slowly and reach reproductive maturity later than do conspecifics reared with nonrelatives (16). Normally, sexual maturation would thus be delayed until after dispersal. Young of the meadow vole (*Microtus pennsylvanicus*) do not experience such growth effects, possibly because nonrelatives are more likely to be accessible in their natural habitat (16). Laboratory studies on many small mammals reveal patterns of delayed sexual maturation among individuals reared with siblings (e.g. 1, 103, 236; but see 54). Juvenile female mice (*Mus musculus*) exposed to soiled bedding of first cousins and unrelated males come into estrus at an earlier age than do controls, whereas females exposed to bedding of fathers or uncles reach puberty at the same age as controls (134). Because all odors were deposited by males unknown to the test subjects, these responses reflect discrimination between kin classes that cannot be attributed to familiarity with particular individuals. Social suppression of maturation among kin has also been documented in natural populations. Two-year old female marmots (*Marmota flaviventris*) generally fail to reproduce if their mother or more distant kin are present, but they may reproduce if unrelated adults are present (7). Whether reproductive suppression is modulated by kinship in other taxonomic groups (e.g. fishes; 30) is unknown.

MATE CHOICE Kin recognition mechanisms can mediate behavioral discrimination of mates. Male sweat bees (*Lasioglossum zephyrum*) recognize those females with which they have previously mated, and subsequently tend not to mate with them or their relatives (204, 237). Moreover, a female's attractiveness to a male sweat bee appears to decrease linearly with her relatedness to his previous mate (203). Males of the solitary wasp *Euodynerus foraminatus* remain around their natal nest and readily mate with their sisters although they are not constrained to do so (48). Mate choice is random with respect to kinship in other insects that have been studied (181, and references therein). Under artificial conditions behavioral kin recognition mechanisms seem ineffective in preventing inbreeding in captive primate groups (e.g. rhesus macaques, *Macaca mulatta*) (207), although behavioral mechanisms may not be necessary to avoid inbreeding in wild populations (153). In laboratory tests, Japanese quail (*Coturnix coturnix japonica*) orient more frequently toward unfamiliar first cousins than toward either unfamiliar siblings or unfamiliar third cousins, suggesting they may choose these relatives as mates (12). Quail chicks discriminate between siblings and nonsiblings soon after hatching, even if they are reared together in mixed broods (230). Incest avoidance has been demonstrated in studies of many small mammals (e.g. 52, 71, 101), although results for inbred laboratory stocks are sometimes difficult to interpret. But even estrous female mice (*Mus musculus*) collected from wild populations approach unfamiliar nonsiblings rather than familiar or unfamiliar siblings in a choice apparatus (244).

MECHANISMS OF KIN RECOGNITION

Recognition and Discrimination

Kin biases are evident in both behavioral and ecological responses of individuals to their conspecifics. Differential treatment of relatives and nonrelatives, or of different classes of relatives, constitutes kin discrimination. Kin are recognized either because of their spatial and temporal distribution (indirect recognition), or because of traits they express (direct recognition), or both. Kin recognition, however, need not and should not invariably lead to kin discrimination. Kin discrimination, the expression of recognition abilities, is only expected when its benefits exceed its costs measured in terms of inclusive fitness. The benefits and costs will vary depending on social and ecological conditions, causing discrimination to be context-specific (186, 227). A bird that does not discriminate between its own offspring and others' while feeding them in the nest nonetheless might gather up its own young should a predator appear, or it may avoid mating with them in future years. A failure to discriminate among nestlings could indicate a recognition error, but it need not. Discrimination might be possible but too costly, either because the risk of misidentifying kin as nonkin is greater than the benefit obtained by rejecting nonkin (especially if nonkin are infrequently encountered in a given context), or because nonkin actively resist rejection. For example, attempts to feed only one's own chicks might incite other nestlings to direct interference behaviors toward them. In ejecting foreign young from the nest, parents might sustain damage that would deprive their offspring of further parental care. These are hypothetical costs, of course, but the consideration of factors such as these is essential if studies of kin recognition are to be interpreted within an evolutionary framework. Reeve (186) has formalized the costs and benefits of discrimination in a series of optimization and ESS models.

Behaviorists often consider recognition to be synonymous with discrimination (106, 198) and thus fail to consider the neural and physiological processes by which kinship identity is detected and evaluated. Yet all organisms that discriminate kin (even those lacking nervous systems) presumably can transform information they perceive about conspecifics, or the environment in which these individuals are encountered, into an effective assessment of their kinship identities. This assessment may be imperfect, but nonetheless is likely to be better than random. Recognition, while more difficult to study than discrimination, is not impossible to study (cf 40). Recognition that does not normally result in behavioral discrimination can still be examined by using conditioning paradigms (31), by measuring metabolic or physiological responses (159), or by use of neurobiological techniques (113, 136). Recognition is expected to be context-dependent even in the absence of selection favoring context-dependent discrimination (227). An individual regularly encountered in specific contexts may be more readily distinguished from nonkin in those contexts than in other novel locations or situations. Contextual information provided by indirect mechanisms often is important in the ontogeny of direct recognition mechanisms.

Behavioral discrimination should be influenced by many factors, the effects of which may be difficult to predict. Consequently these variables are unlikely to be adequately simulated or controlled in laboratory experiments. Inconsistent experimental results on kin discrimination tendencies of particular species, even in repeated experiments of the same investigators on a single population, may indicate that abilities to recognize kin are variably expressed (231). Ecologists are principally interested in the consequences of discrimination rather than its underlying processes, but how the expression of recognition is modulated by environmental and social factors is an important problem that so far has attracted little attention. Kinship needs to be more generally considered when analyzing how ecology influences behavior in natural populations.

Components of Recognition

This survey reveals not only that kin discrimination is common in many contexts, but also that with few exceptions (e.g. parental and alloparental care) it often occurs by direct rather than indirect mechanisms. This should not be surprising. Direct kin recognition is possible (*a*) if individuals can be categorized as relatives or nonrelatives based on memory of the extent and contexts of one's previous social interactions with them (20), or (*b*) if relatives express some traits in common, either because they have been exposed to the same environmental factors (69) or because the traits are genetically determined (18, 72, 132). In the first case, kinship classifications may be based on *individual* recognition; in the second case, kinship classifications may be based on *group* or *class* recognition (91, 102, 227).

Individual and group recognition mechanisms are difficult to consider separately (227) because genetic relatives share a larger number of phenotypic traits than do nonrelatives. In both cases, traits (*labels*) expressed by individuals are perceived by conspecifics and compared with some model (*template*). How well the labels match the template is evaluated by some criterion (*decision rule*) to determine whether the label bearer is recognized. Individual recognition represents one extreme in which matches are based on many labels and decision rules are very precise to maximize the probability that each individual is uniquely recognized. Class recognition may involve the same neural and physiological processes, but the precision of matches necessary to elicit recognition is dictated by the extent of label variation present in the kin group or class to be identified. Species recognition may also be accomplished by the same processes, but the precision of matches necessary to identify conspecifics is still lower. Whether the same labels are used for each of these types of recognition is unknown in most cases (see 205), but if they are, "mistaken" individual recognition can result in kin recognition (203, 227). Mistakes are also inevitable in group or class recognition systems, as kin sometimes may be identified as nonkin and vice versa (72, 132). Kin discrimination based on individual recognition may be most common in animals with relatively complex nervous systems, and individual recognition can be selected for reasons other than kin identification (e.g. behavioral reciprocity, dominance hierarchies) (96, 227). Abilities to recognize classes of conspecifics may also be secondary consequences of recognition systems selected for a variety of reasons unrelated to behavioral nepotism (e.g. incest avoidance or immune function) (49).

Evidence that individuals discriminate kin that they have not previously encountered, or discriminate between different classes of kin and nonkin that they have always encountered together, holds particular fascination for behavioral ecologists. In the majority of cases in which kin biases are apparent, kinship is confounded with other variables, particularly familiarity and spatial distribution. Yet the "cleaner" experimental design afforded by these studies allows kinship effects to be examined separately from those associated with other types of social interactions. Many organisms can discriminate unfamiliar kin, or among familiar kin and nonkin (e.g. 27, 75, 83, 105, 106, 121, 166, 222). Yet in natural conditions kin discrimination is often based on familiarity and spatial distribution, and these cues can serve as reliable indicators of kinship identity. Experimental studies generally show that even if organisms can discriminate kin from nonkin when familiarity and proximity provide no basis for discrimination, these cues when available strongly influence behavioral tendencies. For example, individuals experimentally reared in social isolation may discriminate kin from nonkin (e.g. larvae of the amphibians *Bufo americanus* and *Rana cascadae*), but if reared in a socially mixed environment they fail to discriminate between familiar kin and nonkin (27, 166, 222). Similarly, results of several studies on rodents suggest that individuals can discriminate between unfamiliar siblings and unfamiliar nonsiblings (or half-siblings), but in usual conditions these effects are masked by much stronger preferences to interact with familiar individuals even if they are nonkin (83, 121).

Experimental analyses of kin recognition systems entail studies of (*a*) how the template is formed, (*b*) how labels communicate kinship identity, and (*c*) what algorithm characterizes the decision rule. The template might be genetically determined or learned. If genetically determined, the template may be coded by a single allele or linkage group, or it may more generally reflect the composition of the genome. If learned, the template may be based on conspecifics to which one has been exposed during specific circumstances or ontogenetic stages, on spatially proximate conspecifics or those with which one is presently familiar, or on oneself. Even a learned template might be genetically constrained by differential learning tendencies. For example, individuals may be more adept at learning certain cues similar to their own. Labels may be genetically determined (84, 203), environmentally influenced (e.g. by diet or nest materials; 69), or both (43). Labels may be socially transferred among group members or not; if environmentally influenced, labels may converge among kin (212), but genetic labels can also be transferred (138). Finally, the overlap in perceived labels with those represented in the template may be assessed by acceptance or rejection paradigms. Various algorithms have been proposed and modeled for systems in which labels (and indirectly, templates) are genetically determined (18, 49, 72, 132), and for systems in which labels and templates are environmentally determined (70). Recognition based on single allelic differences (cf "green beard" effects; 51a) does not truly constitute kin recognition. However, recognition may be possible if labels are encoded by highly polymorphic loci which are more likely to be shared by close kin than by more distant kin or nonkin (227). Alleles of the major histocompatibility complex (*MHC, H-2, HLA*) in vertebrates (17), fusibility alleles in marine invertebrates (88, 194), and the self-incompatibility alleles of plants (189, 219) may fulfill these requirements, and their possible roles in mediating kin recognition are being actively studied.

Ontogeny of Recognition

Although genetic analyses promise to provide important insights into kin recognition mechanisms, initial findings suggest that even when labels are genetically determined, templates are influenced by social experience. For recognition systems to be effective, labels and templates must match within the specifications set by the decision rule. Ontogenetic studies provide a powerful method for evaluating when and how each component develops and how the components interact in effecting recognition. By manipulating subjects' opportunities to interact socially with conspecifics during development and by choosing appropriate behaviors as assays of recognition, genetic and ontogenetic factors influencing recognition can be pinpointed.

Labels and templates both can be characterized with regard to their plasticity (225). Kin discrimination tendencies of some organisms suggest that templates are genetically encoded or become crystallized through an imprinting-like process so that they are resistant to modification through social experience. The labels, once established, also may remain unchanged if they are genetically coded or environmentally fixed (e.g. the *Polistes* scented-candle model; 70). Prior to dispersing from an oviposition site, *Bufo americanus* larvae form templates based on labels of surrounding siblings (which may be maternally acquired) (222). Neither the tadpoles' labels nor their templates are influenced by subsequent social interactions with nonkin (222, 225). Similarly, larval *Cataglyphis cursor* ants apparently form a template based on colony odors they experience during the first days after hatching, and this template persists through metamorphosis and into adulthood unchanged by subsequent social experience (116). Even if individuals bear constant labels throughout their lives, however, their templates may change. Sweat bees (*Lasioglossum zephyrum*) recognize their nestmates by their genetically determined labels (84, 203). The labels are not socially alterable, but the bees' templates do appear to change in response to the kinship composition of the nest (37; also see 73). When adult bees are isolated from their nest, they gradually lose the ability to discriminate between nestmates and non-nestmates (129). *Polistes* wasps bear both endogenous and acquired label components which appear to be learned not by larvae or pupae but only by adults (69, 70). Gadagkar (68) has proposed asymmetric rearing experiments as a tool to further probe the relationship between the ontogeny of labels and templates.

Recognition systems are constrained by social and ecological conditions when labels vary ontogenetically or as a result of social interactions. Variable labels are not uncommon. For instance, woodlice (*Hemilepistus reaumuri*) express genetically determined labels, but when conspecifics interact they adsorb the labels of those with which they come in contact, leading to a changing composite "badge" for each kin group (138). The kin recognition system breaks down when nonsiblings exchange labels, as these individuals become temporarily unacceptable to their families. Consequently, young actively avoid neighboring burrows and nonsiblings after emerging from their burrow; indeed, agonism between families may have been selected primarily to maintain the integrity of the kin recognition system (138). Woodlice learn the labels of their young soon after they emerge, but their templates remain plastic to match changes in the composite family-group label. Aside from changing due to social interactions, recognition labels may reflect temporally variable environmental factors. Colony odors of many social insects (32, 104, 154, 212) and recognition labels of some mammals (135, 178) vary in response to changes in food or nesting materials, and templates must concurrently change to accommodate these labels. Even if labels do not incorporate environmental factors, they may change ontogenetically. For example, in birds, plumage cues can potentially identify kin (15), but an individual's juvenile plumage may be very different from its plumage as an adult. Recognition labels of known kin might need to be repeatedly relearned as individuals mature (230). A recognition system in which changes in labels were not "tracked" by a variable template would be effective only if individuals were somehow insulated from environmental or social perturbations. The ability of *Rana cascadae* tadpoles to discriminate between unfamiliar siblings and unfamiliar nonsiblings has been cited as possible evidence of a "genetic recognition system" (27). Yet the template, if genetically specified, would not match the tadpoles' labels which apparently change when sib groups are allowed to interact socially in laboratory tanks (166).

Genetically determined templates are generally inappropriate for evaluating environmentally or socially influenced labels (224).

CONCLUSIONS

Despite the skepticism with which early experimental reports of kin recognition were received (95, 127), evidence of recognition abilities in diverse phyletic groups has rapidly accumulated during the past few years. The widespread occurrence of kin recognition systems in animals, and possibly also in plants, provides new impetus for the development of kinship-based models of sociality. Kin recognition mechanisms may arise and be maintained in response to selective factors independent of those favoring nepotism. Once established, however, these mechanisms can facilitate the evolution of complex behavioral responses to the social environment.

The mechanisms by which kin can be identified are remarkably diverse. Yet, with few exceptions, knowledge of how particular organisms respond to their kin remains largely fragmentary. Even less is known about the ecological determinants of kin recognition. The properties of kin recognition systems may be determined to a greater extent by ecological conditions than by phylogenetic constraints. Indeed, recognition mechanisms of some species seem well tailored to their habitat and life-history patterns, and recognition mechanisms of closely related species living in different habitats sometimes vary widely. Yet studies of numerous species fail to find evidence of kin discrimination in contexts in which the advantages of kin recognition appear clear. An ecological perspective on kin recognition demands the integration of functional studies evaluating the costs and benefits of discrimination with mechanistic studies determining the processes by which kin are identified.

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