KIN RECOGNITION IN GROUND SQUIRRELS AND OTHER RODENTS

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Significant advances have been made in understanding kin recognition as it pertains to nepotism (preferential treatment of kin) and mate choice (optimization of inbreeding and outbreeding). Yet complementary knowledge about how animals discriminate conspecifics on the basis of genetic relatedness remains unclear for most species. Because of the diversity of their scent sources and highly developed olfactory systems, rodents present a unique opportunity for examining chemical communication and kin recognition as a function of sociality. I review general processes of kin recognition and summarize mechanisms of recognition used by rodents. As a case study, I also examine recognition systems of ground squirrels, relating odor production and perception to differences in patterns of nepotism. Belding's ground squirrels (*Spermophilus beldingi*) produce ≥ 2 odors (from oral and dorsal glands) that correlate with relatedness (kin labels), and they are able to use these odors to make precise discriminations among their unfamiliar relatives. Thus, *S. beldingi* can recognize their distant female kin and male kin, even though these kin are not treated nepotistically (e.g., through cooperative territory defense or alarm call production). Furthermore, *S. beldingi* use these kin labels and recognition abilities to interact differentially with conspecifics as a function of relatedness. In ground squirrels and in other rodents, components of the kin recognition process (production of recognition cues, discrimination of these cues, and differential treatment of conspecifics) have evolved differentially among even closely related species. Kin recognition abilities in the absence of nepotism might reflect selection for inbreeding avoidance mechanisms, in addition to sex-biased natal dispersal. Together, data and the review demonstrate that recognition abilities cannot be predicted on the basis of sociality alone and suggest that comparative analyses, by multiple assays of discrimination, might be necessary to understand variation in the function of kin recognition within and across species.

Key words: ground squirrels, kin discrimination, kin recognition, mate choice, nepotism, odors, olfactory behavior, rodents, *Spermophilus*

The adaptive significance of kin recognition, as it relates to nepotism (preferential treatment of kin) and mate choice (optimal inbreeding and outbreeding), has been studied extensively in a variety of taxa (Bateson 1983; Fletcher and Michener 1987; Hepper 1991a; Sherman et al. 1997; Shields 1982). For some species, particularly those well suited to laboratory studies, proximate mechanisms by which animals recognize kin are well understood, yet complementary knowledge of both functions and mechanisms of recognition typically is lacking for most species. An understanding of kin recognition systems can be important for explaining interspecific variation in population cycles, nepotistic patterns, dispersal,

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and inbreeding avoidance (Blaustein et al. 1987; Charnov and Finerty 1980; Hepper 1991a; Pusey and Wolf 1996; Sherman et al. 1997). Here, I first discuss various mechanisms underlying kin recognition and then review literature on kin discrimination among rodents. As a case study, I discuss kin recognition abilities of Belding's ground squirrels (*Spermophilus beldingi*), a species that exhibits a variety of nepotistic behaviors. Finally, I discuss how kin recognition can be used in other contexts, such as inbreeding avoidance, and how sociality might influence recognition abilities, and I suggest future research.

Kin recognition is an internal process of assessing genetic relatedness that can be inferred through kin discrimination—the observable, differential treatment of conspecifics on the basis of cues that correlate with relatedness (kin labels). Thus, an absence of discrimination or of differential treatment of conspecifics cannot be interpreted as a lack of recognition ability. Kin recognition involves 3 components: production of unique phenotypic cues or labels, perception of these labels and the degree of correspondence of these labels with a "recognition template" (these components composing the mechanisms of recognition), and action taken by the animal as a function of the perceived similarity between its template and an encountered phenotype (Beecher 1982; Gamboa et al. 1991; Holmes and Sherman 1982; Reeve 1989; Sherman et al. 1997). Chemical cues provide information about species, sex, dominance, and individuality in a variety of rodents (Brown and Macdonald 1985; Johnston 2003), and they also can serve as kin labels if odors vary with genetic relatedness.

Mechanisms of kin recognition.—Several mechanisms for the perception component of kin recognition have been proposed (Alexander 1979; Barnard 1990; Blaustein 1983; Holmes and Sherman 1982; Waldman et al. 1988). First, animals can be recognized indirectly from spatial cues, with individuals encountered in a particular area (e.g., nest or burrow) treated as kin regardless of true relatedness (e.g., mother–offspring recognition via natal burrows—Holmes and Sherman 1982). Second, recognition can be based on familiarity via prior association: animals learn the phenotypes of individuals during early development (e.g., siblings and parents) and later discriminate these familiar relatives from unfamiliar animals. Third, as with prior association, animals learn their own phenotypes or those of their familiar kin, but later they can compare or match the phenotypes of *unknown* animals to this learned recognition template (phenotype matching). Phenotype matching requires a correlation between phenotypic and genotypic similarity so that individuals with traits that most closely match an animal's template are its closest kin. Site-specific spatial recognition is considered "indirect" recognition because nonphenotypic cues serve as the basis for discrimination, whereas prior association and phenotype matching are forms of "direct" recognition because discrimination is based on bearers' traits, such as odors or vocalizations (Holmes and Sherman 1982; Waldman et al. 1988). Fourth, recognition could be mediated by "recognition alleles," which cause expression of a phenotypic cue, recognition of that cue in others, and preferential treatment of individuals bearing the cue (Dawkins 1976; Hamilton 1964; Holmes and Sherman 1982). This mechanism has not been the focus of much research because, conceptually, it could result in cooperation with nonkin that happen to express that cue; thus, such cue-based cooperation is unlikely to spread (Dawkins' [1976] "green-beard" effect). Because most theoretical and empirical research on kin recognition focuses on prior association and phenotype matching, I will not address the spatial or recognition-allele mechanisms further.

Although prior association and phenotype matching involve a comparison between encountered phenotypes and templates, prior association leads to recognition

of previously encountered familiar individuals, whereas phenotype matching, through generalization of recognition templates, permits recognition of unfamiliar kin (Reeve 1989; Sherman et al. 1997). Phenotype-matching abilities can be demonstrated empirically by cross-fostering young at birth and later testing their ability to recognize unfamiliar littermates (this assumes that kin cues are not learned in utero—e.g., Mateo and Johnston 2000a; see also Hepper 1987a, 1991b) or by testing the ability of normally reared individuals to recognize unfamiliar kin such as older full siblings or paternal half-siblings. A more robust demonstration of phenotype matching would involve manipulation of recognition templates with subsequent changes in patterns of social interactions (Porter et al. 1983).

Certain social contexts can favor recognition on the basis of either prior association or phenotype matching (Holmes and Sherman 1982; see also Bekoff 1981; Charnov and Finerty 1980). Prior association is sufficient for kin recognition when relatives predictably interact in the absence of nonkin, such as at nest sites or in exclusive home ranges. Through direct association, individuals learn and become familiar with their relatives and can later recognize them as kin even if encountered in a different spatial location. This mechanism is commonly implicated in parent–offspring recognition and recognition when litter size is >1 or when young remain with their natal group. However, prior association will lead to recognition mistakes if nonkin are encountered during the learning phase (e.g., communal nesters), or if close kin are not encountered until some time later (e.g., nonlittermate siblings). Phenotype matching would be favored in such situations because it allows discrimination among individuals without prior association, by comparing their cues to a learned recognition template. In mammals, this mechanism would be expected when males mate with multiple females (permitting recognition of paternal half-siblings), communal nesting

(allowing females to discriminate against familiar but unrelated young), natal or breeding dispersal (allowing males to recognize their older brothers or fathers), or overlap of generations, particularly in long-lived species (Holmes and Sherman 1982; Sherman and Holmes 1985). Although not often relevant to rodents, phenotype matching would also be favored in cases of intra- or interspecific parasitism. Comparison of conspecifics' cues to own cues (self-referent phenotype matching) might be favored when females mate multiply so that young can discriminate among their maternal full and half-siblings (Mateo and Johnston 2000a).

Kin recognition in rodents.—Kin recognition abilities have been studied most extensively in mice, rats, and ground squirrels. Because of the variety of species studied, and to facilitate discussion of recognition across rodent species, I have summarized the available literature on the mechanisms used for recognition in Table 1. House mice (*Mus musculus*; *M. musculus domesticus*), white-footed deermice (*Peromyscus leucopus*), and rats (*Rattus norvegicus*) can discriminate between unfamiliar kin and nonkin (Aldhous 1989; Barnard and Fitzsimons 1988, 1989; Grau 1982; Kareem and Barnard 1982, 1986; Winn and Vestal 1986). Cactus mice (*P. eremicus*) treat familiar nonkin as kin, although it is unknown whether they can discriminate among unfamiliar kin and nonkin (Dewsbury 1982). Spiny mice (*Acomys cahirinus*) also can use phenotype matching to discriminate among conspecifics, but continued exposure to kin cues appears necessary for maintenance of this recognition ability (Porter 1988; Porter et al. 1983; see also Dewsbury 1988a). Male oldfield mice (*Peromyscus polionotus rhoadsi*) preferentially associate with more distantly related females regardless of female reproductive status, suggesting that this monogamous species can use phenotype matching to assess relatedness to unfamiliar individuals (Ryan and Lacy 2003). Odor cues associated with

urine, which contains by-products of the major histocompatibility complex (MHC), can serve as kin labels in rats and mice (Boyse et al. 1991; Brown and Eklund 1994; Brown et al. 1978), and the MHC also could be the basis of kin discrimination in other rodents. Most studies of rodent kin recognition have focused on odor cues, given the importance of chemical communication in this order, although the production component could involve other modalities (see ''Discussion'').

The predictions in the preceding section concerning social systems and recognition mechanisms are supported in some rodents (Table 1). For example, female gray squirrels (*Sciurus carolinensis*) treat close kin amicably and form winter nesting groups with them, but sympatric female fox squirrels (*S. niger*) do not. This is likely due to interspecific variation in philopatry, because female *S. carolinensis* remain in their natal areas and continue to interact with kin, whereas natal dispersal by both sexes of *S. niger* precludes kin interactions (Koprowski 1996). In *S. carolinensis*, interactions between pairs of distant kin that are not normally encountered during early development (e.g., grand-relatives) are often agonistic, suggesting that prior association rather than phenotype matching mediates their kin-differentiated behaviors. However, it is possible that distant kin are recognized without being treated preferentially.

The social and ecological systems of beavers (*Castor canadensis*) present a potential problem for recognizing kin. Beavers are long-lived (up to 9 years), young of both sexes disperse along waterways, and settlement usually occurs close to natal dens, so it is likely that they will encounter unfamiliar nonlittermate siblings after dispersal. In such cases, they can use phenotype matching to recognize their unfamiliar kin, likely using anal gland odors as kin labels (Sun and Müller-Schwarze 1997, 1998).

In species that nest communally, kin recognition is likely mediated by phenotype matching, particularly if there is a risk of offspring mixing before mothers become familiar with their own young. Maras (*Dolichotis patagonum*) typically share warrens because den sites are limited, but females attempt to prevent unrelated young from nursing, suggesting that mothers are able to recognize their own offspring (Taber and Macdonald 1992). Degus (*Octodon degus*) are communal nesters and might nurse communally, yet mothers are able to discriminate between their own and their nestmate's offspring, even though they are equally familiar with all young (S. A. Jesseau et al., in litt.). Although it was originally thought that naked mole-rats (*Heterocephalus glaber*) inbreed within their underground colonies, current data suggest outbreeding through periodic dispersal (Braude 2000). Accordingly, Ciszek (2000) demonstrated that female naked mole-rats prefer to mate with unfamiliar noncolony members over colony members, although their ability to discriminate through phenotype matching has not yet been tested.

Kin recognition in ground-dwelling squirrels.—Kin recognition in ground-dwelling squirrels has been studied in detail, in part because they exhibit wide intra- and interspecific variation in sociality and nepotism (e.g., alarm call production, territory defense, hibernaculum sharing, and patterns of infanticide—Holmes and Sherman 1982; Michener 1983; Schwagmeyer 1988). Results of cross-fostering studies indicate that *S. beldingi*, *S. lateralis*, *S. parryii*, and *S. richardsonii* can discriminate among conspecifics according to relatedness and prior association (Davis 1982; Holmes 1994, 1995; Holmes and Sherman 1982), whereas *Cynomys ludovicianus* (black-tailed prairie dogs), *S. columbianus*, and *S. tridecemlineatus* appear to discriminate on the basis of prior association alone (Hare and Murie 1996; Holmes 1984b; Hoogland 1995). The latter studies focused on social interactions (e.g., agonism, nasal investigations, play) of free-living or temporarily captive individuals as indicators of discrimination. However, odor perception

TABLE 1. Summary of available data on kin recognition abilities of rodents; in all cases, discrimination appears to be based on odor cues.

Species[a]	Sociality[b]	Prior association[c]	Phenotype matching[d]	Test design[e]	Reference
Sciuridae					
Sciurus carolinensis (gray squirrel)	Territorial; polygamous	Yes			Koprowski 1996
S. niger (fox squirrel)	Territorial; polygamous	Possible			Koprowski 1996
Cynomys ludovicianus (black-tailed prairie dog)	Highly social; polygamous	Yes	No	1	Hoogland 1995
Spermophilus beldingi (Belding's ground squirrel)	Social; polygamous	Yes	Yes	1	Holmes 1984a, 1986a, 1986b; Holmes and Sherman 1982; Mateo 2002
S. columbianus (Columbian ground squirrel)	Social; polygamous	Yes	No	1	Hare 1992; Hare and Murie 1996; King 1989; King and Murie 1985; Stevens 1998
S. lateralis (golden-mantled ground squirrel)	Asocial; polygamous	Yes	Yes	1	Holmes 1995; Mateo 2002
S. parryii (Arctic ground squirrel)	Highly social; polygamous	Yes	Yes	1	Holmes and Sherman 1982
S. richardsonii (Richardson's ground squirrel)	Social; polygamous	Yes	Yes	1	Davis 1982, 1984; Hare 1998b; Michener 1974; Michener and Sheppard 1972
S. tridecemlineatus (thirteen-lined ground squirrel)	Asocial; polygamous	Yes	No	1	Holmes 1984b
Tamias townsendii (Townsend's chipmunk)	Solitary	Yes	Yes	1	Fuller and Blaustein 1990
Castoridae					
Castor canadensis (North American beaver)	Monogamous pair and young	Yes	Yes		Sun and Müller-Schwarze 1997, 1998
Muridae					
Arvicola terrestris (water vole)	Family groups	Yes			Potapov and Evsikov 1995
Clethrionomys rufocanus (gray red-backed vole)	Territorial; promiscuous	Yes			Ims 1989; Ims and Andreassen 1991; Kawata 1987
Lasiopodomys mandarinus[f] (mandarin vole)	Monogamous	Yes	Possible	1	Fadao et al. 2000
Microtus arvalis (common vole)	Female family groups; solitary males; polygynous	Yes			Heise and Rozenfeld 2002
M. canicaudus (gray-tailed vole)	Territorial; monogamous to polygamous	Yes	No	1	Boyd and Blaustein 1985; Wolff et al. 1994

TABLE 1.—Continued.

| Species[a] | Sociality[b] | Discriminate conspecifics according to | | Test design[e] | Reference |
		Prior association[c]	Phenotype matching[d]		
M. montanus (montane vole)	Territorial; monogamous to polygynous	Yes	No	1	Berger et al. 1997
M. ochrogaster (prairie vole)	Monogamous	Yes	No	1	Gavish et al. 1984; Kohli and Ferkin 1999; McGuire and Getz 1981; Paz y Miño and Tang-Martinez 1999; Phillips and Tang-Martinez 1998; Smale et al. 1990
M. pennsylvanicus (meadow vole)	Territorial; promiscuous to polygamous	Yes	No	1	Ferkin 1988; Ferkin and Rutka 1990
M. pinetorum (pine vole)	Family units; range of mating systems	Yes			Brant et a. 1998; Solomon and Rumbaugh 1997
Ondatra zibethicus (muskrat)	Monogamous with occasional polygyny	Yes			Caley and Boutin 1987
Mesocricetus auratus (golden hamster)	Solitary and territorial; polygamous?	Yes	Yes	1	Heth et al. 1998; Mateo and Johnston 2000a; Todrank et al. 1998
Meriones unguiculatus (Mongolian gerbil)	Colonial with extended family groups	Yes	No	2	Ågren 1981, 1984; Halpin 1976
Acomys cahirinus (spiny mouse)	Gregarious; communal nesting	Yes	Yes	1	Porter 1988; Porter et al. 1983
Mus musculus musculus and *M. m. domesticus* (house mouse)	1 male and several females to communal groups; polygamous	Yes	Yes	1, 3	Aldhous 1989; Barnard and Fitzsimons 1988, 1989; D'Amato 1993; Kareem and Barnard 1982, 1986; Winn and Vestal 1986
Rattus norvegicus (rat)	1 male and several females to territorial colonies	Yes	Yes	1, 3	Hepper 1983, 1987a, 1987b
Peromyscus leucopus (white-footed deermouse)	Social; polygamy to monogamy	Yes	Yes	1, 2, 3	Grau 1982; Halpin and Hoffman 1987; Keane 1990
P. maniculatus (deermouse)	1 male and several females; polygynous	Yes			Dewsbury 1988b
P. eremicus (cactus mouse)	Monogamous?	Yes	No	1	Dewsbury 1982
Bathyergidae					
Cryptomys (common mole-rat)	Eusocial; 1 breeding pair	Yes			Burda 1995
Heterocephalus glaber (naked mole-rat)	Eusocial; polyandry	Yes			Ciszek 2000; Clarke and Faulkes 1999; O'Riain and Jarvis 1997
Octodontidae					
Octodon degus (degu)	Colonial	Yes	Yes		S. A. Jesseau, W. G. Holmes and T. M. Lee, in litt.

tests could be used to determine whether these species cannot discriminate on the basis of relatedness or can discriminate but do not do so in the contexts in which they were tested (Mateo 2002).

Components of kin recognition in Belding's ground squirrels.—I describe in detail the production, perception, and action components of kin recognition in *S. beldingi*, one of the few species for which both mechanisms and functions of kin recognition are well understood. Belding's ground squirrels mate multiply, exhibit sex-biased natal dispersal and philopatry, are long-lived, and produce large litter sizes—traits that favor the ability to recognize kin through both prior association and phenotype matching. They also exhibit a variety of nepotistic behaviors, including cooperative territory defense and alarm call production. Nepotism is restricted to close female kin only (e.g., mothers, daughters and sisters); distant female kin and male kin are not treated preferentially (Sherman 1977, 1981). To determine whether these kin are not treated nepotistically because they are not recognized, I examined the production of kin labels by *S. beldingi* and their perceptual ability to discriminate among various classes of kin (Mateo 2002). I also examined whether these recognition abilities can mediate social interactions by examining social relationships among unfamiliar kin and nonkin.

MATERIALS AND METHODS

Study animals.—Belding's ground squirrels are group-living, burrowing rodents found in alpine and subalpine regions of the western United States (Jenkins and Eshelman 1984). They are socially active aboveground between April and August and hibernate the remainder of the year. Each mother produces 1 litter annually of 5–8 young, which are reared in isolation for 25–28 days in an underground burrow (natal burrow). Young first come aboveground (emerge) as nearly weaned, 4-week-old juveniles (Sherman and Morton 1984). Because mothers nest in equal proximity to close and distant kin (Sherman 1981), juveniles emerge into a social environment that includes unfamiliar juveniles and adults that vary in genetic relatedness. Two to 3 weeks after natal emergence, juvenile females establish their own burrow system within 25 m of their natal burrow, whereas juvenile males begin to disperse 250–500 m from their birthplace (Holekamp 1983).

I focused on odors from *S. beldingi* oral and dorsal glands because of their potential role in ground squirrel social recognition (Halpin 1985; Kivett et al. 1976). Most sciurids engage in frequent nasal contacts, in which an individual smells the oral region (containing large apocrine glands in the mouth corners) of another animal for several seconds. Investigations often precede amicable and agonistic social interactions, particularly among unfamiliar animals, suggesting that oral gland secretions might facilitate identification of conspecifics. Size of the dorsal gland field, which extends caudally from the scapular region and contains small apocrine

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[a] Species names and taxonomic organization follow Wilson and Reeder (1993).

[b] Sociality refers to a brief description of a species' social system and mating patterns, where known.

[c] Data indicate that animals can discriminate among kin classes on the basis of prior association (e.g., familiar sibling versus unfamiliar agemate).

[d] Data indicate that animals can discriminate among equally familiar kin classes (e.g., maternal full- and half-siblings) or among equally unfamiliar kin classes (e.g., cousins and nonkin).

[e] Experimental design used to test for phenotype-matching ability: 1 = animals were cross-fostered between unrelated mothers and tested with unfamiliar full siblings; 2 = animals were tested with older, nonlittermate full siblings; 3 = animals were tested with unfamiliar kin such as cousins or paternal half-siblings.

[f] Considered by many to be in the genus *Microtus*.

glands, increases with sociality across *Spermophilus* species (Kivett et al. 1976), suggesting that these odors also might be used for social recognition.

Animal housing.—Research was conducted at the Sierra Nevada Aquatic Research Laboratory near Mammoth Lakes, California (37.649°N, 118.971°W). Pregnant females were live-trapped and housed in a laboratory building at the research station, where they gave birth and reared their young (Mateo and Holmes 1997). Litters probably comprised full siblings and maternal half-siblings because of multiple mating by females (Hanken and Sherman 1981). When young were 25–28 days of age, they and their mothers were transferred to outdoor enclosures at the research station (3–4 litters/enclosure) to be subjects or odor donors in odor discrimination tests. Animals were individually marked with a combination of hair dye and ear tags. Each open-air enclosure (10 by 10 by 2 m) included natural vegetation, laboratory food and water, and 4 buried nestboxes connected to the surface by plastic tunnels (Mateo and Holmes 1997).

Juveniles (>50 days old) served as subjects in the odor tests, and both juveniles and adults served as odor donors. Adult female donors had ceased lactating ≥2 weeks before tests. Some *S. beldingi* were collected from a site where they have been observed and marked since 1992. Therefore, maternal relatedness of some kin (e.g., grandmother, half-aunt, or the mother's nonlittermate sister), was known with certainty because juveniles were marked within 48 h of their natal emergence and before they started mixing with other juveniles. Because of multiple paternity in *S. beldingi* (Hanken and Sherman 1981), relatedness among some nondescendent kin (e.g., siblings) was unknown. Therefore, coefficients of relatedness for three-quarter siblings (offspring of 2 sisters mated with the same male), aunts (mother's littermate sister), and cousins (offspring of the referent's mother's brother) were averages of calculations assuming individuals (the 2 sisters or the mother and her sister or brother) were full siblings or were half-siblings. Because of controlled mating in captivity, some siblings were known to be full siblings. Animals were maintained on similar diets (Purina mouse chow #5015) for >1 week before testing to minimize diet-related variation in odors.

General methods for odor tests.—Odors were collected from donors on 1-cm^3 polyethylene cubes (Ann Arbor Plastics, Inc., Ann Arbor, Michigan) ≤15 min before use with methods developed by Harris and Murie (1982) for *S. columbianus*. Secretions were collected by rubbing a cube 8 times, either anteroposteriorly along both mouth corners or cephalocaudally along the dorsal gland field, depending on which odor was needed for an odor test. Observers were blind to the identity of donors. For tests, cubes were placed at burrow entrances in the enclosure for simultaneous investigation by all animals in the enclosure. Although >1 animal could investigate a set of cubes at a given time, presence of conspecifics did not make ground squirrels more or less likely to investigate cubes, nor did it influence their duration of investigation. The total duration of investigation of each odor (time spent smelling or licking an odor) was recorded during 30-min test periods. Those data were log transformed (and verified for normalization with Kolmogorov–Smirnov tests) and analyzed with 2-tailed dependent *t*-tests or repeated measures analyses of variance (ANOVAs) and 2-tailed general linear contrasts (SPSS Inc. 1998). Individuals served as the unit of analysis because my previous odor discrimination tests have not revealed a litter effect. That is, variance in investigation duration was equal or greater within litters than between, suggesting that investigation durations are not influenced significantly by family differences.

Production component.—With the use of a habituation–discrimination task, subjects were presented with either oral or dorsal odor from an unrelated individual (the "referent") for 3–4 habituation trials and then tested with similar odors from several individuals varying in relatedness to the referent (discrimination trials). During habituation trials, an unscented cube was presented along with the cube containing the referent's odor to verify that animals habituated to the odor rather than cubes; data on investigation of unscented cubes are not included here. After the habituation trials, test odors were presented in a balanced order, 2 at a time, with the habituation odor presented after the 1st test session to "remind" animals of the appropriate referent. Trials were separated by 24 h.

If odor differences correlate with genetic differences, then as odor donors become less related to the referent, their odors should be less sim-

ilar to the referent's and therefore should be investigated more by subjects (Halpin 1986; Johnston 1981). Due to trapping distances (>100 m) between subjects and odor donors (or their mothers), they were unlikely to have been familiar or closely related (Sherman 1981; J. M. Mateo, in litt.). Therefore, subjects could only use qualities of the odors themselves to discriminate among them. Data from test trials and the final habituation trial were compared with ANOVAs. Partial correlations controlled for test order effects when necessary. Individuals were used only once as subjects. For each habituation–discrimination task, a group of enclosure-housed *S. beldingi* ($n = 23$–24; 3–4 mothers and their offspring) served as subjects. Animals were included in the analysis if they investigated at least 1 cube during each of the habituation and discrimination trials.

Perception component.—A preference task was used to determine whether *S. beldingi* can use oral and dorsal odors to discriminate among their unfamiliar kin and nonkin. Differential investigation of classes of cues, such as kin versus nonkin, indicates spontaneous discrimination of the cues and reflects animals' perceptual abilities to assess correlates of relatedness. If *S. beldingi* spontaneously discriminate between cues of distant kin and nonkin, for example, one could infer that they have the ability to recognize their distant kin, but this does not lead to nepotistic behaviors (Sherman 1977, 1981).

To determine whether ground squirrels discriminate among classes of their own unfamiliar kin, I used preference tasks in which 2–3 odors (either oral or dorsal) were presented simultaneously to juveniles living in enclosures during a 1-trial test. If odors of nonkin match juveniles' recognition templates less than odors of distant kin, then nonkin odors should be perceived as more novel and investigated longer than odors from distant kin (Halpin 1986; Johnston 1981; Mateo and Johnston 2000b). Juveniles were tested with odors from their own unfamiliar kin, and each individual was a subject in 1 or 2 preference tasks. Juveniles that were related to the odor donors were housed with other unrelated litters to provide species-typical social experiences and to expose subjects to a range of conspecific odors. Animals were included in analyses if they investigated ≥ 1 cube.

Action component.—When kin recognition abilities are demonstrated in a given species, it is necessary to demonstrate a causal link between this ability and differential treatment of kin. Therefore, I observed social behaviors of related and unrelated *S. beldingi* to determine whether kin discrimination, in the absence of prior association, influenced patterns of social interactions. I focused on rates of play and nasal investigations among juveniles. Although play is not considered a nepotistic behavior, it is thought to lay a foundation for adult kin preferences and nepotism and therefore is likely to vary with kinship (Holmes 1994; Michener 1983).

Three litters ($n = 14$ juveniles total) and their mothers were housed in an enclosure for 11 days. Two of the mothers were littermate sisters (field-collected, so either full or half-sisters) that mated in captivity with 1 male; the 3rd unrelated mother mated with a 2nd male. Pairs of juveniles therefore were full siblings (offspring of 1 female; average coefficient of relatedness, $r = 0.50$), three-quarter siblings (offspring of the 2 sisters; $r = 0.34$), or nonkin (offspring of unrelated females; $r = 0$). Social behaviors (play, nasal investigation, agonism) between pairs of juveniles were recorded daily from 0700–1200 h (additional details in Holmes and Mateo 1998). Observers were blind to the juveniles' relatedness. Poisson regressions were used to compare rates of behaviors among juvenile pairs as a function of relatedness. These analyses examine the effect of relatedness while controlling statistically for effects of sex and weight differences of pairs of juveniles, factors known to affect rates of play (Holmes 1994).

Results

Production component.—Habituation–discrimination tasks indicated that *S. beldingi* produced odors that were more similar among close kin than distant kin (kin labels). In the test of oral gland odors, animals investigated odors more as relatedness of the test odor donors to the referent decreased (adult odors: $n = 14$ subjects, $F = 11.25$, *d.f.* $= 4, 52$, $P < 0.001$; Fig. 1a; juvenile odors: $n = 11$, $F = 2.79$, *d.f.* $= 4, 49$, $P < 0.05$; Fig. 1b). Thus, ground squirrels perceived odors of a referent's distant kin as less similar to the referent's odor than odors of close kin. Tests with dorsal gland odors yielded similar results (adult odors: n
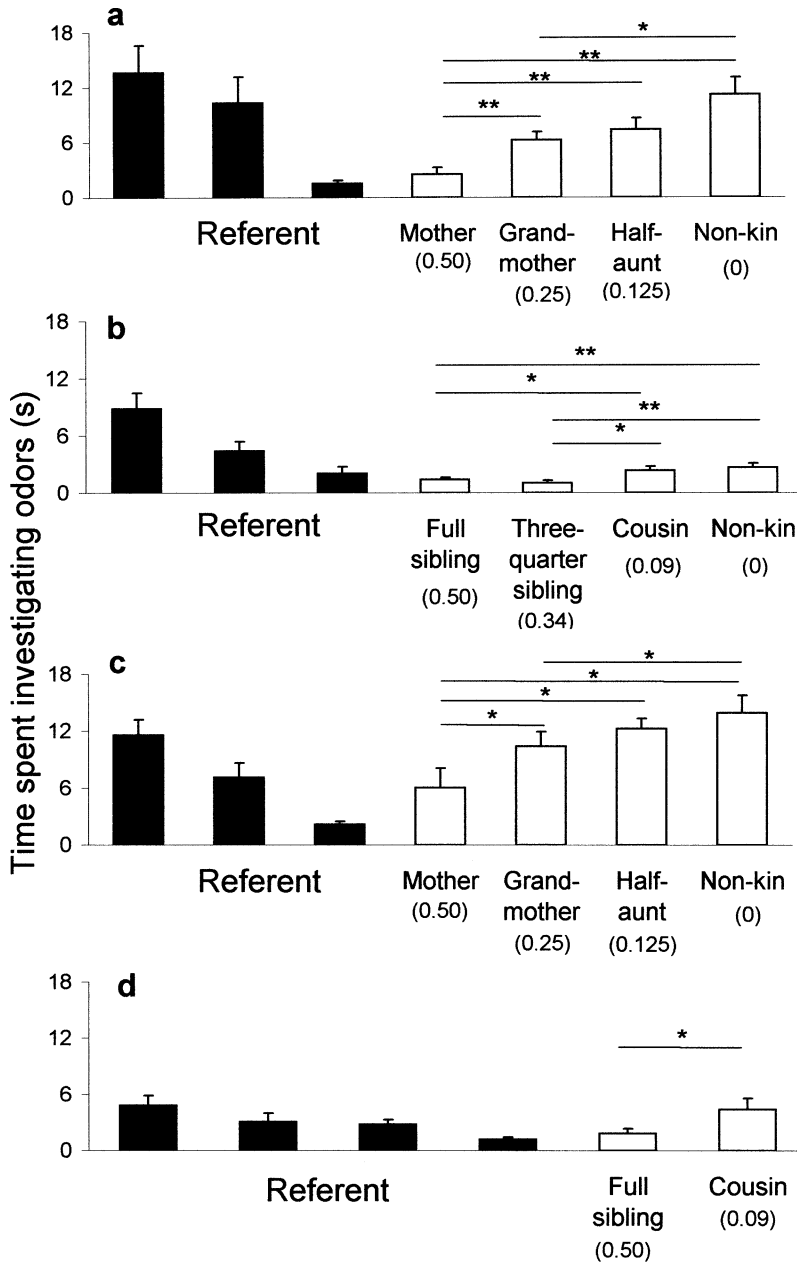
FIG. 1.—Duration of investigation ($\bar{X} + SE$) of odors by subjects in habituation–discrimination tasks. Solid bars represent investigation of the referent odor (3–4 habituation trials), and open bars represent investigation of test odors (discrimination phase) collected from kin and nonkin of the referent. Numbers below category labels are estimated coefficients of relatedness between the referent and test odor donor. a) Test of *Spermophilus beldingi* oral gland odors with the referent's mother, grandmother, half-aunt (mother's nonlittermate sister), and nonkin. b) Test of *S. beldingi* oral gland odors with the referent's full sibling, three-quarter sibling (offspring of 2 sisters mated with the same male), cousin (offspring of the referent's mother's brother), and nonkin. c) Test of *S. beldingi* dorsal gland odors with the referent's mother, grandmother, half-aunt (mother's nonlittermate sister), and nonkin. d) Test of *S. beldingi* dorsal gland odors with the referent's full sibling and cousin. Due to

$= 13$, $F = 11.39$, $d.f. = 4, 44$, $P < 0.001$; Fig. 1c; juvenile odors: $n = 11$, $F = 7.17$, $d.f. = 2, 20$, $P < 0.01$; Fig. 1d). In the test of juvenile dorsal odors, subjects were not tested with three-quarter sibling or nonsibling odors in the discrimination phase due to inclement weather. Across all tests, investigation of odors was related inversely to the degree of kinship between odor donors and the referent, indicating that both oral and dorsal odors of *S. beldingi* varied linearly with relatedness.

Perception component.—Juveniles investigated oral odors of their nonkin longer than odors of their unfamiliar three-quarter sibling, whereas investigation of their unfamiliar cousin's odor was intermediate ($n = 7$ juvenile subjects, repeated measures ANOVA $F = 12.87$, $d.f. = 2, 12$, $P < 0.001$; Fig. 2a). Juveniles investigated the oral odor of their aunt significantly longer than that of their grandmother as well ($n = 7$, paired $t = 3.19$, $d.f. = 6$, $P = 0.02$; Fig. 2b), where coefficients of relatedness differ by only ~0.06. They also investigated unfamiliar dorsal gland odors of their nonkin longer than those of their half-aunt ($n = 7$, paired $t = 2.63$, $d.f. = 6$, $P = 0.04$; Fig. 2c). More important, however, juveniles discriminated between cousin and nonkin odors (Fig. 2a) and between half-aunt and nonkin odors (Fig. 2c), inferring they were able to recognize their unfamiliar distant kin ($r \leq 0.125$).

Action component.—Social behaviors of juveniles varied as a function of relatedness, and discrimination was likely due to investigation of kin labels, particularly oral gland odors. Rates of play between pairs of juveniles declined as relatedness decreased (Fig. 3a), and juveniles were more likely to
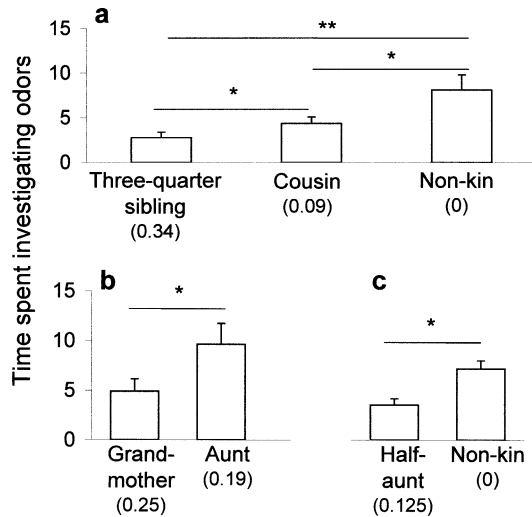

FIG. 2.—Duration (s) of investigation ($\bar{X} + SE$) of *S. beldingi* odors collected from unfamiliar kin of subjects during preference tasks. Numbers below category labels are estimated coefficients of relatedness between subjects and odor donors. a) Investigation of oral gland odors of unfamiliar kin collected from subjects' three-quarter siblings (offspring of 2 sisters mated with the same male), cousin (offspring of the subject's mother's brother), and nonkin. b) Investigation of oral gland odors collected from subject's grandmother and aunt. c) Investigation of dorsal gland odors collected from subject's half-aunt (mother's half-sister), and nonkin. Horizontal bars and asterisks represent differences in investigation of odors (* $P < 0.05$, ** $P < 0.01$) by repeated measures ANOVAs or paired t-tests (Mateo 2002).

play with their three-quarter siblings than with nonkin, even though both groups were unfamiliar at the start of the study (overall likelihood ratio $\chi^2 = 58.24$, $d.f. = 2$, $P < 0.0001$). Kin discrimination was likely facilitated by odor cues because nasal inves-

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inclement weather at the end of the study, the final discrimination test with three-quarter siblings and nonkin was not completed. Horizontal bars and asterisks represent differences in investigation of odors (* $P < 0.05$, ** $P < 0.01$) by repeated measures ANOVAs. Although not depicted, in all tests, investigations of test odors were significantly longer than investigation of the referent odor during its last presentation in the habituation phase. Figs. 1a and 1c from Mateo 2002.
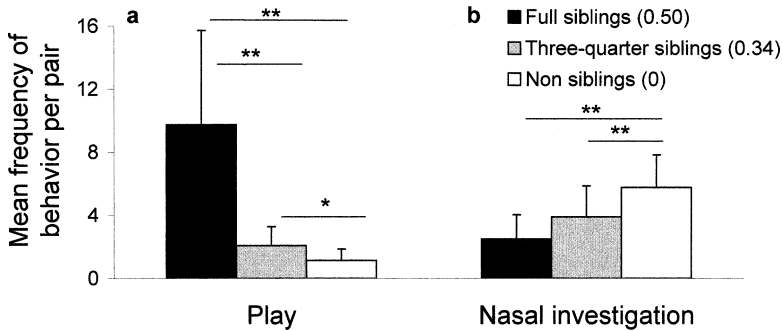
FIG. 3.—Mean frequencies (+95% *CI*) of a) play and b) nasal investigations between pairs of juveniles as a function of relatedness. Horizontal bars and asterisks represent differences in behavior frequencies (* $P < 0.05$, ** $P < 0.01$) by Poisson regression analyses. Mean frequencies are adjusted statistically by the regression model for effects of sex of each juvenile in a pair and the weight difference between juveniles in each pair.

tigations were higher among nonkin than either three-quarter siblings or full siblings (overall $\chi^2 = 13.44$, *d.f.* = 2, $P < 0.002$; Fig. 3b). Those results suggested that kin discrimination abilities described above (Figs. 1 and 2) were used in social behaviors, allowing juveniles to preferentially interact with kin over nonkin, even in the absence of prior association.

DISCUSSION

Belding's ground squirrels produce ≥2 odors—one from oral glands and one from dorsal glands—that vary with relatedness (production component; Fig. 1), and these oral and dorsal secretions can be used by *S. beldingi* to discriminate among various classes of unfamiliar kin (perception component; Fig. 2). Kin labels are critical for recognition of unfamiliar relatives via phenotype matching (Holmes 1986a, 1986b; Holmes and Sherman 1982), and the combination of ≥2 odor sources to kin labels might facilitate more accurate assessments of kinship than would a single odor (Beecher 1988). Indeed, ground squirrels are able to discriminate very small differences in relatedness among their kin, such as between their cousin and nonkin (a difference in relatedness of ~0.09) and between their grandmother and aunt (a difference of ~0.06; Fig. 2). I used male and female sub-

jects and male and female odor donors (this study; J. M. Mateo, in litt.); thus, I knew that males produced kin labels and could recognize their unfamiliar kin, even though they are not treated nepotistically nor do they act nepotistically (Sherman 1977, 1981). Therefore, the limits of nepotism in *S. beldingi* are not due to constraints on recognition abilities. Ground squirrels can recognize their distant female kin and their male kin, but this does not lead to preferential treatment of those kin.

Odor perception tests suggest that Belding's ground squirrels can use odors to recognize their relatives (Fig. 2); yet, it is necessary in this, and other species, to demonstrate the link empirically between recognition cues and differential treatment of kin classes. Observations of play behavior and nasal investigations among *S. beldingi* juveniles indicate that relatedness does influence social interactions, even among unfamiliar individuals (action component; Fig. 3). Differential behaviors among full siblings, three-quarter siblings, and nonkin are likely mediated by odor discrimination because nasal investigations, which precede most social interactions, were inversely proportional to rates of play among kin classes. Given the density of juveniles in the enclosure, play partner preferences were unlikely influenced by variation in avail-

ability of kin. In previous studies of juveniles in these enclosures, nearest neighbor distances of kin and nonkin were indistinguishable (Holmes 1994, 1995). In addition, mothers do not directly influence development of juvenile social relationships, either by limiting their spatial movement or by preventing their young from playing with nonlittermates (Holmes and Mateo 1998). Thus, odor-based kin discrimination, even in the absence of prior association, can facilitate formation of juvenile social relationships, which are hypothesized to be precursors of adult kin preferences and nepotistic relationships (Holmes 1994; Michener 1983).

Components of recognition across rodents.—To date, most research on kin recognition in rodents has focused on the perception component, examining abilities of animals to discriminate on the bases of familiarity and relatedness (Table 1). Olfaction typically is assumed to be the modality underlying recognition, yet few studies have verified which particular odor sources are used for discrimination. Future work could focus on the production component, determining the extent to which traits vary with kinship, and thus potentially could be used as kin labels (e.g., Fig. 1; see also Johnston 2003). After cues are identified, our understanding of how they evolved (and perhaps whether they evolved specifically for kin recognition—Grafen 1990) would be enhanced by a quantitative assessment of the correlation between genetic similarity and odor similarity. For example, gas chromatography and mass spectrometry have revealed that beaver anal gland secretions, but not their castoreum, are more similar among kin than nonkin and can be used for phenotype matching (Müller-Schwarze 1992; Sun and Müller-Schwarze 1997, 1998). Finally, for a complete understanding of kin recognition, we need to determine whether discrimination and resulting kin-biased behaviors are indeed adaptive. That is, do individuals in fact increase their fitness by performing nepotistic behaviors or by rejecting kin as mates (Pusey and Wolf 1996; Sherman 1977, 1981)? Evidence of a kin bias alone is insufficient to posit a function for kin recognition abilities.

Sociality and kin recognition abilities.— Kin selection theory predicts that recognition components (production, perception, and action) will evolve with sociality, depending in part on species' social systems, rates of interactions with kin, and costs and benefits of nepotism (Beecher 1988; Reeve 1989; Sherman et al. 1997). However, data on *S. beldingi* and other rodents (Table 1) suggest that sociality alone cannot always be used to predict recognition abilities. For example, despite the wide range of social systems among *Microtus*, including group size, patterns of natal dispersal, and frequency of multiple mating, social interactions and reproductive behaviors of all species examined to date appear to be influenced by prior association and not relatedness (Berger et al. 1997; Boyd and Blaustein 1985; Fadao et al. 2000; Ferkin and Rutka 1990; Paz y Miño and Tang-Martinez 1999; Sera and Gaines 1994). Although lack of kin-based discrimination by voles during dyadic encounters has been interpreted as a lack of recognition abilities, use of multiple assays of discrimination, such as odor perception tests and observations of social interactions, might be necessary to reveal kin recognition abilities (Mateo 2002).

Among ground-dwelling squirrels in particular, social systems alone have been poor predictors of kin recognition abilities or of the mechanisms underlying recognition. For example, some species and some kin classes within species do not exhibit preferential treatment of kin, even though they have the ability to discriminate among conspecifics according to genetic relatedness (through phenotype matching—Fuller and Blaustein 1990; Holmes 1995; Mateo 2002). Likewise, evidence of kin recognition ability does not necessarily mean that an animal makes use of this ability. For example, oral gland odors of golden-mantled

ground squirrels, *S. lateralis*, also are kin distinct and can be used to discriminate among kin (Mateo 2002), even though this species shows no evidence of nepotistic behaviors except between mothers and their dependent young (Michener 1983). These recognition abilities might function in contexts other than nepotism.

Kin recognition and mate choice.—Kin recognition mediates nepotistic behaviors (dispensing benefits only to close kin), mate choice decisions (optimizing costs and benefits of inbreeding and outbreeding), or both (Bateson 1983; Hepper 1991a; Sherman et al. 1997; Shields 1982). Given the predominance of male natal dispersal among rodents, it has been argued that additional mechanisms of inbreeding avoidance (i.e., recognizing kin) are unnecessary (Blaustein et al. 1987; Dewsbury 1988a; Dobson 1982; Faulkes and Bennett 2001; Ferkin et al. 1992; Holekamp 1983), yet few data are available to support this prediction (cf. Hoogland 1995; Potts et al. 1991; Pusey and Wolf 1996). Males also might remain where they mate year after year and thus run the risk of mating with their daughters (Davis and Murie 1985; Hoogland 1995; Murie and Harris 1984; J. M. Mateo, in litt.), and males might return to their natal area several years after dispersing, again creating a potential need for recognizing kin during mating. Future studies could focus on how kin recognition abilities influence mate choice behaviors, including choice among distantly related kin (e.g., Ryan and Lacy 2003). Although it has been argued that all kin recognition mechanisms are organized similarly (Sherman et al. 1997), for most species, it is unknown whether there are commonalities in mechanisms they use for nepotism and mate choice. Kin recognition abilities of *S. lateralis* (Mateo 2002), for example, a nonnepotistic species, might function in inbreeding avoidance, even though males disperse from their natal area (Michener 1983).

Other functions of social recognition.— Recognition through phenotype matching might be used to assess relatedness among both nonkin and kin. If recognition templates are continually updated, then animals could learn traits of nonkin later in life and subsequently be able to identify relatives of those nonkin. Such recognition abilities have been demonstrated in mice and beavers (Aldhous 1989; Porter 1988; Sun and Müller-Schwarze 1997). Phenotype-matching abilities of Belding's ground squirrels also can be extended to nonkin: after becoming familiar with a group of unrelated conspecifics, *S. beldingi* discriminated among odors of that group's relatives (Holmes 1986b; J. M. Mateo, in litt.). That a variety of species can discriminate among unrelated animals suggests that recognition templates of adults can be updated, and perhaps need to be (Mateo and Johnston 2000b), well after young leave the natal nest. Phenotype matching among nonkin might facilitate social relationships within a colony (Hare 1992), formation of winter groups of communally nesting rodents (Wolff 1985), and recruitment of dispersing young into new groups (Holekamp 1983).

Ability to discriminate among conspecifics according to genetic relatedness might function for (and in some cases might have evolved for—Grafen 1990) recognition at other social levels, facilitating discrimination among species, populations, or individuals (Colgan 1983). Indeed, if genetic similarity changes predictably along these organizational levels, then a single heritable recognition cue can mediate recognition at each level (Heth and Todrank 2000). This could be especially true of mammalian odors that are often complex mixtures of several to hundreds of compounds (Albone 1984). In addition to indicating an animal's identity, an odor could reveal its sex, reproductive status, health, or even location (Brown and Macdonald 1985; Ferkin and Johnston 1993; Ferkin et al. 1994; Harris and Murie 1984; Kavaliers et al. 1997; Penn and Potts 1998). The meaning of cues across multiple social contexts is a relatively unknown area of animal communication.

Future directions.—Most empirical studies of kin recognition in rodents have focused on olfactory discrimination of conspecifics (Table 1). Relatedness potentially could be assessed through other modalities, such as vibrational signaling (Randall 1993), visual behavioral cues (Michener 1973), or vocalizations (Hare 1998a; see also Insley 2001; Rendall et al. 1996). Although phenotype matching would be difficult if production cues do not vary predictably with kinship (e.g., foot-drumming signatures—Randall 1993), such cues could be used for recognition when prior association correlates with relatedness, such as for parent–offspring recognition. Future work should address the potential for other modalities to mediate recognition, such as ultrasonic vocalizations (e.g., Balcombe 1990; Scherrer and Wilkinson 1993), and whether there are multiple, overlapping cues to identity. The use of multiple modalities might simply be redundant or could indicate differential importance in varying contexts. Likewise, most research has focused on direct mechanisms of recognition, yet there might be instances when indirect spatial cues suffice for kin recognition. This might be expected in short-lived, sedentary species with little overlap of generations or in species with restricted dispersal.

Our understanding of rodent kin recognition is far from complete (Table 1). For many species, kin recognition is inferred through population structure, inbreeding avoidance, or settlement patterns, but we know little about their actual recognition abilities. For other species, we have extensive information about mechanisms underlying their recognition abilities but do not yet know contexts in which recognition is expressed. Future studies should target particular gaps in our knowledge, such as production and perception of recognition cues in *Microtus* (to determine whether voles indeed cannot discriminate on the basis of relatedness); frequency of kin interactions in relatively solitary species such as *Aplodontia rufa*, *Erethizon dorsatum*, or *Agouti*

paca; potential for kin-differentiated behaviors in large rodents that live in 1-male groups (e.g., *Myocastor coypus*, *Lagostomus maximus*, *Hydrochoerus hydrochaeris*); or recognition in closely related species that vary in sociality (e.g., *Ctenomys*—Lacey and Wieczorek 2003; Lacey et al. 1997, 1998). These comparative studies would allow us to relate demographic traits such as longevity, reproductive rates, dispersal, and overlap of generations to the presence of kin associations (Lambin and Yoccoz-Nigel 1998) and thus contexts in which kin recognition is or is not expressed. With such information, we could determine whether an absence of behavioral discrimination is due to lack of recognition (no discrimination among kin classes), demographic patterns such as dispersal or mortality (nepotism or inbreeding avoidance are not socially possible), or evolutionary reasons (fitness benefits do not outweigh costs of nepotism or inbreeding avoidance).

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