

# Kin-recognition abilities and nepotism as a function of sociality

Jill M. Mateo

Department of Psychology, Uris Hall, Cornell University, Ithaca, NY 14853-7601, USA (jmm52@cornell.edu)

Despite widespread interest in kin selection and nepotism, relatively little is known about the perceptual abilities of animals to recognize their relatives. Here I show that a highly nepotistic species, Belding's ground squirrels (*Spermophilus beldingi*), produces odours from at least two sources that correlate with relatedness ('kin labels'), and that ground squirrels can use these odours to make accurate discriminations among never before encountered ('unfamiliar') kin. Recognition odours appear to vary linearly with relatedness, rather than in an all-or-none fashion, allowing precise estimates of kinship even among distant relatives. Thus *S. beldingi* are able to recognize their distant kin and male kin, even though they do not treat them preferentially. I also show that a closely related species (*S. lateralis*) similarly produces kin labels and discriminates among kin, although it shows no evidence of kin-directed behaviour. Thus, contrary to a commonly held assumption, kin favouritism and recognition abilities can evolve independently, depending on variation in the costs and benefits of nepotism for a given species.

**Keywords:** kin discrimination; kin recognition; nepotism; ground squirrels; olfactory behaviour

## 1. INTRODUCTION

Since Hamilton's seminal work on inclusive-fitness theory (Hamilton 1964), significant advances have been made in understanding the functions of kin recognition in facilitating nepotism (preferential treatment of kin) and mate choice (Bateson 1983; Hepper 1991; Sherman *et al.* 1997). However, the mechanisms by which animals discriminate conspecifics based on correlates of genetic relatedness remain largely enigmatic (Sherman *et al.* 1997). For example, nepotism among closely related female kin ('close' kin), but not distant kin or male kin, has been well documented in Belding's ground squirrels (*Spermophilus beldingi*; Sherman (1977, 1980, 1981)), yet the sensory and perceptual mechanisms by which they recognize relatives are unknown.

Kin recognition is the process of assessing genetic relatedness; recognition is inferred through kin discrimination, or differential treatment of conspecifics based on cues that correlate with relatedness (Gamboa *et al.* 1991). Kin-recognition systems involve three components: the production of kin labels, the perception of these labels by another individual and their similarity to that individual's learned recognition template (these two components comprising the mechanism of recognition), and the action or behaviours taken, if any, by the individual (e.g. nepotism, inbreeding avoidance (Holmes & Sherman 1982; Beecher 1988; Reeve 1989; Gamboa *et al.* 1991; Sherman *et al.* 1997)).

Kin recognition in *S. beldingi* is mediated by at least two mechanisms (Holmes & Sherman 1982). First, animals can learn the phenotypes of related individuals during early development (e.g. siblings), and later discriminate these familiar relatives from unfamiliar animals ('prior association'). Second, animals can learn their own phenotypes and/or those of their familiar kin, and later compare or match the phenotypes of unknown animals with this learned template ('phenotype matching'). Although both mechanisms involve a comparison between encountered

phenotypes and recognition templates, prior association leads to recognition of previously encountered familiar individuals, whereas phenotype matching permits 'recognition' of unfamiliar kin, through generalization of learned recognition templates (Holmes & Sherman 1982; Sherman *et al.* 1997). This distinction has implications for the evolution of kin-directed behaviours because phenotype matching permits more refined kin-differentiated behaviours than prior association, such as nepotism directed towards previously unfamiliar kin or discrimination among equally familiar full and half maternal siblings.

Nepotism is favoured when Hamilton's rule,  $rb - c > 0$ , is satisfied, where  $r$  is the coefficient of relatedness between two individuals,  $b$  is the benefit to the recipient and  $c$  is the cost to the actor (Hamilton 1964). A lack of behavioural discrimination, therefore, may be due to a lack of recognition ability (a mechanistic explanation) or to a failure to satisfy Hamilton's rule (an evolutionary explanation). Sherman proposed that *S. beldingi* do not behave nepotistically towards distant kin, such as aunts or cousins (e.g. through cooperative territory defence or alarm-call production), either because they have not evolved the ability to recognize distant kin or because Hamilton's rule is not satisfied (benefits do not outweigh costs (Sherman 1980, 1981)). These alternatives have not been tested, despite their implications for the evolution of nepotism in this and other species. To assess whether limits of nepotism in *S. beldingi* reflect a lack of recognition or a failure to satisfy Hamilton's rule, I evaluated their production of kin labels and their ability to discriminate among cues of unfamiliar kin. I conducted odour-discrimination tests with groups of temporarily captive ground squirrels housed in one of four large, outdoor enclosures. I focused on odours from oral and dorsal glands because these cues are individually distinct and are used in scent-marking behaviours (J. M. Mateo, unpublished data), and because they have been implicated in social recognition (particularly through nasal investi-

gations of the oral gland (Kivitt *et al.* 1976)). Both oral and dorsal glands are apocrine glands (Kivitt *et al.* 1976), but it is unknown if their odours are similar chemically.

Kin-recognition theory predicts that selection will drive the elaboration of recognition components, 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; Pfennig 1999). Thus, species that are not nepotistic may not produce kin labels or they may not have the ability to discriminate among them. Therefore I also examined the recognition system of golden-mantled ground squirrels (*S. lateralis*), an asocial species that shows no evidence of nepotistic behaviour except between mothers and their dependent young (Michener 1983).

## 2. METHODS

### (a) *Study species*

Belding's ground squirrels are group-living, burrowing rodents found in alpine and subalpine regions of the western USA (Jenkins & Eshelman 1984). They are socially active above ground between April and August and hibernate for the remainder of the year. Each mother produces one litter annually of 5 to 8 pups, which is reared for 25 to 28 days in an underground burrow (the natal burrow). Young first come above ground (emerge) as nearly weaned, four-week-old juveniles (Sherman & Morton 1984). Because mothers nest in equal proximity to close and distant kin (Sherman 1980), the juveniles emerge into a social environment that includes unfamiliar juveniles and adults who vary in genetic relatedness. Two to three weeks after natal emergence, juvenile females establish their own burrow system within 25 m of their natal burrow, whereas juvenile males begin to disperse permanently from their birthplace (Holekamp 1984). Golden-mantled ground squirrels are sympatric with *S. beldingi* throughout most of its range and show similar seasonal patterns (Michener 1983; J. M. Mateo, personal observation). In addition, *S. lateralis* have oral and dorsal glands and exhibit scent-marking and nasal-investigation behaviours that resemble *S. beldingi*'s (but at a lower rate; Kivitt *et al.* 1976; J. M. Mateo, personal observation).

### (b) *Animal housing*

Ground squirrels were studied at the Sierra Nevada Aquatic Research Laboratory (SNARL; near Mammoth Lakes, CA, USA). Pregnant females were live-trapped and housed in a laboratory building at SNARL where they gave birth and reared their young (see Mateo & Holmes (1997) for details). Litters probably comprised maternal full- and half-siblings because of multiple mating by females (Schwagmeyer 1990). When the young were 25–28 days of age, they and their mothers were transferred to outdoor enclosures at SNARL (three to four litters per enclosure) to serve as subjects or donors for odour tests. Individuals within an enclosure moved about and interacted freely. Each 10 × 10 × 2 m<sup>3</sup> open-air enclosure included natural vegetation, laboratory food and water, and four buried nestboxes connected to the surface by plastic tunnels.

Juveniles (more than 50 days old) served as subjects, and both juveniles and adults served as odour donors (see § 2c). Adult female donors had ceased lactating two weeks or more before the tests. Some *S. beldingi* were collected from a site where they have been observed and marked since 1992. Therefore maternal relatedness of some kin was known with certainty (e.g. grand-

mother, sibling, half-aunt), as juveniles are marked within 48 h of their natal emergence and before they start mixing with other juveniles. Paternal half-siblings ( $n = 8$ ) resulted from controlled matings in captivity (one male mated with two females collected more than 100 m apart and were therefore presumed to be not closely related; J. M. Mateo, personal observation); thus  $r = 0.25$ . Half-aunts (mother's non-littermate sisters) were collected from the field and were probably sired by males different from the mother's sire (Sherman 1980); thus  $r = 0.125$ . Because of multiple paternity in *Spermophilus* (Schwagmeyer 1990), relatedness among non-descendent kin was unknown. Therefore the coefficients of relatedness for three-quarter siblings (offspring of two sisters mated with the same male), aunts (mother's littermate sisters) and cousins (offspring of the referent's mother's brother) are averages of calculations assuming individuals were full siblings or half-siblings. Animals were maintained on similar diets for one week or more before testing to minimize environmental variation in odours. Details of trapping, marking and housing animals are in Mateo & Holmes (1997).

### (c) *Odour-testing methods*

Odours were collected from donors on 1 cm<sup>3</sup> polyethylene cubes 15 min or less before use. Secretions were collected by rubbing a cube eight times anterior–posteriorly along both mouth corners or cephalo–caudally along the dorsal-gland field. For tests, cubes were placed at each of the four burrow entrances in the enclosure for simultaneous investigation by all animals in the enclosure. Although more than one animal could investigate a set of cubes at a given time, the presence of conspecifics did not make ground squirrels more or less likely to investigate cubes, nor did it influence their duration of investigation (J. M. Mateo, unpublished data). In addition, animals typically re-emerged from burrows one by one after cube placement, and the majority of investigations occurred during this initial emergence. The total number of contacts each subject made with each cube (subject's nose within 1 cm of a cube) and the total duration of contact (time spent smelling or licking an odour) were recorded during 30 min test periods. Observers were blind to the identity of odour donors. Although some subjects were involved in more than one test (see § 2e), statistical comparisons were made only within tests and thus the data are considered independent.

### (d) *Odour-production experiments*

First, it was tested whether ground squirrels produce kin labels that are more similar among close than distant kin and thus convey information about relatedness. I used an habituation–discrimination task in which subjects were presented with an odour from an unrelated individual (the 'referent') for 3 to 4 habituation trials, and then tested with odours from several individuals varying in relatedness to the referent (discrimination trials). Odour donors and subjects lived in separate enclosures. Due to distances between where they were trapped (more than 100 m), subjects were unlikely to have been closely related to the odour donors (J. M. Mateo, unpublished data), and therefore were unfamiliar with and unrelated to the odour donors. All trials were separated by 24 h. During habituation trials, an unscented cube was presented along with the cube containing the referent's odour, to verify that subjects habituated to the odour rather than the cubes. Subjects smelled the scented cube significantly longer than the unscented cubes during the first 2 to 3 habituation trials, and were considered habituated to the

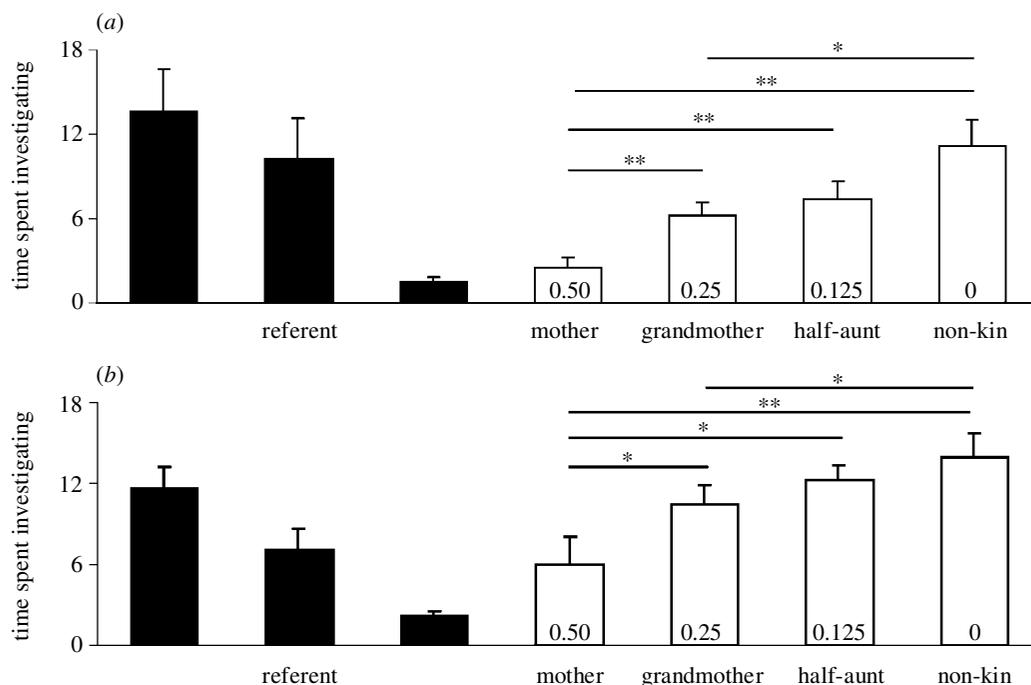


Figure 1. Duration of investigation (mean (s) + s.e.) of odours by subjects in habituation–discrimination tasks. Black bars represent investigation of the referent odour (three habituation trials) and open bars represent investigation of test odours (discrimination phase), collected from the referent’s mother, maternal grandmother, half-aunt (mother’s half-sister) and non-kin. (a) Test of *Spermophilus beldingi* dorsal-gland odours. (b) Test of *S. beldingi* oral-gland odours. The numbers inside the bars are estimated coefficients of relatedness between the referent and test-odour donor. Horizontal bars and asterisks represent significant differences in investigation of odours ( $*p < 0.05$ ,  $**p < 0.01$ ) based on repeated-measures ANOVAs. Although not depicted, in both studies investigations of test odours were significantly longer than investigation of the referent odour during its last presentation in the habituation phase. Two additional habituation–discrimination tests, using *S. beldingi* oral and dorsal odours from a referent’s full sibling, three-quarter sibling (offspring of two sisters mated with the same male), cousin (offspring of the referent’s mother’s brother) and non-kin yielded similar results.

scent when they did not smell the cubes differentially (detailed data on investigation of unscented cubes are not presented). After the habituation trials, test odours were presented during two discrimination trials, two odours at one time in a balanced order, with the habituation odour presented *ca.* 18 h after the first test trial to ‘remind’ subjects of the appropriate referent.

The perceived dissimilarity of test stimuli, relative to the referent’s odour, is reflected in the magnitude of the response differences to the test odours, because novel stimuli are usually attended to more than familiar stimuli (Johnston 1981; Smith 1983; Halpin 1986; Stoddard 1996; Mateo & Johnston 2000b). Thus, if odour differences correlate with genetic differences, then as test-odour donors become less related to the referent, their odours should be less similar to the referent’s, and therefore should be investigated more by subjects. Because subjects were unrelated to and unfamiliar with the odour donors, subjects could only use the qualities of the odours themselves to discriminate among them. After investigation, durations were log transformed and tested for normality with Kolmogorov–Smirnov tests, repeated-measures ANOVA and two-tailed general linear contrasts were used to compare data from the discrimination trials and the final habituation trial. Partial correlations controlled for test-order effects when necessary. For each habituation–discrimination task (e.g. figure 1a), a group of enclosure-housed *S. beldingi* ( $n = 23–24$ ) served as subjects. Animals were included in the analysis if they investigated at least one cube during each of the habituation and discrimination

trials. Each individual was used as a subject in only one habituation–discrimination task.

#### (e) Odour-perception experiments

To determine if ground squirrels can discriminate among classes of their own unfamiliar kin, I used preference tasks in which two to three odours were presented simultaneously to juveniles living in enclosures during a one-trial test ( $n = 7–10$  juveniles per test living in one enclosure). If odours of non-kin match juveniles’ recognition templates less than odours of distant kin, then non-kin odours should be perceived as more novel and investigated longer than distant-kin odours (Johnston 1981; Smith 1983; Halpin 1986; Stoddard 1996; Mateo & Johnston 2000b). Juveniles were tested with odours from their own unfamiliar kin, and each individual was a subject in one (figure 2c) or two (figure 2a,b; figure 3b,c) preference tasks. Juveniles, which were related to the odour donors, were housed with other unrelated litters to provide species-typical social experiences and to expose the subjects to a range of conspecific odours. Animals were included in the analyses if they investigated at least one cube. Odour donors lived in enclosures separate from the juveniles. Differential investigation of classes of odours, such as kin versus non-kin, indicated spontaneous discrimination of the odours and reflected the animals’ perceptual abilities to assess correlates of relatedness and ‘recognize’ unfamiliar kin. These data were log transformed (and verified for normalization with Kolmogorov–Smirnov tests) and analysed with two-tailed

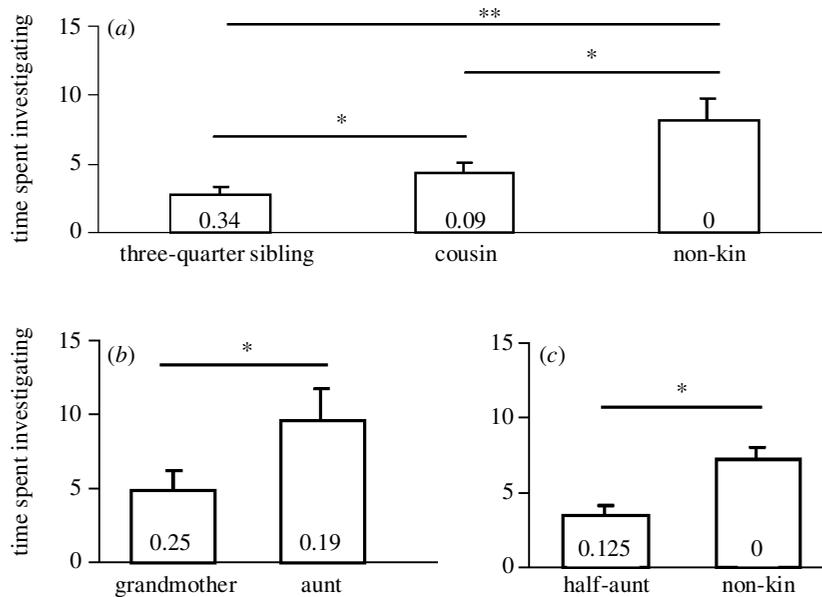


Figure 2. Duration of investigation (mean (s) + s.e.) of *Spermophilus beldingi* odours collected from subjects' unfamiliar kin during preference tasks. (a) Investigation of oral-gland odours of unfamiliar kin, collected from subjects' three-quarter sibling (offspring of two sisters mated with the same male), cousin (offspring of the subjects' mother's brother) and non-kin. (b) Investigation of oral odours collected from subjects' grandmother and aunt. (c) Investigation of dorsal-gland odours collected from subjects' half-aunt (mother's half-sister) and non-kin. The numbers inside the bars are estimated coefficients of relatedness between subjects and odour donors. Horizontal bars and asterisks represent significant differences in investigation of odours ( $*p < 0.05$ ,  $**p < 0.01$ ) based on repeated-measures ANOVAs or paired *t*-tests.

dependent *t*-tests or repeated-measures ANOVAs and two-tailed general linear contrasts.

#### (f) *Comparative analysis of kin discrimination abilities*

The habituation–discrimination task and preference task were also used to determine if *S. lateralis* produce kin labels and if they can discriminate among odours of their kin. I did not use *S. lateralis* as subjects for the habituation–discrimination task because a lack of discrimination could have been due to a lack of differential odour production (no kin labels) or to a lack of discrimination abilities (perceptual deficit). In addition, preliminary data suggested few *S. lateralis* would investigate cubes repeatedly over a 5 to 6 day testing period. Because *S. beldingi* have the ability to discriminate among their own kin labels (figure 1*a,b*), I used them as subjects in the habituation–discrimination task with *S. lateralis* odours. Those data indicated that *S. lateralis* do produce kin labels (figure 3*a*), so I next tested *S. lateralis* with their own relatives' odours in the subsequent one-trial preference tasks (figure 3*b,c*).

### 3. RESULTS

#### (a) *Odour-production experiments*

In the habituation–discrimination task, subjects investigated *S. beldingi* dorsal odours more as relatedness of the test-odour donors to the referent decreased (*n* equals seven males, six females from four litters;  $F_{4,44} = 11.39$ ;  $p < 0.001$ ; figure 1*a*). That is, subjects perceived odours of referents' distant kin as less similar to the referent's odour than odours of its close kin. Similar results were found with oral-gland odours (*n* equals seven males, seven females from four litters;  $F_{4,52} = 11.25$ ;  $p < 0.001$ ; figure 1*b*), indicating that *S. beldingi* produce odours from at least two sources that vary with relatedness. However,

in this task subjects did not appear to discriminate between odours of individuals that were closely related to each other (e.g. referent's grandmother and half-aunt), nor did subjects discriminate between the referent's distant kin and non-kin (e.g. compare half-aunt and non-kin in figure 1*a,b*), perhaps because subjects were unrelated to the donors.

#### (b) *Odour-perception experiments*

Preference tasks were therefore used to determine if juvenile *S. beldingi* can discriminate among odours of their own unfamiliar kin, and in particular whether they could discriminate between odours of their distant kin and non-kin. In general, investigation increased as the odour donors' relatedness to the juveniles decreased. Juveniles investigated oral odours of their non-kin significantly longer than odours of their unfamiliar three-quarter sibling, whereas investigation of their unfamiliar cousin's odour was intermediate (*n* equals four males, three females from one litter; repeated-measures ANOVA  $F_{2,12} = 12.87$ ;  $p < 0.001$ ; figure 2*a*). Juveniles investigated oral odour of their aunt significantly longer than that of their grandmother as well (*n* equals four males, three females from one litter; paired  $t_6 = 3.19$ ;  $p = 0.02$ ; figure 2*b*), where coefficients of relatedness differ by only ca. 0.06. They also investigated unfamiliar dorsal-gland odours of their non-kin significantly longer than those of their half-aunt (*n* equals five males, two females from one litter; paired  $t_6 = 2.63$ ;  $p = 0.04$ ; figure 2*c*). More important, however, juveniles were able to recognize their unfamiliar distant kin ( $r \leq 0.125$ ), as they discriminated between cousin and non-kin odours (figure 2*a*) and between half-aunt and non-kin odours (figure 2*c*; compare with figure 1*a,b*).

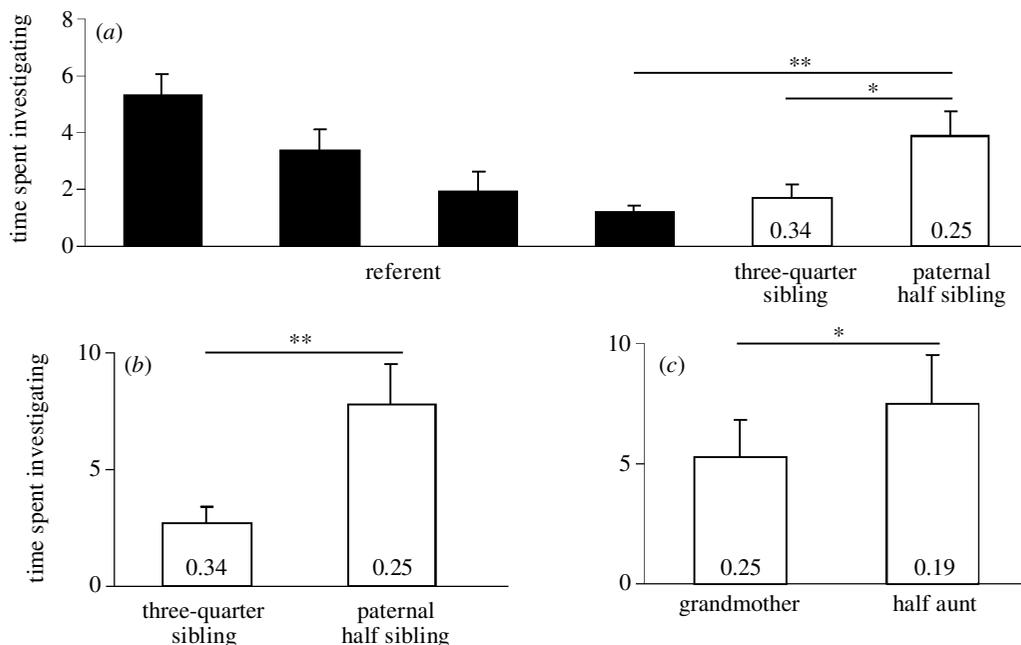


Figure 3. Duration of investigation (mean (s) + s.e.) of oral-gland odours collected from *Spermophilus lateralis*. (a) Results of test to determine if *S. lateralis* produce kin labels, using a habituation–discrimination task. The black bars represent investigation of the referent (habituation phase) odour and the open bars represent investigation of test odours (discrimination phase), collected from the referent’s three-quarter sibling (offspring of two sisters mated with the same male) and paternal half-sibling. The numbers inside the bars are estimated coefficients of relatedness between the referent and test-odour donor. Horizontal bars and asterisks represent significant differences in responses to odours ( $*p < 0.05$ ,  $**p < 0.01$ ) based on repeated-measures ANOVAs. (b,c) Results of tests to determine if *S. lateralis* are able to discriminate among odours of their unfamiliar kin, using preference tasks. (b) Investigation of odours collected from subjects’ three-quarter sibling and paternal half-sibling. (c) Investigation of odours collected from subjects’ unfamiliar grandmother and aunt (mother’s full or half-sister). In b and c, the numbers inside the bars are estimated coefficients of relatedness between subjects and odour donors. Horizontal bars and asterisks represent significant differences in investigation of pairs of odours ( $*p < 0.05$ ,  $**p < 0.01$ ) based on paired *t*-tests.

### (c) Comparative analysis of kin discrimination abilities

Contrary to the prediction that non-nepotistic species lack mechanisms for kin recognition, oral odours of *S. lateralis* do vary with relatedness. Subjects in an habituation–discrimination task investigated test odours more as relatedness of the donors to the referent decreased ( $n$  equals nine males, five females from four litters; repeated-measures ANOVA  $F_{2,24} = 7.53$ ;  $p = 0.003$ ; figure 3a). In addition, *S. lateralis* could use these odours to discriminate among their unfamiliar kin, as juveniles in preference tasks investigated odours of their paternal half-sibling significantly longer than those of their three-quarter sibling ( $n$  equals six males, five females from two litters; paired  $t_{10} = 4.82$ ;  $p < 0.001$ ; figure 3b) and odours of their aunt significantly longer than odours of their grandmother ( $n$  equals six males, six females from two litters; paired  $t_{11} = 3.03$ ;  $p = 0.01$ ; figure 3c).

## 4. DISCUSSION

Belding’s ground squirrels produce odours from at least two sources that vary with genetic relatedness (oral and dorsal apocrine glands; figure 1a,b). Such kin labels are critical for ‘recognition’ of unfamiliar relatives via phenotype matching (figure 2a–c; Holmes & Sherman 1982; Holmes 1986a,b), and the contribution of multiple odours to kin labels may facilitate more precise assessments of

relatedness than would single odours (Beecher 1988). Not only are there heritable components to *S. beldingi* recognition odours (because donors were maintained on similar diets in captivity), but the odours vary in such a way as to permit linear assessments of relatedness rather than threshold or all-or-none estimates (e.g. families sharing a common odour; see also Smith (1983) and Hepper (1987)). However, ground squirrels did not appear to discriminate between distant-kin and non-kin odours if they were unrelated to the odour donors (figure 1a,b; although a lack of discrimination does not indicate a lack of recognition (Gamboa *et al.* 1991)), suggesting that prolonged experience with close kin and/or own cues, perhaps during early development, may be necessary for precise estimates of kinship (see also Mateo & Johnston 2000a).

Although *S. beldingi* adults do not treat distant kin nepotistically (e.g. grandmothers, aunts or cousins (Sherman 1980, 1981)), they are able to recognize these individuals as relatives (figure 2a–c). Thus by comparing unfamiliar odours to their recognition templates, ground squirrels can discriminate among more kin classes than their nepotistic behaviours would suggest. These results indicate a dissociation in the evolution of recognition components, such that all *S. beldingi* kin classes produce discriminable cues, but only close kin are recipients of nepotism. In addition, sex differences in nepotism (only females behave nepotistically) cannot be explained by sex differences in discrimination abilities. I used both males

and females as subjects (this study) and as odour donors (Mateo & Johnston 2000b; J. M. Mateo, unpublished data), and I found that males, like females, produce kin labels and can recognize their kin. This suggests a further dissociation in the components, because males are not treated nepotistically, nor do they act nepotistically (see also Holmes & Sherman 1982; Holmes 1986a). Thus despite a mechanism for recognizing kin classes, decision rules for the expression of kin favouritism by *S. beldingi* differ between males and females as well as among close and distant kin (Hamilton 1964; Reeve 1989).

Golden-mantled ground squirrels (*S. lateralis*), which are closely related to *S. beldingi* but are not nepotistic, are also able to discriminate among classes of their kin (figure 3b–c). Therefore there has been a dissociation in the elaboration of *S. lateralis*' recognition components as well. They produce kin labels and have the perceptual ability to recognize kin, but neither males nor females use this recognition mechanism to treat relatives preferentially (see also Holmes 1995). The reasons for this remain a puzzle, given that *S. beldingi* and *S. lateralis* share similar ecologies, but only one species behaves nepotistically. Kin-recognition abilities in the absence of nepotism may reflect a failure to satisfy Hamilton's rule (e.g. inclusive-fitness benefit does not exceed cost of nepotism) and/or selection for inbreeding-avoidance mechanisms, even in species with sex-biased natal dispersal.

With these data, *S. beldingi* and *S. lateralis* are among the few species for which we understand both the mechanisms and functions of kin recognition mediating nepotistic behaviours. These results suggest a need to re-evaluate current thinking about nepotism, in particular the assumption that a lack of nepotism is due to a lack of recognition ability (Gamboa *et al.* 1991), and in general the expectation that sociality can be used to predict patterns of recognition abilities. Furthermore, these results should focus attention on understanding why and how recognition components become dissociated. For example, there has been much theoretical and empirical interest in why cuckolded male birds invest in unrelated young, yet few studies consider whether young birds produce kin labels or whether males can discriminate among these labels (Beecher 1988; Kempenaers & Sheldon 1996; see also Hatchwell *et al.* 2001). Such a recognition mechanism is required before preferential investment in own young can evolve. Finally, Grafen (1990) has argued that the only 'true' cases of kin recognition are those for which the mechanisms of recognition evolved specifically for that purpose. By contrast, however, my data suggest that kin-based odour production and perceptual abilities may be widespread traits in *Spermophilus*, perhaps by-products of the influence of the major histocompatibility complex on odours and the highly developed olfactory systems of rodents (Brown & MacDonald 1985; Brown & Eklund 1994; see also Gamboa *et al.* 1986), and that these traits have been co-opted for nepotistic purposes, but only in some species and among some kin classes.

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## REFERENCES

- Bateson, P. P. G. 1983 Optimal outbreeding. In *Mate choice* (ed. P. P. G. Bateson), pp. 257–277. Cambridge University Press.
- Beecher, M. D. 1988 Kin recognition in birds. *Behav. Genet.* **18**, 465–482.
- Brown, J. L. & Eklund, A. 1994 Kin recognition and the major histocompatibility complex: an integrative review. *Am. Nat.* **143**, 435–461.
- Brown, R. E. & MacDonald, D. W. 1985 *Social odours in mammals*, vol. 1. New York: Oxford University Press.
- Gamboa, G. J., Reeve, H. K. & Pfennig, D. W. 1986 The evolution and ontogeny of nestmate recognition in social wasps. *Ann. Rev. Entomol.* **31**, 431–454.
- Gamboa, G. J., Reeve, H. K. & Holmes, W. G. 1991 Conceptual issues and methodology in kin-recognition research: a critical discussion. *Ethology* **88**, 109–127.
- Grafen, A. 1990 Do animals really recognize kin? *Anim. Behav.* **39**, 42–54.
- Halpin, Z. T. 1986 Individual odors among mammals: origins and functions. *Adv. Study Behav.* **16**, 39–70.
- Hamilton, W. D. 1964 The genetical evolution of social behaviour, I. II. *J. Theor. Biol.* **7**, 1–52.
- Hatchwell, B. J., Ross, D. J., Fowlie, M. K. & McGowan, A. 2001 Kin discrimination in cooperatively breeding long-tailed tits. *Proc. R. Soc. Lond. B* **268**, 885–890.
- Hepper, P. G. 1987 The discrimination of different degrees of relatedness in the rat: evidence for a genetic identifier? *Anim. Behav.* **35**, 549–554.
- Hepper, P. G. 1991 *Kin recognition*. Cambridge University Press.
- Holekamp, K. E. 1984 Natal dispersal in Belding's ground squirrels (*Spermophilus beldingi*). *Behav. Ecol. Sociobiol.* **16**, 21–30.
- Holmes, W. G. 1986a Identification of paternal half-siblings by captive Belding's ground squirrels. *Anim. Behav.* **34**, 321–327.
- Holmes, W. G. 1986b Kin recognition by phenotype matching in female Belding's ground squirrels. *Anim. Behav.* **34**, 38–47.
- Holmes, W. G. 1995 The ontogeny of littermate preferences in juvenile golden-mantled ground squirrels: effects of rearing and relatedness. *Anim. Behav.* **50**, 309–322.
- Holmes, W. G. & Sherman, P. W. 1982 The ontogeny of kin recognition in two species of ground squirrels. *Am. Zool.* **22**, 491–517.
- Jenkins, S. H. & Eshelman, B. D. 1984 *Spermophilus beldingi*. *Mammalian Species* **221**, 1–8.
- Johnston, R. E. 1981 Attraction to odors in hamsters: an evaluation of methods. *J. Comp. Physiol. Psychol.* **95**, 951–960.
- Kempenaers, B. & Sheldon, B. C. 1996 Why do male birds not discriminate between their own and extra-pair offspring? *Anim. Behav.* **51**, 1165–1173.
- Kivitt, V. K., Murie, J. O. & Steiner, A. L. 1976 A comparative study of scent-gland location and related behavior in some northwestern nearctic ground squirrel species (Sciuridae): an evolutionary approach. *Can. J. Zool.* **54**, 1294–1306.
- Mateo, J. M. & Holmes, W. G. 1997 Development of alarm-call responses in Belding's ground squirrels: the role of dams. *Anim. Behav.* **54**, 509–524.
- Mateo, J. M. & Johnston, R. E. 2000a Kin recognition and the 'ampit effect': evidence of self-referent phenotype matching. *Proc. R. Soc. Lond. B* **267**, 695–700.
- Mateo, J. M. & Johnston, R. E. 2000b Retention of social recognition after hibernation in Belding's ground squirrels. *Anim. Behav.* **59**, 491–499.
- Michener, G. R. 1983 Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In

- Advances in the study of mammalian behavior* (ed. J. F. Eisenberg & D. G. Kleiman), pp. 528–572. Shippensburg, PA: American Society of Mammalogists.
- Pfennig, D. W. 1999 Cannibalistic tadpoles that pose the greatest threat to kin are most likely to discriminate kin. *Proc. R. Soc. Lond. B* **266**, 57–61.
- Reeve, H. K. 1989 The evolution of conspecific acceptance thresholds. *Am. Nat.* **133**, 407–435.
- Schwagmeyer, P. L. 1990 Ground squirrel reproductive behavior and mating competition: a comparative perspective. In *Contemporary issues in comparative psychology* (ed. D. A. Dewsbury), pp. 175–196. Sunderland, MA: Sinauer Associates.
- Sherman, P. W. 1977 Nepotism and the evolution of alarm calls. *Science* **197**, 1246–1253.
- Sherman, P. W. 1980 The limits of ground squirrel nepotism. In *Sociobiology: beyond nature/nurture?* (ed. G. W. Barlow & J. Silverberg), pp. 505–544. Boulder: Westview Press.
- Sherman, P. W. 1981 Kinship, demography, and Belding's ground squirrel nepotism. *Behav. Ecol. Sociobiol.* **8**, 251–259.
- Sherman, P. W. & Morton, M. L. 1984 Demography of Belding's ground squirrels. *Ecology* **65**, 1617–1628.
- Sherman, P. W., Reeve, H. K. & Pfennig, D. W. 1997 Recognition systems. In *Behavioural ecology: an evolutionary approach* (ed. J. R. Krebs & N. B. Davies), pp. 69–96. Oxford: Blackwell Scientific.
- Smith, B. H. 1983 Recognition of female kin by male bees through olfactory signals. *Proc. Natl Acad. Sci.* **80**, 4551–4553.
- Stoddard, P. K. 1996 Local recognition of neighbors by territorial passerines. In *Ecology and evolution of acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 356–376. Ithaca, NY: Comstock Publishing Associates.

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