



## The causal role of odours in the development of recognition templates and social preferences

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Despite decades of theoretical interest in the role of kin recognition in mate choice and nepotism, data on both the mechanisms and functions of recognition are available for only a few species. Even less common are demonstrations of direct causal links between the production and perceptual components of recognition and subsequent social preferences. Belding's ground squirrels, *Spermophilus beldingi*, produce odours that vary with kinship and can be used to discriminate classes of kin. However, the links between odours, recognition templates and differential treatment of conspecifics have not been shown empirically. Here I examined whether the manipulation of odour recognition templates influences juvenile behaviours. I induced recognition errors by exposing young to odours from a foreign mother before natal emergence. According to phenotype-matching mechanisms, developing young should incorporate all encountered odours into their kin template and later treat individuals matching the template as kin. As in previous studies, the most preferred play partners were littermates, but young also interacted preferentially with juveniles from the foreign family, whose odours were similar to the foreign mother and therefore matched their templates, compared with unfamiliar, unrelated juveniles. This preference for juveniles of the foreign family could not be due to relatedness or direct familiarity prior to emergence. Patterns of nasal investigations mirrored those of play bouts. This is a novel demonstration of a causal link between recognition cues, recognition templates and 'kin'-differentiated behaviours, and highlights the potency of social odours during development on later social dynamics.

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Significant conceptual advances have been made on the functions of kin recognition as it pertains to nepotism and mate choice in mammals, amphibians and insects (Hamilton 1964; Bateson 1983; reviewed in: Fletcher & Michener 1987; Hepper 1991). Yet, for many taxa, empirical data are available on either the functions or the mechanisms of recognition, but not both. In addition, causal links between recognition mechanisms and differential treatment of conspecifics are rarely shown. This verification is critical when considering the evolution of kin recognition in and across species (Alexander 1990; Grafen 1990). Here I explored the link between mechanisms and functions of kin recognition in Belding's ground squirrels, *Spermophilus beldingi*.

Kin recognition is an unobservable internal process of assessing genetic relatedness that is inferred from kin discrimination, the observable differential treatment of conspecifics based on cues that vary with relatedness. An understanding of kin recognition involves three components: (1) the production of unique phenotypic cues or labels, (2) the perception of these labels and their degree of correspondence with a recognition template or memory of cues

and (3) the action taken by an animal as a function of the similarity between its template and an encountered phenotype (Hamilton 1964; Beecher 1982; Sherman & Holmes 1985; Waldman 1987; Reeve 1989; Gamboa et al. 1991; Mateo 2003, 2004). Production and perception components comprise the mechanism of recognition, three types of which will be described here. In prior-association or familiarity-based recognition, animals learn the labels of related individuals during early development (e.g. siblings) and later discriminate these familiar individuals from unfamiliar animals. In phenotype matching, animals can learn their own phenotypes and/or those of their familiar kin and later compare or match the phenotypes of unknown animals to this learned template. Both of these mechanisms involve comparisons between phenotypes and templates, but familiarity leads only to recognition of familiar individuals, whereas phenotype matching, through generalization from templates, permits recognition of unfamiliar kin (Holmes & Sherman 1982; Sherman et al. 1997; Mateo 2004). Finally, in context-based recognition, discrimination is based on spatial cues, timing of births or mating exclusivity (see Mateo 2004).

Social recognition is mediated by olfactory cues in a variety of taxa (insects: Jaisson 1991; Gamboa 1996; Dani et al. 2004; amphibians: Waldman 1991; mammals: Brown & MacDonald 1985; Halpin 1986; Swaisgood et al. 1999; Beauchamp & Yamazaki 2003;

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Johnston 2003; Ables et al. 2007; fish: Olsén et al. 1998; Neff & Sherman 2003; possibly birds: Zelano & Edwards 2002; Bonadonna et al. 2003; Bonadonna & Nevitt 2004), including ground-dwelling squirrels (Kivett et al. 1976; Halpin 1984). Odours also mediate recognition in *S. beldingi*, and nasal investigations often precede social interactions. Dorsal gland odours (from a field of small apocrine glands on the back) and oral odours (from large apocrine glands in the corner of the mouth) are both individually distinct and kin distinct, and are the primary cues used for social recognition (Holmes 1984; Mateo 2002, 2006a, b).

Belding's ground squirrels are group-living rodents that are active between April and August and hibernate the remainder of the year. Each mother produces one litter annually of five to eight pups (typically multiply sired; Hanken & Sherman 1981; J. M. Mateo, personal observation), which is reared in an underground natal burrow. Young first emerge above ground as nearly weaned, 25–27-day-old juveniles (Sherman & Morton 1984; J. M. Mateo, personal observation). Females nest near both close and distant kin as well as nonkin (Sherman 1980; J. M. Mateo, personal observation), so juveniles encounter unfamiliar conspecifics that vary in relatedness. Two to three weeks after emergence, juvenile males begin to disperse, whereas females are largely philopatric (Holekamp 1984).

Female philopatry has favoured the evolution of nepotistic behaviours. Females with close kin (e.g. mothers, daughters, sisters) are more likely to give potentially fatal alarm calls than are females without close kin alive (Sherman 1977). During lactation, when females defend natal burrows against potential infanticide, they are less agonistic towards close kin than they are towards nonkin or distant kin (aunts, cousins; Sherman 1981). As adults, maternal half sisters are more agonistic than full sisters, suggesting discrimination of equally familiar littermates that vary in relatedness. The results of several studies show that this differential treatment of familiar and unfamiliar kin by *S. beldingi* is accomplished through both familiarity and phenotype matching (Holmes & Sherman 1982; Holmes 1986a, b, 1994, 1997; Mateo & Johnston 2000b; Mateo 2002). Contrary to Sherman's (1980, 1981) prediction, *S. beldingi* are able to recognize distant female kin and male kin (Mateo 2002), even though they are not treated preferentially.

Juvenile social interactions are thought to lay a foundation for adult nepotistic behaviours (Michener 1983; Holmes 1994). Play-partner preferences form shortly before and after natal emergence; *S. beldingi* juveniles prefer to play with their littermates more than they do nonlittermates, and males play more often than females. Juveniles also prefer to share sleeping burrows with littermates over nonlittermates. Continued interactions with mothers after emergence are important for crystallization of typical littermate preferences; however, kin preferences can form in a mother's absence if juveniles interact with littermates exclusively for several days after emergence, including at night. Cross-fostering halves of litters at 18 days of age significantly affects play preferences, with the highest rates of play occurring between familiar littermates, then familiar fostermates, then littermates reared apart, and finally unfamiliar nonlittermates. These data show an effect of both relatedness and familiarity on the development of play-partner preferences, but cross-fostering at 25 days of age (about 2 days before natal emergence) prevents the development of preferences, illustrating the importance of the timing of experience (Holmes 1994, 1997; Holmes & Mateo 1998). *Spermophilus beldingi* pups cross-fostered at birth to unrelated mothers can discriminate bedding and oral odours of their familiar foster mother from those of an unfamiliar, unrelated female as early as 15 days of age, based on orientation towards and olfactory investigation of the odours, thus showing an ability to detect and differentiate social odours well before emergence (J. M. Mateo, unpublished data). Therefore, experiences prior to natal emergence influence the formation of kin

preferences, but these preferences are not stable until sometime after emergence, perhaps because odours used for recognition are not fully developed until about 30 days of age (Mateo 2006a). Odour-discrimination abilities probably directly mediate kin-differentiated behaviours. For example, I found that juveniles played preferentially with their  $3/4$  siblings (offspring of two sisters that mated with the same male) over nonkin, even though both groups were unfamiliar at the start of the study, and they investigated nonkin more often than they did their  $3/4$  siblings (Mateo 2003).

Although it is likely that *S. beldingi* do use odours to recognize kin, the causal link between odours, recognition templates and differential treatment of kin classes needs to be shown empirically. I manipulated the development of odour recognition templates to examine how they influence juvenile behaviours. This approach is similar to that used with social insects, where recognition cues such as cuticular or comb wax hydrocarbons are manipulated, or nest guards are exposed to new odours and subsequent social interactions observed (e.g. Pfennig et al. 1983; Tsutsui 2004). Here, instead of changing individuals' odours, recognition errors were induced by exposing juveniles to odours from a 'foreign' family before natal emergence. According to phenotype matching, young should incorporate all odours they encounter during early development (e.g. prior to emergence) into their kin template and later treat individuals matching the template as kin (Holmes & Sherman 1982; Blaustein 1983; see also Crozier's 1987 Gestalt model of odour perception). Odours of nonkin can be incorporated into recognition templates (Holmes 1986b, 1997; Mateo 2002), so olfactory receptors are not specific to family odours.

## METHODS

### Animals

I observed ground squirrels at the Sierra Nevada Aquatic Research Laboratory (SNARL; near Mammoth Lakes, CA, U.S.A.) in the summer of 2006. The University of Chicago (protocol no. 71255) and University of California at Santa Barbara (protocol no. 532) approved this study, which adhered to standards set forth by the U.S. National Institutes of Health for animal research. I had permits from California Fish & Game and the United States Forest Service. I live-trapped pregnant females from a site in Lundy Canyon (2316 m) and housed them in a laboratory building at SNARL where they gave birth and reared their young. Because of trapping distances between females (>200 m), mothers were unlikely to have been closely related or to have mated with the same males (J. M. Mateo, unpublished observations of mating behaviours and female dispersal). Mothers were housed singly in stainless steel cages (61 × 45 × 35 cm) that included a nestbox (28 × 20 × 20 cm) fitted with a 6 cm diameter entry hole and a removable top. Females gave birth and reared their young in this nestbox, which contained wood shavings for bedding. I also provided mothers with paper towels that they took into their nestbox and shredded, creating a fluffy, full nest. I gave animals Purina mouse chow (no. 5015) and water ad libitum and occasionally supplemented the food with dandelions, vegetables and sunflower seeds. I maintained the building on a 13:11 h light:dark cycle, with temperature regulated by a combination of a heater, portable air conditioner and automatic fans. I refer to young of the year as pups prior to the age of emergence (about 30 days of age) and juveniles thereafter.

### Odour Transfers

I studied two groups of four females each and their offspring (Group 1: 15 male, 15 female juveniles total; Group 2: 13 male, 15 female juveniles); within each group, females gave birth within

24 h of each other. Within each group, I transferred odours (described below) reciprocally between two pairs of females, starting 5 days after birth and continuing every other day for 25 days. I did not begin transfers on the day of birth to avoid disturbing the recently parturient mothers. In Group 1, I transferred odours between Mom A and Mom B and between Mom C and Mom D. I used the same schema for Group 2. I refer to pairs of juveniles of Mom A (or B, C or D) as Littermates; pairs of juveniles of Mom A and Mom B are termed Indirectly Exposed (as are juveniles of Mom C and Mom D) and pairs of juveniles of Mom A and Mom C (or D) are termed Not Exposed (as are juveniles of Moms B and C or Mom D). I used a reciprocal transfer because dyadic social interactions are more likely to be influenced if both participants are exposed. For odour transfers, I rubbed two 3 cm<sup>3</sup> polyethylene cubes on a female's oral glands eight times each and two cubes on her dorsal gland field eight times each and placed the four cubes inside the nestbox of the recipient female. In addition, I transferred bedding from the middle of the donor's nest, loosely filling a 0.47-litre cup. Two days later I removed the used cubes from the nestboxes and placed fresh cubes and bedding inside; I washed cubes with hot water and unscented soap and allowed them to air dry. Two individuals not involved in data collection conducted the odour transfers. No mother ejected bedding or cubes from her nestbox after transfer. Bedding becomes compressed with movement of the mother and the pups, so addition of new bedding did not result in passive loss through the entrance of the nestbox either.

#### Observation of Social Interactions

When young were 30 day of age (when kin templates are largely formed; Holmes 1997), I transferred them and their mothers to outdoor enclosures at SNARL, with one group of four litters in each enclosure. Each 10 × 10 × 2 m open-air enclosure included natural vegetation, laboratory food (Purina mouse chow no. 5015) and water, and four buried nestboxes connected to the surface by plastic tunnels (see Figure 1 in Holmes 1994). Individuals moved about within the enclosures, above and below ground, and interacted freely as they would in the wild. I positioned each litter in the enclosure an equal distance from an Indirectly Exposed litter and a Not Exposed litter. I individually marked juveniles with a combination of hair dye (blue-black, Lady Clairol Co., Stamford, CT, U.S.A.) and coloured-vinyl discs attached to eartags (National Band & Tag Co., Newport, KY, U.S.A.). I individually marked adult females with dye and eartags. I weighed juveniles at the beginning and end of data collection, and averaged the two weights for each individual for use in data analyses, using the absolute difference in mean body weights for each pair of juveniles.

I and my assistants recorded play bouts (motor patterns including one or more of the following: nudging with nose, chasing, pouncing on, biting or chewing on, swiping or boxing with forepaws, clasping or mounting, or wrestling), agonism (long chases > 3 m, or fights with growls or squeals) and nasal investigations (nose of one individual in direct contact with the body of another; ad libitum sampling; Altmann 1974) for 14 days between 0700 and 1300 hours (one day's collection of social interaction data for both groups was suspended because of rain). A play bout had to last more than 3 s to be scored; repeated bouts by a pair were not scored unless at least 30 s had lapsed. We did not score play bouts involving three or more juveniles. Two people observed each group, allowing us to record 95% of all social interactions (Holmes 1994; Mateo 2003). Observers were blind to odour treatments of the litters. We placed plywood and hardware-cloth gazebos (76 × 61 × 46 cm), fitted with water bottles, over the burrow entrances each night after the animals were asleep. These gazebos prevented the animals from leaving their burrow in the morning. We noted the sleeping-burrow locations of each animal shortly

after all *S. beldingi* awoke and emerged above ground; once we located all animals, we removed the gazebos and began collecting social interaction data. I used multiple disc colours and dye marks for each litter to minimize the likelihood that observers would learn the identity of littermates through shared burrow use in the mornings. At the conclusion of the study, I released juveniles with their mothers at each mother's original trap location (for details on releases, see Mateo & Johnston 2000b).

#### Analyses

I used Poisson regressions (SAS v. 9.1, SAS Institute, Cary, NC, U.S.A.) to compare rates of behaviours between juvenile pairs as a function of prior odour exposure, sex of the pair and weight differences (the last two factors are known to affect rates of play; Holmes 1994; Mateo 2003). I examined independent effects of these variables on rates of play and nasal investigation by testing each variable separately while holding the other two variables constant. I used Wald tests for pairwise comparisons following significant overall regressions. Agonism was too infrequent for statistical analysis.

## RESULTS

#### Play-partner Preferences

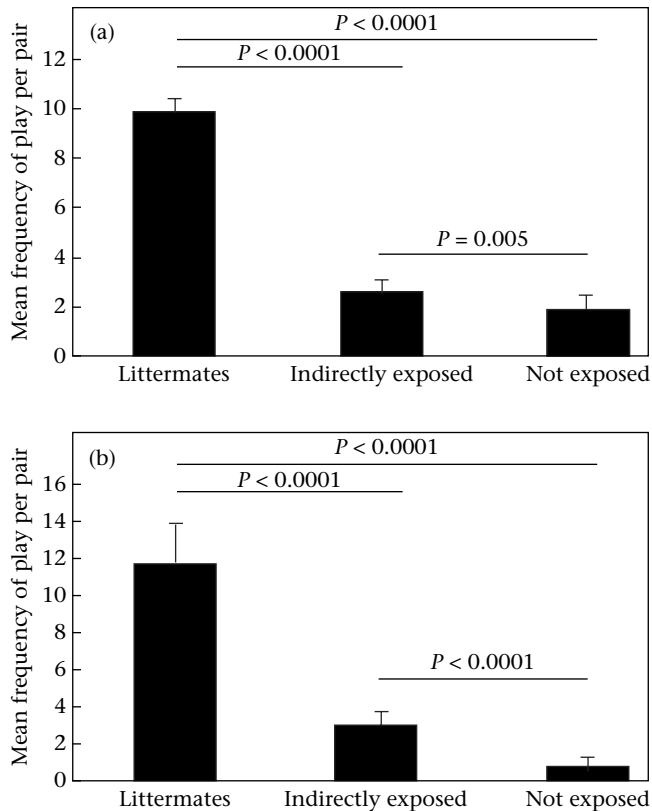
Rates of play between Group 1 juveniles were highest between Littermates, but Indirectly Exposed juveniles also played significantly more often than Not Exposed pairs of juveniles (overall likelihood ratio:  $\chi^2_2 = 393.67$ ,  $P < 0.0001$ ; Fig. 1a). The sex of the pair influenced rates of play (overall likelihood ratio:  $\chi^2_2 = 8.64$ ,  $P = 0.013$ ), with female–female pairs playing significantly less often than male–male pairs or male–female pairs (Wald comparisons:  $P = 0.005$  and  $P = 0.015$ , respectively). I found similar results for Group 2 juveniles (overall likelihood ratio:  $\chi^2_2 = 395.88$ ,  $P < 0.0001$ ; Fig. 1b), with Littermate pairs playing significantly more often than Indirectly Exposed and Not Exposed pairs, and Indirectly Exposed pairs playing together significantly more often than Not Exposed pairs. Sex also influenced rates of play in Group 2 (overall likelihood ratio:  $\chi^2_2 = 6.79$ ,  $P = 0.034$ ), with female–female pairs playing significantly less often than male–male pairs or male–female pairs (Wald comparisons:  $P = 0.028$  and  $P = 0.020$ , respectively). Weight differences between members of a pair did not influence rates of play in either group (Group 1:  $\chi^2_2 = 0.01$ ; Group 2:  $\chi^2_2 = 0.32$ ;  $P_s > 0.57$ ).

#### Nasal Investigations

Rates of nasal investigations between juveniles were similar to play rates, being lowest between Not Exposed pairs (overall likelihood ratios: Group 1:  $\chi^2_2 = 16.12$ ,  $P = 0.0003$ ; Group 2:  $\chi^2_2 = 103.41$ ,  $P < 0.0001$ ; Fig. 2). There were no significant sex differences in rates of nasal investigations (Group 1:  $\chi^2_2 = 0.32$ ; Group 2:  $\chi^2_2 = 0.24$ ;  $P_s > 0.85$ ). I found no effects of weight differences in Group 1 ( $\chi^2_2 = 0.99$ ,  $P = 0.32$ ), but in Group 2, investigations decreased as weight differences between individuals in a pair increased ( $\chi^2_2 = 7.10$ ,  $P = 0.008$ ).

#### Sleeping-partner Preferences

In Group 1, juveniles of the four litters spent 97.0%, 98.5%, 98.9% and 96.6% of their nights, respectively, with their mother in their assigned burrow. One juvenile spent two nights with its Indirectly Exposed litter, and one juvenile in another litter spent one night with them. Five juveniles spent one night each with a Not Exposed litter. In Group 2, juveniles spent 100%, 100%, 98.9% and 85.7% of

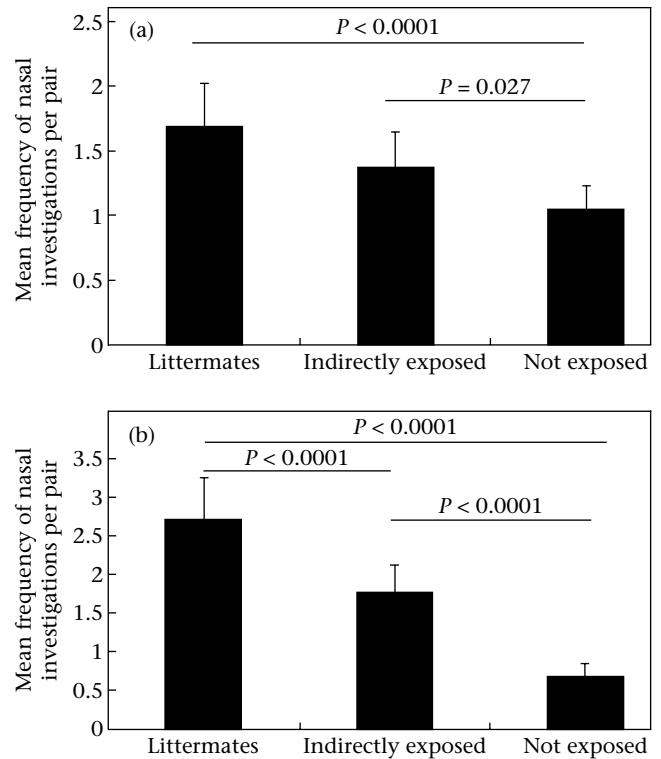


**Figure 1.** Mean frequencies (+95% confidence interval) of play between pairs of juveniles in (a) Group 1 and (b) Group 2 as a function of odour exposure. Littermate pairs were offspring of a common mother; Indirectly Exposed: juvenile pairs were reciprocally exposed to the odours of each other's mother prior to natal emergence; Not Exposed: juveniles had no prior odour experience. Horizontal bars represent differences in play frequencies based on Wald tests on pairwise group comparisons, following significant Poisson regression analyses. Mean frequencies are adjusted statistically by the regression model for effects of the sex of each juvenile in a pair and the weight difference between juveniles in each pair.

their nights with their mother in their assigned burrow. In the third litter, one juvenile spent one night with a Not Exposed litter; their mother spent the last night of the study in the burrow of a Not Exposed female. In the last litter, one juvenile spent all 14 nights with its Indirectly Exposed litter. This male played with Indirectly Exposed juveniles more often than it played with Littermates or Not Exposed juveniles ( $\bar{X} = 20.6, 7.2$  and  $0.9$  play bouts with each group, respectively).

## DISCUSSION

Although play is not considered a nepotistic behaviour, it is thought to lay a foundation for adult kin preferences and nepotism, and therefore is likely to vary with kinship (Michener 1983; Holmes 1994). Prior work has shown well-developed discrimination abilities in young *S. beldingi* (Holmes 1986a, b; Mateo 2002, 2006a) and clear play-partner preferences based on kinship and familiarity (Holmes 1994, 1997; Holmes & Mateo 1998; Mateo 2003). Play also probably solidifies recognition mechanisms that will be used in mate choice contexts, and thus, will be used by males and females to recognize all kin classes. In this study I manipulated the learned recognition templates of juveniles to determine whether early odour exposure to a foreign family, in the absence of direct prior association or relatedness, influenced patterns of juvenile social interactions.



**Figure 2.** Mean frequencies (+95% confidence interval) of nasal investigations between pairs of juveniles in (a) Group 1 and (b) Group 2 as a function of odour exposure (see Fig. 1 for definitions). Horizontal bars represent differences in investigation frequencies based on Wald tests on pairwise group comparisons, following significant Poisson regression analyses. Mean frequencies were adjusted statistically by the regression model for effects of the sex of each juvenile in a pair and the weight difference between juveniles in each pair.

As in previous studies (Holmes 1994, 1997; Holmes & Mateo 1998; Mateo 2003), juveniles in the present study played most frequently with their littermates, because littermates were most familiar and they most closely matched juveniles' recognition templates (Fig. 1). Young have more exposure to their family odours than they do to foreign odours, through direct proximity to their mother and littermates before emergence and closer association with littermates than nonlittermates after emergence. Indirectly Exposed litters played together more often than Not Exposed litters, probably because odours of the former matched juveniles' recognition templates, and thus, these animals were perceived as related according to phenotype matching mechanisms. The preference for Indirectly Exposed juveniles could not be due to relatedness or to prior direct familiarity in the natal nest. Not Exposed litters were treated as nonkin and did not play frequently, because their odours did not match templates well. Exposure to odours in the natal nest when templates are being learned and social preferences are developing was salient to young ground squirrels and facilitated a preference for individuals (or their kin; see below) bearing those odours.

Other studies with mammals have manipulated pup exposure to odours and examined subsequent odour or social preferences (e.g. Brunjes & Alberts 1979; Porter et al. 1983; Leon et al. 1987; Shah et al. 2002), but these studies used artificial odours rather than natural odours of conspecifics and thus did not test species-typical social development. Honeybee, *Apis mellifera*, guards that are briefly exposed to non-nestmate odours show an increased likelihood of allowing those non-nestmates into the hive. The plasticity of adult honeybee templates is important given the rapid turnover of hive odours that influence bee odours, but it is unclear how long new templates are maintained since the guard position is



short-lived (~1 day), nor is it clear whether other worker types also change templates (Breed et al. 2004; Couvillon et al. 2007). Hauber et al. (2000) manipulated recognition templates by changing the visual cues of isolated cowbird, *Molothrus ater*, nestlings during template formation, but they did not test the effects of this manipulation on later social preferences with functional outcomes.

In my current design, *S. beldingi* pups did not have direct contact with pups of the foreign family while in the natal nest, and they may not have had indirect contact with them either, thereby preventing incorporation of those odours into acquired templates. That is, pups became familiar with the foreign mother's odours on the cubes and in the bedding transferred into their nestboxes, but it is unclear to what extent they experienced odours of foreign pups. Young do not produce detectable oral gland odours until 21 days of age, several days before emergence, and these odours are not individually distinct until after emergence (Mateo 2006a). Pups excrete inside the nestbox, and those odours may get transferred with the bedding, but pups produce very few faecal boli and urine is not individually distinct (and it is unknown whether it is kin distinct; Mateo 2006b). Therefore, it is likely that most of the transferred odours were from the mother. As a result, upon first encounter in the enclosure, the odours of Indirectly Exposed juveniles would be unfamiliar, preventing recognition via prior association. Odours of Indirectly Exposed juveniles would therefore have to be matched to recognition templates, which included the mother of those juveniles, for evaluation of their degree of 'relatedness'. This phenotype-matching mechanism has been shown for *S. beldingi* before (Holmes 1986a, b; Mateo 2002; and for other species; e.g. Waldman 1981; Getz & Smith 1983; Porter et al. 1983; Brown et al. 1993; Mateo & Johnston 2000a; Wahaj et al. 2004; Hain & Neff 2007), as evidenced by differential treatment of maternal full and half siblings and recognition of previously unfamiliar paternal half siblings, for example. But here I provide the first evidence that such discriminations are mediated directly through recognition templates comprising odours encountered during early development (even though individuals bearing those odours were not encountered directly), and that unfamiliar kin of individuals represented in those templates are treated as kin when later encountered. Familiarity can also mediate social decisions, which probably explains why, at the proximate level, rates of play were highest among littermates. In contrast, phenotype matching would be necessary for deciding how to interact with unfamiliar individuals, particularly if the behaviour involved has functional costs.

Patterns of nasal investigation were similar to those of play, with rates higher between littermates than nonlittermates, and higher between Indirectly Exposed juveniles than Not Exposed pairs (Fig. 2). Rates of play and nasal investigation can correlate positively (Holmes & Mateo 1998) or negatively (Mateo 2003) with kinship. The reason for the different outcomes is unclear, as the same methodologies and facilities were used. Regardless, in all studies, there were significant differences in nasal investigations between groups as a function of relatedness or odour exposure, indicating discrimination of individuals based on direct cues (sensu Waldman 1987). The direction of the differences is less meaningful than is the presence or absence of differences. There were no sex differences in investigation rates after controlling for prior odour exposure and weight differences. This finding is consistent with those of previous studies on odour discrimination abilities of *S. beldingi*, in which there was no evidence of sex differences in investigation of oral or dorsal odours as a function of familiarity with or relatedness to the odour donors (Mateo 2002, 2006a, b). My results here show that both males and females use odours to guide their play behaviours as juveniles, and may continue to use odours as adults, to discriminate among conspecifics according to relatedness during mating or in nepotistic contexts.

My manipulation of the recognition template does not parallel typical *S. beldingi* development. That is, unlike the cases of brood parasites or communal nursing (e.g. Hoogland 1995; Manning et al. 1995; Andersson & Åhlund 2000; Hauber et al. 2000; Hayes 2000; Lopez-Sepulcre & Kokko 2002; Griffin & West 2003), young do not experience the odours of anyone other than their mother and littermates until after natal emergence, unless an already emerged juvenile wanders into their burrow. At Tioga Pass, CA, U.S.A., Sherman (1980) observed 6 of 173 (3.5%) newly emerged juveniles moving into another burrow over 4 years of study. At my site in Rock Creek Canyon, CA, over 15 years I have never observed a transfer (personal observation). However, that preferences could be altered illustrates the importance of odours in early social development.

Sleeping-partner preferences mirrored play-partner preferences, with juveniles spending most nights with their mother and littermates. One juvenile spent all nights in the burrow of the female to which he was indirectly exposed as a pup, and he later played more often with those juveniles than with his own littermates. Of the newly emerged juveniles that transferred burrows at Tioga Pass, Sherman (1980) observed three females as yearlings, and noted that they treated their adoptive family as kin rather than as their genetic family. Holmes & Mateo (1998) found that night-time associations with kin crystallize *S. beldingi* kin preferences, such that if mothers are removed from enclosures before nocturnal emergence, juvenile burrow use is not discriminating and littermate preferences and sleeping-partner preferences do not develop. These previous data suggest that preferences (action component) solidify after natal emergence, although it is unclear whether templates (perception component) as described here also change as a result of postemergence experiences. Templates are probably updated as the odours of littermates develop (Mateo 2006a), but new individuals should not be incorporated into them, as it would result in recognition errors and the treatment of nonkin as kin.

My results here show a causal link between odour exposure and subsequent social preferences in *S. beldingi*, because play preferences with nonlittermates could not be due to relatedness or direct familiarity prior to emergence. Rather, pups learned the odours of the foreign mother in the nestbox prior to emergence and incorporated them into their recognition templates. Later, juveniles treated individuals bearing odours similar to that mother as kin, although not as closely related as littermates. It is unknown how long Indirectly Exposed individuals would be treated as kin during their first summer, or whether the preferences would be maintained after hibernation and into adulthood (littermate but not nonkin preferences are retained after hibernation; Mateo & Johnston 2000b) and be expressed through nepotistic behaviours or mate choice preferences. These results illustrate the potency of odours on the social dynamics of *S. beldingi* and suggest that early odour experiences may be more important in other species than previously suspected. Furthermore, because recognition templates are potentially important for habitat selection, food choice, social bonds and mate preferences, understanding their development and degree of plasticity is important for conservation efforts (Reed 2004). In group-living species, social recognition can mediate cooperation, competition, mate choice and parent-offspring interactions. Although the adaptive functions of recognition are clear, how relatedness is assessed accurately is not well understood.

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