



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

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