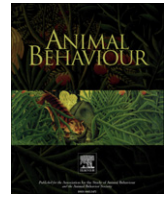




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Self-referent phenotype matching and long-term maintenance of kin recognition

Jill M. Mateo*

Department of Comparative Human Development & The Institute for Mind and Biology, The University of Chicago

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Self-referential phenotype matching, or using one's own cues as a referent for recognizing kin, is expected in species with multiple paternity or maternity to discriminate among full siblings and half-siblings, or in nepotistic contexts to accurately assess relatedness. It would also facilitate optimal inbreeding and outbreeding. Self-matching has been predicted for Belding's ground squirrels, *Urocitellus beldingi*, yet previous work could not rule out the possibility that animals use family cues rather than or in addition to their own cues for recognition. After hibernation, *U. beldingi* recognize their littermates but not previously familiar nonkin. Kin templates, including cues of mother and littermates, may be maintained throughout life, or, they may be lost during hibernation with memories of unrelated individuals, in which case self-matching must be used to create a new template in the spring. Using a cross-fostering design, these two possibilities were tested with olfactory discrimination tests after ground squirrels aroused from hibernation. Yearlings recognized their siblings, but not fostermates they had been reared with since birth, demonstrating that kin templates are lost over winter and self-matching is used to recognize kin after hibernation. Results are discussed in terms of plasticity of kin recognition systems, the costs and benefits of maintaining social memories, and the contexts in which templates are updated.

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Accurate discrimination of conspecifics according to genetic relatedness is a crucial prerequisite for nepotistic behaviours and facilitates mate choice to optimize inbreeding versus outbreeding. The adaptive significance of kin recognition in these contexts has been extensively studied (Bateson 1983; Hamilton 1987), yet complementary knowledge of the proximate mechanisms by which animals recognize kin is lacking. Kin recognition is an internal process of assessing genetic relatedness that is inferred by kin discrimination, the observable differential treatment of conspecifics based on cues that vary with relatedness. An understanding of kin recognition involves three components: the production of unique phenotypic cues, or 'labels', the perception of these labels and their degree of correspondence with a 'recognition template', or a stored representation or memory of these labels (these two components are the mechanism of recognition), and the action taken by an animal as a function of the similarity between its template and an encountered individual (Beecher 1982; Sherman & Holmes 1985; Reeve 1989; Gamboa et al. 1991; Mateo 2003, 2004). Recognition can be based on prior association, as animals learn the labels of related individuals during early development (e.g. siblings) and later discriminate these familiar individuals from

unfamiliar animals. Or, 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 (phenotype matching).

Both recognition mechanisms involve comparisons between phenotypes and templates, but prior association leads to recognition of familiar individuals only, whereas phenotype matching through generalizations from templates permits 'recognition' of unfamiliar kin (Holmes & Sherman 1982). This distinction has implications for the evolution of kin-directed behaviours because phenotype matching permits more precise discrimination than familiarity, such as discrimination of previously unfamiliar kin or discrimination among equally familiar full siblings and half-maternal siblings. Finally, in context-based recognition, discrimination is based on spatial cues, timing of births or mating exclusivity, rather than on cues of individuals themselves (Mateo 2004).

Self-referential phenotype matching, using one's own cues as a referent for recognizing kin (hereafter 'self-matching'; also dubbed the 'armpit effect' by Dawkins 1982), should be favoured in species with multiple paternity or maternity to discriminate among full siblings and half-siblings or when individuals commonly encounter older (or younger) siblings after dispersal (Holmes & Sherman 1982; Lacy & Sherman 1983; Sherman 1991). It would also be favoured in intra- and interspecific brood parasitism and communal nesting, when individuals encountered early in life might not be kin and thus would be poor referents (reviewed in

* Correspondence: J. M. Mateo, Department of Comparative Human Development & The Institute for Mind and Biology, 5730 South Woodlawn Avenue, The University of Chicago, Chicago, IL 60637, U.S.A.

E-mail address: jmateo@uchicago.edu.

Hauber & Sherman 2001; Mateo 2004). Several recent studies have described results consistent with self-matching, but their design could not rule out the use of other referents (fish: Olsén et al. 1998; Neff & Sherman 2005; Thunken et al. 2009; tadpoles: Villinger & Waldman 2008; birds: Petrie et al. 1999; Shorey et al. 2000; small mammals: Sherborne et al. 2007; primates: Alberts 1999; Smith et al. 2003; humans: Jacob et al. 2002; Platek et al. 2008).

Kin recognition abilities have been studied most broadly in rodents (reviewed in Mateo 2003), although several species in other taxa have been elegantly studied (Beecher 1988; Getz 1991; Waldman 1991; Blaustein & Waldman 1992; Gamboa 1996; Pfennig et al. 1999). Social recognition is mediated by olfactory cues in a variety of taxa (insects: Jaisson 1991; Gamboa 1996; Dani et al. 2004; Lihoreau & Rivault 2009; amphibians: Waldman 1991; mammals: Brown & MacDonald 1985; Halpin 1986; Swaisgood et al. 1999; Beauchamp & Yamazaki 2003; Johnston 2003; Brennan & Kendrick 2006; fish: Olsén et al. 1998; Neff & Sherman 2003; Ward et al. 2007; birds: Zelano & Edwards 2002; Bonadonna & Nevitt 2004; Mardon & Bonadonna 2009), including ground-dwelling squirrels (details in Mateo 2003). Odours also mediate recognition in *U. beldingi* and vary among individuals and kin classes (Holmes 1984; Mateo 2002, 2006b). In addition to indicating an animal's individual identity, sex or relatedness, an odour may also reveal an individual's location, reproductive status or even genetic quality (Brown & MacDonald 1985; Penn & Potts 1998).

Belding's ground squirrels, *Urocitellus beldingi* (Helgen et al. 2009), exhibit nepotism among certain classes of close female kin, including production of potentially risky alarm calls and cooperative defence of territories. Females with close kin (e.g. mothers, daughter, sisters) are more likely to give alarm calls than females with no close kin. During gestation and lactation, when females defend natal burrows against potential infanticide, they are less agonistic towards close kin than nonkin or distant kin (aunt, cousin). Maternal half-sisters are more agonistic than full sisters, suggesting discrimination of equally familiar littermates that vary in relatedness (Sherman 1980). They also have the potential for inbreeding, such as between fathers and daughters or siblings (J.M.M., unpublished data), again favouring accurate kin recognition. *Urocitellus beldingi* can use both familiarity and phenotype matching to recognize kin (Holmes & Sherman 1982; Holmes 1986a, b, 1997; Mateo 2002). Odours from oral and dorsal glands vary among individuals and kin classes in *U. beldingi* and mediate social recognition (Mateo 2002, 2006a).

Holmes & Sherman predicted self-matching for *U. beldingi* because these ground squirrels can discriminate between equally familiar maternal full siblings and half-siblings and between unfamiliar paternal half-siblings and unfamiliar nonkin (Holmes & Sherman 1982; Holmes 1986b), yet their data could not exclude the possibility that animals use family cues rather than or in addition to their own cues (see Mateo & Holmes 2004). It is not possible to deprive animals of experience with their own recognition cues and still observe normal behaviours, so novel experimental approaches are necessary. The cross-fostering design that Holmes and I recommended for testing self-matching (single-transfer design; Mateo & Holmes 2004) is not practical for all species, and would be difficult with *U. beldingi* because of the sample size needed and the constraints of once-per-year seasonal reproduction. A combination of cross-fostering and memory loss provides an alternative tool to test self-matching. After hibernation, *U. beldingi* no longer discriminate behaviourally between odours of previously familiar and unfamiliar nonkin, indicating that memory of familiar individuals is lost during the winter. Yet they can still discriminate between odours of littermates and nonlittermates, indicating that kin recognition abilities are maintained throughout hibernation (Mateo & Johnston 2000).

What proximate mechanism(s) underlies this kin recognition ability in the spring? First, kin templates, formed early in development and incorporating cues of mother and rearingmates, may be maintained throughout a ground squirrel's life. Perhaps there is less cost (or more of a benefit) in maintaining a kin template than in maintaining separate memories of specific individuals. Alternatively, kin templates may be lost during hibernation with memories of individuals, in which case *U. beldingi* must use self-matching to create a new template in the spring (see also Mateo 2004). Both alternatives involve matching unfamiliar cues to learned templates, but it is unknown whether animals use their close kin as referents after hibernation or whether templates are formed anew based on an individual's own odours. Here I experimentally tested the hypothesis that templates are not maintained during hibernation and are recreated each spring through self-matching.

METHODS

Animals and Housing

Belding's ground squirrels are group-living, burrowing rodents found in alpine and subalpine regions of the western United States (Jenkins & Eshelman 1984). They are socially active above ground between April and August and hibernate the remainder of the year. Each mother produces one litter annually of five to eight pups, which is reared in an underground natal burrow for 25–28 days, when young first emerge above ground (Sherman & Morton 1984). Because mothers nest in equal proximity to close and distant kin (Sherman 1980; J.M.M., unpublished data), juveniles emerge into a social environment that includes unfamiliar conspecifics that 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 from their birthplace (Holekamp 1984).

I studied ground squirrels at the Sierra Nevada Aquatic Research Laboratory (SNARL; near Mammoth Lakes, CA, U.S.A.). The University of Chicago (no. 71255) and University of California at Santa Barbara (no. 532) approved this study, which adhered to standards set forth by the U.S. National Institutes of Health for animal research and the ASAB/ABS *Guidelines for the Treatment of Animals in Behavioural Research and Teaching*. I had permits from California Fish & Game and the U.S. Forest Service. In 2007 I live-trapped pregnant females from a site in Rock Creek Canyon (group 1, see below) and Junction Campground near Yosemite National Park (group 2) and housed them in a laboratory building at SNARL where they gave birth and reared their young. Litters probably comprised full siblings and maternal half-siblings because of multiple mating by females (Hanken & Sherman 1981; J.M.M., unpublished data). I cross-fostered pups nonreciprocally among litters that were born within 24 h of each other, with halves of litters being transferred depending on litter sizes and sex ratios. Specifically, approximately two to four pups from Mother A were placed in Mother B's nestbox. At the same time, approximately two to four pups from Mother B were placed in Mother C's nestbox. Thus each mother reared both genetic and foster young ('nonreciprocal multiple transfer design'; details in Mateo & Holmes 2004). Group 1 comprised three litters (no fourth litter was born in time to be included) with 9 males and 7 females. Group 2 comprised four litters with 9 males and 13 females. Mothers readily accept newborn foster pups (Holmes & Sherman 1982; Holmes 1986b, 1997), and none were rejected in this study.

At about 25 days of age, I transferred juveniles and their mothers to large outdoor enclosures (2 litters/enclosure) so juveniles could interact with conspecifics and continue developing species-typical behaviours (Mateo & Holmes 1999; Mateo 2009). Each 10 × 10 × 2 m

open-air enclosure included natural vegetation, laboratory food and water, and four buried nestboxes connected to the surface by plastic tunnels. Animals were maintained on similar diets (Labdiet no. 5015) throughout the study to minimize environmental variation in odours. Individuals within an enclosure moved about and interacted freely. Details of trapping, marking and housing animals are in [Mateo & Holmes \(1997\)](#). Unfamiliar littermates were placed in separate enclosures so they remained unfamiliar. Unfamiliar, unrelated litters were placed in each enclosure to serve as potential social partners.

At the end of the summer, I transferred three to five juveniles from each litter, including genetic young and foster young, from the outdoor enclosures to the laboratory at SNARL for overwinter housing. The 32 juveniles also included three juveniles from the unrelated litters not involved in the fostering, which would serve as odour donors in the spring. The number of animals overwintered was limited by the number of cages available; the remaining animals were released at the site of their mother's capture. Animals were individually housed in standard plastic cages (38 × 33 × 18 cm; solid sides and bottom, wire lid) and provided with food and water until they showed signs of torpor. Animals could hear the calls and perhaps smell the odours of other individuals, but could not see or touch them. To induce hibernation, I gave animals burlap ($\approx 1.5 \text{ m}^2$ /animal) for nesting material on 20 September 2007, and adjusted the photoperiod and temperature in two steps until 9 October (from a 12:12 h light:dark cycle and 20 °C to an LD 0:24 h cycle, 4 °C; relative humidity ranged from 17 to 75%). Animals shredded the burlap to create a fluffy nest filling the cage; food and water were provided until food was no longer taken and a paper towel, placed on top of the burlap nest, was no longer disturbed. All animals began to hibernate in early November and aroused spontaneously between 7 and 26 April 2008 (terminal arousal was defined as 7 consecutive days of activity). On 24 April, I changed the light:dark cycle to an LD 9:15 h, raised the temperature to 7.2 °C, and provided the animals with food and water. Two animals died during the winter (a male from group 1 and a female from group 2; neither was cross-fostered). On 27 April, I removed the burlap nests from cages and replaced them with pine bedding and a 23 × 8 cm PVC tube for refuge; lights were set to a 12:12 h cycle.

Odour-testing Methods

Starting on 28 April 2008, I tested yearlings in their individual cages with pairs of oral gland odours. At this time animals had been active for a mean \pm SE of 9.7 ± 1.25 days (range 2–26 days) but had not interacted directly (via tactile or visual contact) with other *U. beldingi*. I collected odours from donors on 3 cm³ polyethylene cubes less than 30 min before use, by rubbing cubes eight times anteroposteriorly along both mouth corners. During tests, cubes were suspended approximately 10 cm apart from the wire lids of cages via screws inserted in the middle of each cube. One person collected the odours (to control the pressure applied and thus the amount of odour collected) and coded the cubes (while wearing latex gloves to prevent the transfer of other ground squirrel odours or human odours to the equipment or to the animals). All 30 yearlings were both tested with odours and served as odour donors (donating odours 1–11 times; $\bar{X} \pm \text{SE} = 5.20 \pm 0.476$). Yearlings were tested with three pairs of odours from: (1) a familiar sibling and a familiar fostermate, (2) an unfamiliar sibling of their fostermates and an unfamiliar nonsibling, and (3) a familiar fostermate (different donor than in test 1 whenever possible) and a familiar, unrelated yearling (which lived in the same enclosure as the subject the previous summer). Here, 'familiar' and 'unfamiliar' refer to familiarity during the juvenile summer. All 30 yearlings were tested once each day for three consecutive days (when odour donors were available), with the three pairs of odours presented in

a randomized order for each animal. Whenever possible the two odour donors within a pair were of the same sex (76 of 86 tests). We (myself and two assistants) tested three yearlings at a time, recording each test with separate Sony Digital8 HandyCam camcorders mounted on a tripod adjacent to the cages, which were placed on the laboratory floor. Investigations were recorded for 5 min; the total number of contacts made with each cube (animal's nose within 1 cm of a cube) and the total duration of contact (time spent smelling or licking an odour) were recorded by two observers blind to the identity of odour donors. Tests were rescored whenever investigation durations differed by more than 1 s.

Analyses and Predictions

Animals were included in the analysis for each test if they investigated at least one cube. Differential investigation of classes of odours, such as a familiar littermate and a familiar fostermate, indicated spontaneous discrimination of the odours. Because the data were not normally distributed and transformations were not successful, I used two-tailed normal-scores tests for analyses of investigations (duration and frequency) of the test odours. This test is similar conceptually to a paired *t* test because the difference between two matched data sets is normalized and compared against a null hypothesis that the mean difference is zero, and is more powerful than a Wilcoxon signed-ranks test for many data sets ([Darlington 1990](#)). I used Mann–Whitney *U* tests to assess sex and group differences in investigation durations and Kruskal–Wallis ANOVAs to examine potential litter effects. I present the data as unadjusted means \pm SE and consider results significant when $P < 0.05$. Two yearlings did not investigate any cubes; four yearlings did not investigate either cube in one test each. The sample sizes further varied for each test because not all yearlings had all of the necessary odour donors available (test 1: $N = 21$; test 2: $N = 24$; test 3: $N = 21$).

If kin templates are maintained over hibernation, then yearlings should still recognize their previously familiar siblings and fostermates because their odours were incorporated into templates during early development (no discrimination in test 1). Discrimination between odours of nonlittermates and either fostermates or siblings of fostermates (tests 2 and 3) would provide further evidence that kin templates were maintained. Yearlings could only achieve this discrimination through phenotype matching, generalizing from their memories of familiar fostermates' odours in their templates. Alternatively, if kin templates are lost, then yearlings must rely on their own odours for recognition (self-matching). In this case a yearling would be able to recognize its previously familiar siblings, by comparing their odours to its own (discrimination in test 1). But the yearling would no longer recognize its fostermates, despite being reared with them the previous summer, because its fostermates' odours would not be similar to its own (no discrimination in tests 2 or 3). I note that investigation of odours from various kin classes can predict differential treatment of individuals bearing those odours, such as rates of play and nasal investigation ([Mateo 2003](#)).

RESULTS

Yearlings investigated odours of their siblings significantly longer than they did odours of their fostermates, both of which they had been reared with as pups (test 1; normal-scores test: $t_{20} = 3.34$, $P = 0.003$; [Fig. 1a](#)), but there was no difference in the frequency of investigation of each cube ($t_{20} = 0.91$, $P = 0.37$; [Fig. 1b](#)). There was no significant difference in their investigation of odours from an unfamiliar sibling of their fostermate and an unfamiliar, unrelated yearling (test 2: duration, $t_{23} = 0.65$, $P = 0.52$; frequency, $t_{23} = 0.16$, $P = 0.87$). Nor did yearlings show behavioural

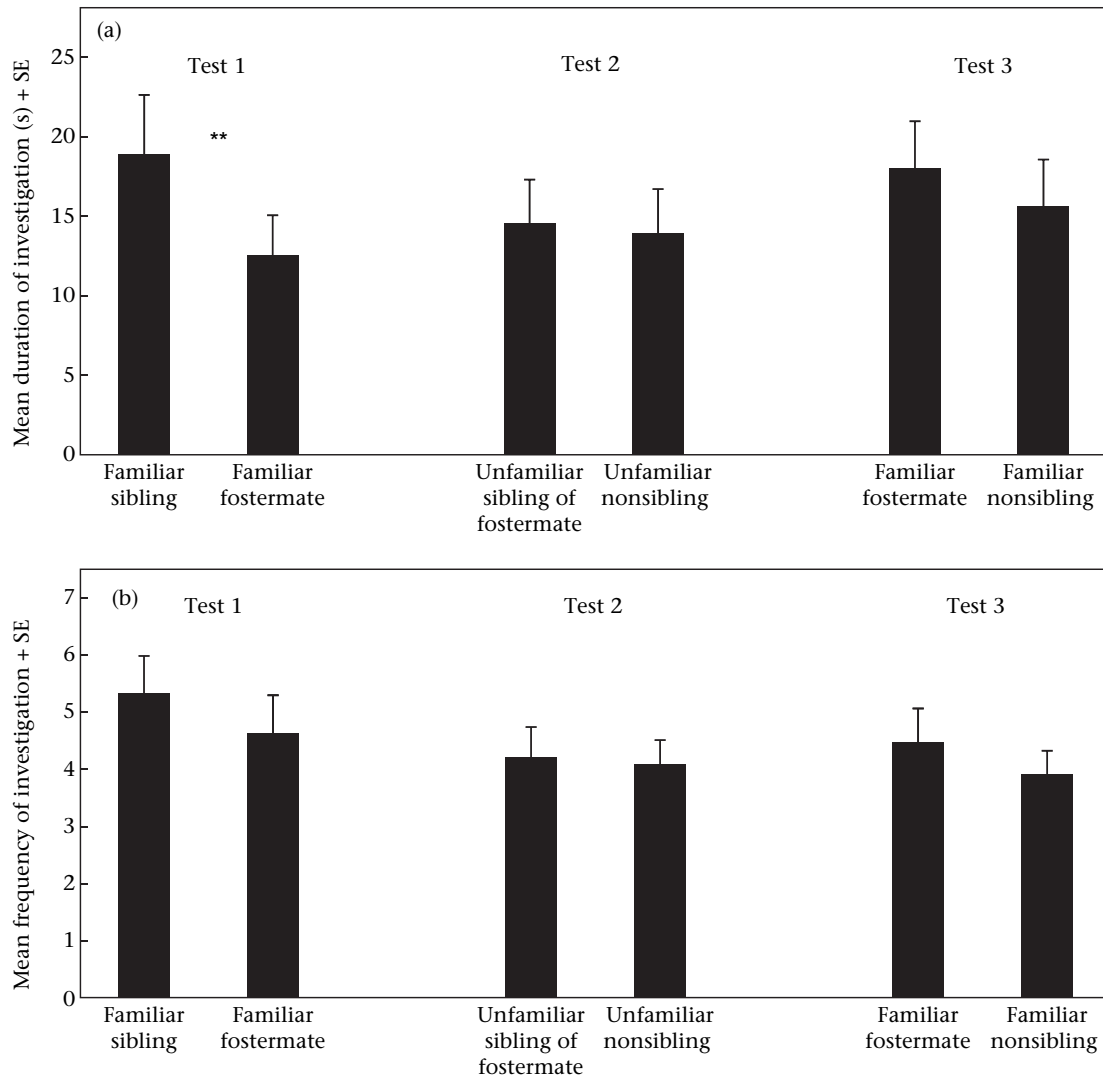


Figure 1. Mean + SE (a) duration of investigation and (b) frequency of contact with oral odours by yearling Belding's ground squirrels after emergence from hibernation. 'Familiar' and 'unfamiliar' refer to whether the odour donor and the ground squirrel were familiar with each other the previous summer. Asterisks represent a significant difference in responses to the two odour types (normal-scores tests: $P < 0.01$).

discrimination of odours of their fostermate and an unrelated yearling they had interacted with the previous summer in the outdoor enclosure (test 3: duration, $t_{20} = 0.64$, $P = 0.53$; frequency, $t_{20} = 1.25$, $P = 0.23$).

There were no sex differences in investigation durations, except for test 2, in which females investigated the odour of the unfamiliar sibling of their fostermate longer than did males (Mann–Whitney U test: $U = 111.5$, $N_1 = N_2 = 12$, $P = 0.02$). Similarly, there were no group differences in investigation durations, with the sole exception of test 2, in which group 2 yearlings investigated the unfamiliar, unrelated odour significantly longer than did group 1 yearlings ($U = 32.0$, $N_1 = 14$, $N_2 = 10$, $P = 0.03$). Within-litter variation in investigation duration was greater than between-litter variation for both cubes for all three tests (Kruskal–Wallis tests: $P_s = 0.63$ – 0.90), indicating that data from multiple individuals in a litter were independent.

DISCUSSION

This 2-year study sought to determine the mechanisms by which Belding's ground squirrels continue to recognize their kin

after a hibernation period of 7–8 months, using a combination of cross-fostering and overwintering. Earlier research on Belding's ground squirrels showed that previously familiar nonkin are no longer recognized after hibernation, but siblings are (Mateo & Johnston 2000). This could be accomplished either through retention of a kin template, or through loss of this template and use of own odours for recognition purposes. Self-referent phenotype matching involves the comparison of another individual's cues to one's own, with the degree of match indicating the degree of relatedness. In this study, yearlings discriminated between odours of their siblings and fostermates, despite having been reared with both since birth (Fig. 1a). This discrimination demonstrates that their kin templates were lost during the winter, as otherwise they would treat both odours similarly because both were equally represented in their template. Yearlings did not discriminate between odours from an unfamiliar sibling of their fostermate and an unfamiliar unrelated yearling, nor between odours from their fostermate and a yearling that they had interacted with during the previous summer similarly. These results are also consistent with the loss of recognition templates and indicate that fostermates were no longer recognized as rearingmates, and were instead

treated as unfamiliar. The self-matching recognition mechanism would not only allow *U. beldingi* to recognize previously familiar siblings in the spring, but also previously unfamiliar kin, such as cousins or paternal half-siblings that had not been encountered before.

Using self-matching to recognize kin after hibernation does not initially appear parsimonious. Rather, one might expect *U. beldingi* to retain memories of their former social partners, particularly potential mates or rivals, to interact with them more efficiently in the spring. The mating period begins a few days after females emerge from hibernation, and involves intense fighting among males and searching for mating partners by both sexes, both of which can be costly (J.M.M., personal observation). These costs could be minimized if adults recall the fighting abilities of males or the quality of opposite-sex conspecifics. That memories and templates are lost may suggest that they are too expensive to maintain during a 7–9-month period of torpor. There is ample evidence of neuronal changes during torpor and hibernation in ground squirrels, including dendritic and synaptic retraction, especially in the hippocampus (Popov & Bocharova 1992; Popov et al. 1992; von der Ohe et al. 2006). Indeed, research on learning and memory in this group has shown cognitive deficits associated with hibernation and the period just after arousal from torpor (Mateo & Johnston 2000; Millesi et al. 2001; Weltzin et al. 2006). Alternatively, rather than being too expensive to maintain, memories may fade during the winter from disuse. That is, because early rearingmates are not encountered for up to 9 months, identification of them is forgotten through passive decay (Wixted 2004).

Functionally, there are at least two explanations for why recognition templates are not maintained. First, kin selection may not favour persistent memories if kin rarely interact year after year. At Tioga Pass, CA, the likelihood that two littermate sisters will both survive hibernation and nest in the same area the following year is about 32%. The likelihood of all other pairs of female kin alive after their first hibernation is less than 20%, with rates decreasing with each year because of mortality (Sherman 1981). At my study site in Rock Creek Canyon, CA, the probability of two or more individuals in a litter being alive the next year as yearlings and living in the meadow ranges from 5 to 35% (8 birth years; J.M.M., unpublished data). *Urocyon beldingi* encounter fewer relatives each season because of predation and overwinter mortality, and since nepotism requires accurate recognition based on genetic relatedness, the use of one's own cues rather than those of kin would permit finely graded discrimination (see also Hain & Neff 2006 for an estimate of costs and benefits of self-matching in bluegill sunfish, *Lepomis macrochirus*). Second, in addition to dispensing nepotism appropriately, self-matching may facilitate identification of optimal mating partners, to avoid extreme inbreeding and outbreeding. Rates of mortality also reduce the need for long-term (> 4 months) memory of unrelated conspecifics. Furthermore, relearning of individuals' cues in the spring to reestablish familiarity may be beneficial if social relationships change (e.g. a neighbour becomes more competitive). Forgetting individuals from the prior year might confer neural advantages as well, reducing cognitive load and facilitating consolidation of new social memories (e.g. Kuhl et al. 2007).

The armpit effect involves the use of one's own cues for recognition, but does it involve the use of a template? In the spring, animals smell their own odours and match them against strangers to assess relatedness. It is not clear, however, whether they create a new template each spring, or instead match newly encountered odours to a current assessment of their own odour (called 'online processing' by Hauber & Sherman 2001). Odours of other individuals are learned and recalled (Holmes & Sherman 1982; Holmes 1984; Mateo 2006a), consistent with the formation of new

recognition templates by yearlings and adults, and parsimony would suggest that own odours would be included in this process.

The results could be interpreted as not a loss of kin templates, but rather a shift of the action component. That is, fostermates may be treated as kin during the juvenile year (e.g. Holmes 1997; Mateo 2009), but treated as nonkin during the yearling year as the acceptance threshold (Reeve 1989) becomes more restrictive. In some systems, decisions on how to treat kin classes change without any associated memory or template changes, probably because of shifts in the costs or benefits of the behaviours involved (Couvillon et al. 2008). Although the acceptance threshold in *U. beldingi* may change with age or context (e.g. juveniles show preferential treatment towards distant kin such as cousins, but as adults they do not; Sherman 1980; J.M.M., unpublished data), the experimental design used here points to a loss of the template. The preference task I used to evaluate the perception component uses differential investigation of classes of odours, such as kin versus nonkin, to indicate spontaneous discrimination of the odours, which reflects the animals' perceptual abilities to assess correlates of relatedness. That is, it quantifies what discriminations animals are capable of, rather than how they would treat individuals bearing those odours. I used this assay rather than dyadic interactions, for example, because such interactions involve the action component, and thus confound discrimination abilities with decisions about how to behave. The preference task by design does not entail any such decision, and thus does not have any fitness (or other) cost or benefit to the actor.

Whether animals maintain memories for conspecifics during extended separations such as migration or hibernation is unclear, despite widespread evidence that social relationships are maintained over long periods (Mateo & Johnston 2000). This study will further our understanding of the degree of plasticity in recognition mechanisms, such as the circumstances in which recognition templates are updated or are lost and recreated (see also Pfennig 1999). Several species of social ants and paper wasps show long-term memory of nestmates, even after overwintering, and there is some evidence that their templates, formed through an imprinting-like process, are maintained rather than formed anew each year (Ross & Gamboa 1981; Pfennig et al. 1983; Gamboa 1988; Jaisson 1991; Errard 1994; but see Dapporto et al. 2004; some memories are retained through metamorphosis: Blaustein et al. 1984; Blackiston et al. 2008). For migrating birds, it is unclear whether enduring pair bonds result from site fidelity or from recognition of the same mate each year (Black 1996); vocal recognition can persist from year to year (Godard 1991). Long-term (> 4-year) vocal recognition between mothers and offspring in northern fur seals, *Callorhinus ursinus*, is asymmetrical, although the mechanisms and functions of this recognition are not well understood (Insley 2000). Finally, 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). Knowledge of how long individuals maintain memories of familiar kin and nonkin is important for the design of captive breeding programmes and the release of endangered species into the wild, particularly if familiarity influences the formation and stability of social groups or their mating success. Phenotypic plasticity in recognition mechanisms, particularly in the perceptual components of recognition, is a potentially common occurrence that has widespread implications for social relationships.

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