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Development of Individually Distinct Recognition Cues

ABSTRACT: Despite extensive research on the functions of kin recognition, little is known about ontogenetic changes in the cues mediating such recognition. In Belding's ground squirrels, *Spermophilus beldingi*, secretions from oral glands are both individually distinct and kin distinct, and function in social recognition across many contexts. Behavioral studies of recognition and kin preferences suggest that these cues may change across development, particularly around the time of weaning and emergence from natal burrows (around 25 days of age). I used an habituation-discrimination task with captive *S. beldingi*, presenting subjects with odors collected from a pair of pups at several ages across early development. I found that at 21 days of age, but not at 7 or 14, young produce detectable odors. Odors are not individually distinct, however, until 28 days of age, after young have emerged from their burrows and begun foraging. In addition, an individual's odor continues to develop after emergence: odors produced by an individual at 20 and 40 days of age are perceived as dissimilar, yet odors produced at 28 and 40 days are treated as similar. Developmental changes in odors provide a proximate explanation for why *S. beldingi* littermate preferences are not consolidated until after natal emergence, and demonstrate that conspecifics must update their recognition templates as young develop. © 2006 Wiley Periodicals, Inc. *Dev Psychobiol* 48: 508–519, 2006.

Keywords: development; kin recognition; kin labels; odors; olfactory behavior; rodents; Belding's ground squirrels; *Spermophilus beldingi*

INTRODUCTION

Recognition of conspecifics is mediated through olfactory cues in a variety of taxa (insects: Gamboa, 1996; Jaisson, 1991; amphibians: Waldman, 1991; mammals: Beauchamp & Yamazaki, 2003; Brown & MacDonald, 1985; Halpin, 1986; Johnston, 1990; Swaisgood, Lindburg, & Zhou, 1999; fish: Neff & Sherman, 2003; Olsén, Grahn, Lohm, & Langefors, 1998; perhaps birds: Bonadonna, Hesters, & Jouventin, 2003; Zelano & Edwards, 2002), including many sciurids (details in Halpin, 1984; Kivett, Murie, & Steiner, 1976). Odor cues mediate social recognition in *Spermophilus beldingi*, and can be used to discriminate individuals, kin classes, and sexes (Holmes, 1984; Mateo, 2002, 2006). Individually distinct cues are useful when animals interact repeatedly over time

and when discrimination among multiple familiar individuals is beneficial, such as in parental care, reciprocal altruism, or dominance hierarchies (e.g., Bergman, Beehner, Cheney, & Seyfarth, 2003; Colgan, 1983; Trivers, 1971). Individual recognition is defined here as a cognitive process (without implying any level of processing or awareness) whereby an animal becomes familiar with a conspecific and later discriminates it (or its cues) from other familiar individuals. Recognition is based on unique features of individuals learned through direct experience with those cues and associated with memories of prior interactions with those individuals, rather than based on simple differences in familiarity (Mateo, 2004).

Social recognition processes can be thought of as comprising three components: the production of cues that can be used for recognition (such as unique odors, plumage patterns, or vocalizations); the perception of these cues by other animals, in particular how these cues correspond with a stored memory of familiar individuals' cues (a "recognition template"); and the action taken by an animal if an individual's cues do or do not match its template (see Mateo, 2004). The particular action taken

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can depend on the degree of relatedness between the two individuals (e.g., kin versus nonkin, or classes of kinship) or their degree of familiarity (e.g., neighbor versus non-neighbor), as well as the costs or benefits of the actions. An apparent absence of recognition can be due to proximate factors (lack of production or perception components that together comprise the mechanism of recognition), ultimate factors (lack of action component favoring differential treatment of individuals), or both.

Accurate recognition is essential for parent–offspring relationships, yet there are many examples of parents who invest in young that are not their own, such as in cases of communal nursing, brood parasitism, and extra-pair paternity. Not only must the evolutionary costs and benefits of parent–offspring recognition “failures” be addressed (reviewed in Beecher, 1991; Holmes, 1990; Komdeur & Hatchwell, 1999), but one must also consider the mechanisms underlying such apparent lack of recognition, in particular the nature and development of cues to identity. For example, there has been much theoretical and empirical interest in why cuckolded male birds invest in unrelated young, yet few studies investigate whether young birds even produce kin labels in any modality or whether males can discriminate among these labels (Beecher, 1988; Bouwman, Lessells, & Komdeur, 2005; Kempnaers & Sheldon, 1996; see also Hatchwell, Ross, Fowlie, & McGowan, 2001). Such a recognition mechanism is required before preferential investment in one’s own young can evolve. Indeed, some research has been conducted on identifying cues used for recognition and how recipients learn and use them (via recognition templates; Mateo & Holmes, 2004), yet across taxonomic groups, there has been little work examining the ontogeny of cue development, a necessary precursor for recognition of young by parents and collateral kin (but see Blaustein, O’Hara, & Olson, 1984; Breed, Leger, Pearce, & Wang, 1998; Gamboa, Reeve, Ferguson, & Wacker, 1986; Krutova & Zinkovich, 1997).

Belding’s ground squirrels (*Spermophilus beldingi*) are ideal animals for studying the development of recognition cues. They are group-living, burrowing rodents found in alpine and subalpine regions of the Western United States and Canada (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 burrow (the natal burrow) for 25–28 days until young first comes above the ground (“emerge;” Sherman, 1976; Sherman & Morton, 1984). I refer to <25-day-old *S. beldingi* still confined to their natal burrow as “pups,” ≥25-day-old young which have emerged from their natal burrow as “juveniles,” and animals which are ≥1-year-old as “adults.”

Recognition is important to many aspects of social interactions among *S. beldingi*. Females live an average (\pm SE) of $3.4 \pm .3$ years (up to 12 years) and males live $2.1 \pm .4$ years (up to 9 years; Sherman & Morton, 1984; J. M. Mateo, unpublished data). Therefore, there are ample opportunities for repeated interactions over many years, and memory of individuals’ competitive or cooperative tendencies would facilitate appropriate behaviors toward such individuals (see Mateo & Johnston, 2000; Mateo, 2006). In addition, *S. beldingi* exhibit a variety of nepotistic behaviors, including cooperative territory defence and alarm-call production. Nepotism is directed to close female kin only, such as mothers, sisters, and daughters (Sherman, 1976), although *S. beldingi* can discriminate among a variety of male and female kin classes, such as aunts, cousins, and nonkin, using odor cues (Mateo, 2002, 2003). Recognition of kin is also important for survival behaviors, as juveniles learn anti-predator behaviors from observing their mother’s responses (Mateo & Holmes, 1997).

Until shortly before their young are old enough to emerge aboveground, free-living female *S. beldingi* are equally likely to retrieve their own and alien pups into their nests (Holmes, 1984; Holmes & Sherman, 1982). Holmes (1984) found that captive females also retrieve their own and alien young with equal likelihood when pups are 1, 8, 15, and 22-day-old, but they retrieve 22-day familiar young faster than alien young. He also noticed that females handle 15-day- and 22-day-old alien pups longer before carrying them to their nest, indicating they can discriminate between the two categories of pups but are motivated to tend to both (Holmes, 1990). His data suggest that young *S. beldingi* express some cues for recognition prior to emergence, although discrimination in his studies may have been based on odors acquired from mothers (see below). In addition, juveniles discriminate behaviorally between littermates and nonlittermates around the age of emergence (Holmes, 1994, 1997; Holmes & Mateo, 1998). Because young may be recognized before there is an advantage to being treated preferentially, and because there presumably is no fitness benefit for young to conceal their identity (e.g., Johnstone, 1997), pups may produce distinct odors well before the age of emergence. And, although juveniles may not need to recognize unfamiliar kin via phenotype matching until after natal emergence, they first need to develop kin templates that represent the odors of their close relatives (e.g., littermates and mother). Template development thus depends in part on the production of recognition cues by littermates, and this may select for cues that develop well before natal emergence.

I therefore investigated the development of recognition odors in *S. beldingi* pups and juveniles, focusing on the contribution of oral-gland odors which are both

individually and kin distinct (Mateo, 2002, 2006). Although behavioral discrimination among related and unrelated young occurs before their natal emergence (J. M. Mateo, unpublished data), it is unclear when young first produce distinct odors or whether the odor cues used by mothers and littermates to recognize kin are developmentally stable. Young may acquire their mother's odors during nursing or sleeping (Aldhous, 1989; Gustin & McCracken, 1987; Rasa, 1973; Schultze-Westrum, 1969; see also Sherman, Reeve, & Pfennig, 1997; Waldman, 1991), and this shared odor may serve as a kin label until individuals produce independent odors. Odor cues may change during development and interfere with recognition of young by others, particularly around natal emergence when juveniles' diets change from mother's milk to vegetation and when they come into contact with objects carrying novel odors (e.g., Doane & Porter, 1978; Halpin, 1986; Hepper, 1991; see also Charrier, Mathevon, & Jouventin, 2003 for an example of developmental changes in vocal recognition cues). I used habituation-discrimination tests to determine whether oral odors are individually distinct at 7, 14, 21 (just prior to eye opening and the age of natal emergence), or 28 days of age (shortly after emergence). I also examined whether the odors of peri-emergent *S. beldingi* are stable or if they continue to change across early development, after young have emerged and are foraging on their own, exploring the area around their natal burrow and encountering other ground squirrels.

METHODS

Subjects

I studied ground squirrels at the Sierra Nevada Aquatic Research Laboratory (SNARL; near Mammoth Lakes, CA). Pregnant females were live-trapped and housed in a laboratory building at SNARL where they gave birth and reared their young. Details of trapping, marking, and housing animals are in Mateo & Holmes (1997). Due to 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 data). Litters probably comprised full- and maternal half-siblings because of multiple mating by females. When young were 25–28 days of age, they and their mothers were transferred to outdoor enclosures at SNARL (3–4 litters/enclosure) to serve as subjects or donors for odor tests. Individuals within an enclosure moved about aboveground and belowground and interacted freely as they would in the wild. Each 10 × 10 × 2 m open-air enclosure included natural vegetation, laboratory food (Purina mouse chow #5015) and water, and four buried nestboxes connected to the surface by plastic tunnels.

Juveniles ≤32 days of age served as subjects (see below); juveniles at these ages perform equally well in habituation-discrimination tasks (Mateo, 2002, 2006; Mateo & Johnston,

2000). For the tests of 7, 14, 21, and 28-day-old odors, donors were two littermate sisters living in a different enclosure than the subjects, and thus unfamiliar to them; the same two donors were used for each age tested. For the two studies examining developmental changes in odors, donors were two familiar juvenile sisters living in the same enclosure as the subjects. These two tests were conducted in different years, and thus required different pairs of odor donors. Animals were maintained on similar diets to minimize environmental influences on odors (e.g., Doane & Porter, 1978; Gamba, Berven, Schemidt, Fishwild, & Jankens, 1991; Schellinck, Slotnick, & Brown, 1997).

Odor Collection

Because pup odors may be contaminated by odors from mothers which were transferred to their young (either actively or passively, such as during nursing; e.g., Aldhous, 1989; Horrell & Hodgson, 1992; Porter et al., 1991; Porter, Tepper, & White, 1981), pups were washed with warm water and unscented soap (sodium laurel sulfate; Chemifax, Santa Fe Springs, CA) and dried with a clean towel to remove all odors. Animals were then placed individually under a heat lamp in a container with cotton bedding for 2 hr to allow the reappearance of their own individual odors, if any (e.g., Loughry & McCracken, 1991). Oral odors were collected from “clean” animals with cotton swabs ($n = 4$ swabs per animal; four to five swipes anterior-posteriorly along both mouth corners per swab) and frozen individually in 1.5 mL polypropylene vials (Cole Parmer; Vernon Hills, IL) at -15°C until use up to 16 days later.

To verify that washing removed species-typical odors, some *S. beldingi* ($n = 8$ lactating females) were presented with a swab containing “odor” from a freshly washed 7-day-old pup and a clean unscented swab. There was no evidence of discrimination between the swabs ($t_7 = .486$, $p > .60$; pup swab mean investigation $s \pm \text{SE} = 2.31 \pm .44$; clean swab = $2.014 \pm .54$), indicating that washing removed odors (own or transferred) from donors. I also presented an enclosure-housed group ($n = 1$ adult female plus three males and six juvenile females from three litters) with fresh oral odor and previously frozen oral odor (at -15°C for 4 days) collected from the same adult female. Each swab was swiped 12× on a female's oral gland and then swiped 12× on a cube (cubes described below). Subjects did not differentially investigate cubes with fresh versus frozen odors ($1.65 s \pm .42$ and $2.72 \pm .81$, respectively; $t_9 = 1.502$, $p > .15$). Thus, freezing did not appear to significantly degrade the odors.

Odor Presentation

For the habituation-discrimination tests (described below), swabs were brought to ambient temperature and then swiped on 3-cm³ polyethylene cubes ≤15 min before use. One person swiped the odors onto and coded the cubes (e.g., scented vs. unscented) while wearing latex gloves to prevent the transfer of odors to the equipment. Therefore, observers ($n = 2$) were blind to which cubes were scented. Pairs of cubes (e.g., scented and unscented) were placed by the odor collector 3 cm apart and 1 cm in front of each of four burrow entrances, anchored by 3 cm

screws (inserted in the middle of each cube) for 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 does not make ground squirrels more or less likely to investigate cubes, nor does it influence their duration of investigation (Mateo, 2002, 2006). In addition, animals always went belowground when we entered the enclosure to place the cubes, and typically re-emerged from burrows one by one after cube placement, with the majority of investigations occurring during this initial ~10 min re-emergence period. Each observer monitored two burrows and their cubes, and given the staggered re-emergence of animals, they were able to record data from both burrows without difficulty. 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 an odor) were recorded for 30 min by observers blind to what was on the cubes. If a cube was licked, scent marked, or dislodged, data collection from that pair of cubes ceased. Cubes were washed with hot water and unscented soap after use and allowed to air dry.

Habituation-Discrimination Tests

I used habituation-discrimination tasks to determine at which ages young *S. beldingi* produce individually distinct odors (Halpin, 1986; Johnston, 1993; Mateo, 2006; Schultze-Westrum, 1969). In this task, using the odor-presentation protocol described above, subjects are repeatedly presented with a particular stimulus (here, an individual's odor) until they habituate to it, and then are presented with a novel stimulus (here, another individual's odor; see exception below) to see if the animals dishabituate to it, indicating discrimination of the two stimuli. This task tests for true discrimination of individual conspecifics, because familiarity, sex, and relatedness were controlled and could not be used as a basis for discrimination. Subjects were presented with an odor from an individual ("Individual 1") for three to four habituation trials, and then tested with a similar odor collected from Individual 1's same-sex littermate ("Individual 2") for "discrimination trials." Trials were separated by 24 hr. During habituation trials, an unscented cube was presented along with the cube containing Individual 1's odor, to verify that subjects detected the odor and habituated to it specifically rather than the cubes in general. Subjects typically smell the scented cube significantly longer than the unscented cubes during the first one to two habituation trials (Mateo, 2002, 2006; see exceptions noted below), and were considered habituated to the scent when they no longer smelled the cubes differentially within a trial. For the discrimination trial, Individual 2's odor was presented on one cube with a second, unscented cube.

The perceived dissimilarity of the test stimulus, relative to the habituation odor, is reflected in the magnitude of the response differences to the test odors, because novel stimuli are usually attended to more than familiar stimuli (Halpin, 1986; Johnston, 1993; Mateo, 2002, 2003, 2006; Mateo & Johnston, 2000; Schultze-Westrum, 1969; Stoddard, 1996). Thus, if young ground squirrels produce chemically distinct odors, then Individual 2's odor should be perceived as dissimilar to Individual 1's and be investigated longer than the final

habituation odor. Because new exemplars of odors were used for each of the trials, the only unique difference between the odor stimuli was the source of the odor (i.e., individual identity; familiarity, sex, relatedness, ageclass, and reproductive condition were controlled). A significant decrease in investigation across habituation trials indicated habituation to (and hence recognition of) Individual 1's odor, and a significant increase in investigation from the final habituation trial to the test trial indicated discrimination of Individual 2's odor as distinct from Individual 1's. All animals emerged after cube placement, but some did not investigate the cubes. Therefore, animals were included in an analysis if they investigated at least one cube during each of the habituation and discrimination trials. For the age-change tests, in which donors were familiar to subjects, responses of relatives of the donors were included, as no statistical differences in their responses compared with responses of unrelated subjects were detected (one-way ANOVAs using litter as the main effect; all $ps > .10$). One group of subjects participated in two habituation-discrimination tasks (with 7- and 28-day-old odors).

The tests of 7, 14, 21, and 28-day-old odors use the same two odor donors for each of the habituation-discrimination tasks. Although this design could be considered an example of "simple pseudoreplication" (*sensu* Hurlbert, 1984) because the same odor donors were used for each of the four tests, it was used to maximize internal validity. Although this design constrains broad generalizability of the results, use of the same odor donors at each age is necessary to reveal changes related to age rather than to other factors such as genetic, diet, and metabolic differences. Prior to this study, there was no information about the age at which animals start producing detectable odors or when these odors become individually distinct. Thus, it was imperative to eliminate potential confounds such as individual variation in growth rates, body size, foraging choices, or metabolism, for example. That is, if novel pairs of odor donors were used for each age group, subjects could discriminate between a pair of odors at a given age because of age-related aspects of odor production or because of the unique aspects of the paired odors. In the design used here, individual variation is controlled for, using two same-aged same-sex siblings, and thus, the onsets of odor production and odor distinctiveness could be detected.

Statistical Analyses

Durations of investigation of odors were not normally distributed so data were log-transformed (normal distributions verified with Kolmogorov-Smirnov tests). I analyzed the data with one-tailed tests because repeated presentation of the "habituation" odor should lead to a decrease in investigation of that odor, and if odors are individually distinct, subjects are predicted a priori to investigate the novel odor longer than the habituation odor (e.g., Halpin, 1986; Harrington, 1976; Johnston, Derzie, Chiang, Jernigan, & Lee, 1993; Mateo, 2002, 2006; Murdock & Randall, 2001; Schultze-Westrum, 1969; Zenuto & Fanjul, 2002). Analyses of frequency of investigation of odors are not presented as they were less discriminating than investigation durations. Data are presented as unadjusted means + SE, and because data

from the fourth day of habituation were used in two comparisons (with the Habituation Day 1 odor and with the test odor from Individual 2), I used a Bonferroni correction and set $\alpha = .025$. I conducted power analyses in Systat (version 11.0) when $.025 < p < .10$ (Cohen, 1988). I tested each dataset for litter effects, as each study involved >1 litter. In all cases, between-litter variation was not significantly greater than within-litter variation, and therefore, I used individuals as the unit of analysis. No sex differences were found for any of the statistical comparisons (two-tailed t -tests; all $ps > .10$).

RESULTS

Odors from 7-Day-Old Squirrels

I tested 14 *S. beldingi* juveniles ($n = 6$ males and 8 females from 3 litters, about 33-days-old at the start of study) for their ability to discriminate between the oral odors of two unfamiliar female littermate pups. Subjects showed no evidence of habituation to repeated presentations of odor from a 7-day-old pup (habituation trial 1 vs. trial 4: $t_{13} = 1.77$, $p > .054$; power = .57; Fig. 1A). Further, juveniles did not differentially investigate the scented and unscented cubes on any habituation trial (all $ps > .05$), nor did they investigate the odor of Individual 2

significantly longer than that of Individual 1 on trial 4 ($t_{13} = .709$, $p > .25$). Thus, odors of 7-day-old pups do not appear to be detectable, let alone individually distinct.

Odors from 14-Day-Old Squirrels

Thirteen juveniles ($n = 7$ males and 6 females from 3 litters, about 34 days of age at start of study) were tested for discrimination between oral odors collected from two unfamiliar 14-day-old sisters. Although subjects appeared to habituate to repeated presentations of odor from Individual 1 (habituation trial 1 versus trial 4: $t_{12} = 3.194$, $p < .005$; Fig. 1B), on no habituation trial did they differentially investigate the scented and unscented cubes (all $ps > .05$). In addition, subjects did not smell the novel odor from Individual 2 longer than the odor from Individual 1 on the last habituation trial ($t_{12} = .49$, $p > .31$). The odors of 14-day-old pups thus appear not to be detectable or distinct.

Odors from 21-Day-Old Squirrels

I tested 12 juveniles ($n = 9$ males and 3 females from 3 litters, about 32-day-old at start of study) to determine if

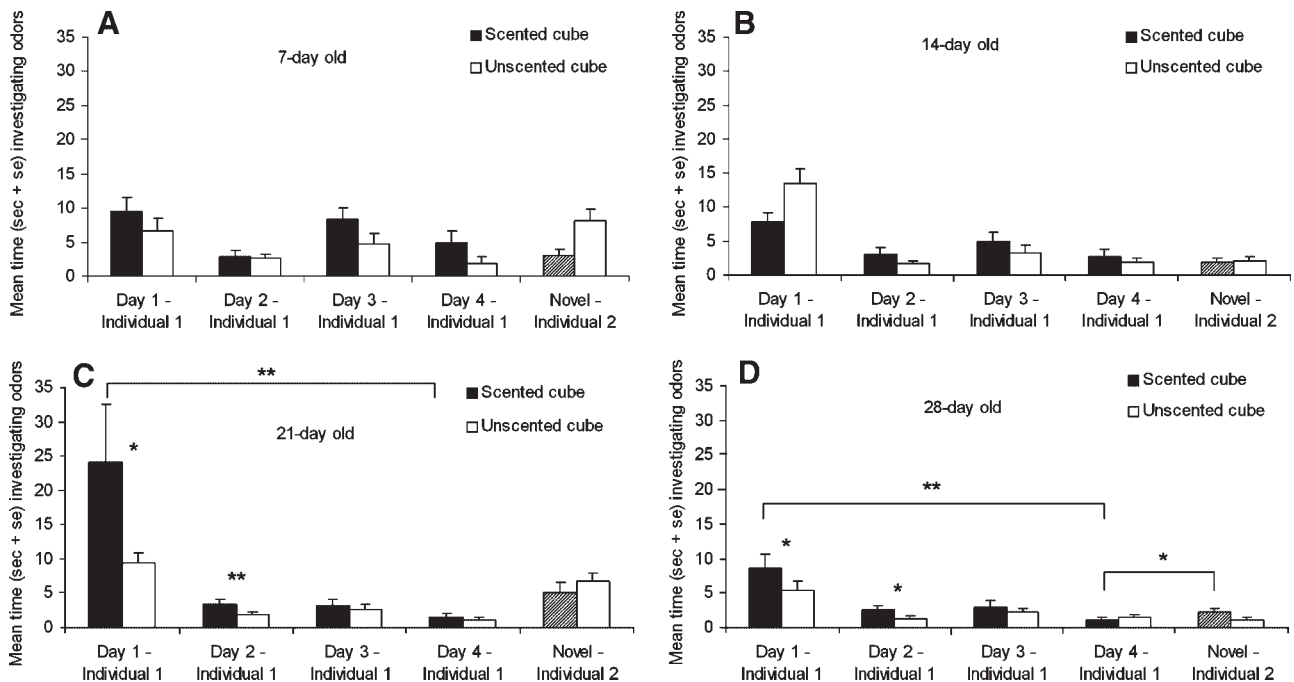


FIGURE 1 Unadjusted mean (\pm SEs) duration of investigation of odors by subjects in habituation-discrimination tasks. (A) 7-day-old donors. (B) 14-day-old donors. (C) 21-day-old donors. (D) 28-day-old donors. Black bars represent investigation of the habituation odor from Individual 1, open bars represent investigation of unscented cubes, and the hatched bar represents investigation of the test odor from Individual 2 during the discrimination trial. Horizontal lines and asterisks indicate significant differences in investigation of odors ($*p < .05$, $**p < .01$) based on paired t -tests on log-transformed data.

they could distinguish between oral odors from two unfamiliar sisters which were collected when they were 21-day-old (just before eye opening and natal emergence). Subjects habituated to the odor from Individual 1 over four trials (habituation trial 1 versus trial 4: $t_{11} = 6.883$, $p < .001$; Fig. 1C). Subjects smelled the scented cube longer than the unscented cube on the first two trials ($t_{11} = 2.583$, $p < .013$; $t_{11} = 3.717$, $p < .002$), but not on the remaining two trials (both $ps > .05$). However, investigation of the odors of Individuals 1 and 2 was not significantly different ($t_{11} = -1.92$, $p > .04$; power = .73). Thus, 21-day-old pups produce detectable odors, but they are not yet individually distinct.

Odors from 28-day-old Squirrels

Fourteen juveniles ($n = 7$ males and 7 females from 3 litters, about 46-day-old at start of study) were tested for discrimination between oral odors collected from two unfamiliar 28-day-old female littermates (shortly after the age of natal emergence). Juveniles habituated to repeated presentations of odor from Individual 1 (habituation trial 1 vs. trial 4: $t_{13} = 4.656$, $p < .001$; Fig. 1D), and investigated the scented cube longer than the unscented cube on trials 1 and 2 ($t_{13} = 2.304$, $p < .02$; $t_{13} = 2.619$, $p < .015$) but not on the subsequent two trials (both $ps > .05$). Subjects investigated the novel odor from Individual 2 significantly longer than the odor from Individual 1 on the final habituation trial ($t_{13} = -2.337$, $p < .02$). Thus, the odors of 28-day-old juveniles are both detectable and individually distinct.

Effect of Weaning on Odors

Individual odors are detectable at 21 days of age (see Fig. 1C), but are not yet distinct, demonstrating that recognition odors continue to develop after natal emergence and weaning. I therefore tested 11 juveniles ($n = 6$ males and 5 females from 3 litters, about 52-days-old at the start of study) with oral odors collected from a familiar female when she was 20 and 40 days of age. Subjects habituated to repeated presentations of the odor collected when the female was 20 days of age ($t_{12} = 2.44$, $p < .017$; Fig. 2A), but when tested with odor from the same animal collected when it was 40 days of age, subjects investigated it significantly longer than the 20 day odor on the last habituation trial ($t_{13} = -3.085$, $p < .005$). Thus, odors change significantly between 20 and 40 days of age, such that subjects perceive them as belonging to different individuals. I therefore repeated the study the following year with odors collected from another familiar female juvenile when she was 28 and 40 days of age. Again, subjects ($N = 7$ males and 6 females from 4 litters, about 42-days-old at start of study) habituated to the donor's

odor at 28 days of age ($t_{12} = 3.881$, $p < .002$; Fig. 2B). In this test, subjects did not behaviorally differentiate between this female's odors collected when she was 28 and 40 days of age ($t_{12} = -1.631$, $p < .065$; power = .63). Thus, odors change significantly before and after natal emergence and weaning, but do not appear to change qualitatively after that time.

DISCUSSION

The series of habituation-discrimination tests presented here was designed to determine when young *S. beldingi* produce individually distinct odors which could be used for social recognition. With odors collected from pups when they were 7- and 14-day-old, subjects did not differentially investigate scented and unscented cubes (Fig. 1A and B), indicating that pups were not producing odors at these ages. Odors collected from the pups when they were 21-day-old (just prior to natal emergence) were detectable, because subjects initially investigated the scented cube longer than the unscented cube, but odors were not yet individually distinct as subjects did not discriminate between the habituation and novel odors (Fig. 1C). At 28 days of age, after the age at which young emerge above ground in the field, the oral odors of the two donors were both detectable and individually distinct (Fig. 1D). These results provide a developmental timeline for the production of unique odors for these two donors, with the onset of distinctiveness corresponding to when young are aboveground and interacting with conspecifics. The same donors were used for each test, the donors were both female, were sisters, and were housed in captivity on a constant diet, and thus, the only unique difference among the odor tests was the age of the donors. Future research can conduct more detailed studies of young between 21 and 28 days of age to pinpoint at exactly what age odors are unique, as well as the degree to which this age differs across *S. beldingi*. The discussion that follows presumes that these results apply to other pairs of young ground squirrels, although additional empirical work is necessary to confirm this.

These results provide a proximate explanation for the success of *S. beldingi* cross-fostering studies. Mothers will accept pups that are not theirs until pups are about 22 days of age, which corresponds with when they start producing recognition odors (Holmes & Sherman, 1982; see also Mateo & Holmes, 2004). Note that captive mothers handle alien pups longer than their own starting at 15 days of age (Holmes, 1990); based on the data presented here, this discrimination in Holmes' study must have been based on mothers' odors transferred to the pups, rather than on the pups' own odors, as young were not washed prior to retrieval experiments. Thus, mothers

might retrieve and care for unrelated, unfamiliar pups prior to the age of emergence because young are not yet producing distinct odors which would reveal their identity. This developmental switch makes adaptive sense as well, as mothers stop retrieving or accepting alien young when they are old enough to stray into her territory and burrow system, thus do not risk investment in unrelated young (for other examples of the onset of parent–offspring recognition when young start mixing see Beecher, 1991; Lefevre, Montgomerie, & Gaston, 1998; Lengyel, Robinson, & Oring, 1998). Similarly, rat pups (*Rattus norvegicus*) begin producing distinct urine odors at 10–11 days of age, well before they are weaned at 21 days (Krutova & Zinkervich, 1997), perhaps because

pups are likely to mix at a young age in communal burrow systems.

Ground squirrels discriminated between odors collected from the same individual at 20 and 40 days of age (Fig. 2A), indicating that the odors were not perceived as similar even though they came from the same individual, but they did not discriminate between odors collected from an individual at 28 and 40 days of age (Fig. 2B; note that additional pairs and ages should be tested, to verify the generalizability of the present results). Recognition cues may not be stable until some time after emergence because of weaning or the metabolic changes associated with independent foraging. In addition, if each juvenile forages on slightly different plants or in different

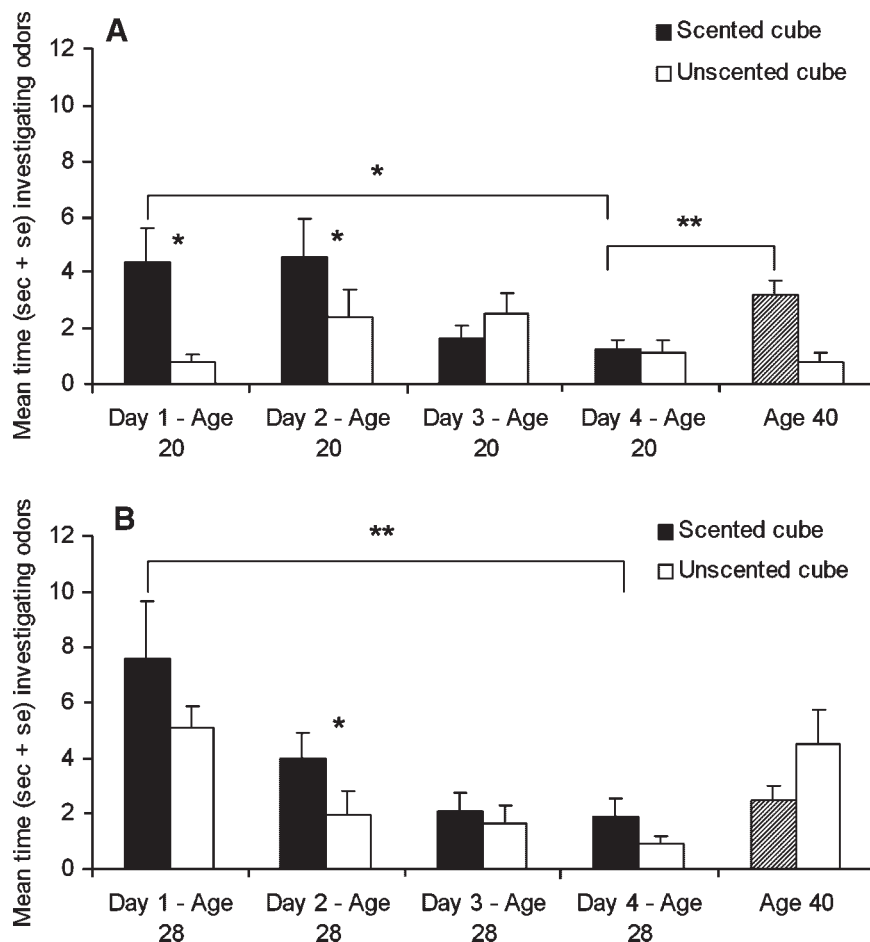


FIGURE 2 Unadjusted mean (+SE s) duration of investigation of odors collected from a female *S. beldingi* by subjects in habituation-discrimination tasks. Black bars represent investigation of the habituation odor collected from the female at a young age, open bars represent investigation of unscented cubes, and the hatched bar represents investigation of the test odor during the discrimination trial collected from the female when she was older. (A) Investigation of odors collected from a female at 20 and 40 days of age. (B) Investigation of odors collected from another female at 28 and 40 days of age. Horizontal lines and asterisks indicate significant differences in investigation of odors (* $p < .05$, ** $p < .01$) based on paired t -tests on log-transformed data.

locations, this may enhance the uniqueness of their odors. (Alternatively, it could be the case that odors continue to change throughout life, and that odors collected 12 days apart were perceived as more similar than odors collected 20 apart. Nevertheless, these perceptual tests indicated that postemergent odors were treated similarly, but pre-emergent and postemergent odors were not.) Whatever the mechanism(s) underlying this ontogenetic change in odor cues, variability in production components across development will also influence the development and stability of *perceivers'* recognition templates. That is, if young are to be recognized properly then mother's and siblings' recognition templates must be updated periodically until young produce stable cues (e.g., Errard, 1994; Mateo & Johnston, 2000). Although juveniles may not need to recognize unfamiliar kin until after natal emergence when they are above ground and can encounter unknown conspecifics, kin templates begin to form prior to emergence and young need to learn the cues of their close relatives (e.g., littermates) even before those cues are stable. Development of the production component (recognition odors), therefore, constrains development of the perception component (kin templates), selecting for cues which begin to develop before young leave the natal nest.

Kin preferences of juvenile Belding's ground squirrels are most evident in their choice of play partners and sleeping partners. Littermate pairs play together three to six times more often than nonlittermate pairs, and distant kin play together more often than nonkin despite both types of juveniles being initially unfamiliar (Holmes, 1994; Holmes & Mateo, 1998; Mateo, 2003). However, if juveniles are reared without their mother after emergence, they play indiscriminately with respect to kinship and do not sleep preferentially with littermates. If their mother is absent but juveniles are spatially restricted for a few days so that they cannot interact with nonlittermates, then their littermate preferences are maintained. Finally, if mothers are absent and juveniles interact freely during the day but sleep with kin only during the initial days after emergence, this also appears to consolidate their kin preferences (Holmes, 1997; Holmes & Mateo, 1998). In other words, because odors are still developing around the age of natal emergence, juveniles must remain in contact with kin—and kin only—during at least part of the day to become familiar with their littermates' odors as they become stable, and later use those odors to guide social interactions with kin. If juveniles spend time with nonkin during the periemergent period, then their odors will be incorporated into kin templates and social behaviors will not be kin-biased. Thus, prolonged experience with kin odors until they are developmentally stable may be necessary for juveniles to be able to accurately generalize from their recognition templates to the odors of their

unfamiliar kin. This process is similar to sexual imprinting, wherein animals must wait for adultlike features to develop in their siblings if they are to avoid mating with them, or similar individuals, at a later age (Bateson, 1966; Bischof & Clayton, 1991; Oetting, Prove, & Bischof, 1995).

Despite extensive research on mammalian odors and scent marking, few studies have been conducted on developmental changes in their recognition cues (but see Blaustein et al., 1984; Breed et al., 1998; Gamboa et al., 1986; Panek, Gamboa, & Espelie, 2001; Waldman, 1991 for invertebrate and amphibian examples). The results of my studies demonstrate that *S. beldingi* produce oral-gland odors that can be used as recognition cues (sensu Beecher's "signature cues;" Beecher, 1982) just prior to their natal emergence, and that the odors become stable sometime after weaning. Young are not treated by mothers or littermates as "familiar" until after 20 days of age (via affiliative and play behaviors; Holmes, 1997; Holmes & Sherman, 1982), which coincides with the production of unique odors. Young emerge above ground at 25–27 days of age, and thus, odors are becoming distinct around the age at which young begin to interact with unfamiliar kin and nonkin, suggesting there is no fitness cost to young for revealing their identity before emergence (Beecher, 1988). Kin templates of young *S. beldingi* also begin to develop prior to emergence (J. M. Mateo, unpubl. data), favoring the production of some recognition cues before natal emergence.

Finally, by comparing responses to odors of young collected before and after the age of emergence, I addressed the question of how production components change across development, which in turn influences the development and stability of perceivers' recognition templates (Hepper, 1991; Sherman et al., 1997). *S. beldingi* do not appear to produce stable individually distinct odors until after weaning (Fig. 2AB), which provides a proximate explanation for why littermate preferences are not consolidated until after natal emergence (Holmes, 1997). Future work could examine changes in odors associated with hibernation, because yearlings no longer recognize previously familiar age-mates after 7 months of hibernation (Mateo & Johnston, 2000). It is possible that yearlings produce odors that are significantly different from those they produced as juveniles, due to further development or long-term torpor, and therefore, are no longer recognizable until conspecifics update their recognition templates after experience with these changed odors.

In this study, I focused on the development of individually distinct odors, rather than kin distinct odors, but because oral odors convey information about both categories of identity (Mateo, 2002, 2006), it is likely that the developmental trajectories for both types of informa-

tion are similar. I note that because I used investigation of odors by conspecifics as a bioassay for odor development, it is possible that pups produced distinct odors at an earlier age, but subjects did not respond differentially to them. I doubt this possibility, as *S. beldingi* discriminate among odors in other contexts (Mateo, 2002, 2003, 2006; Mateo & Johnston, 2000) and likely would have differentially investigated odors if there were salient differences between them. However, gas chromatography/mass spectrometry analyses could determine which compound(s) makes oral glands unique, and at what age these compounds are present in secretions (e.g., Buesching, Waterhouse, & Macdonald, 2002; Lawson, Putman, & Fielding, 2001). Such analyses could also determine if the specific chemical components which make odors individually unique also comprise kin labels.

The age at which recognition cues are first produced, and the subsequent changes in cues, if any, are important when studying at the timing and nature of recognition. For example, if recognition is useful early, then selection may favor cues that develop early. However, if recognition is not useful until later, a different cue may be used for recognition, perhaps one that develops later but is more stable once it appears. In addition, animals cannot reliably make much use of the cues of other individuals until such cues are distinct and stable. Take for instance parent-offspring recognition and selective nursing by mothers. Its onset has typically been interpreted in functional terms, such as the benefits and costs of rejecting unrelated offspring (Hayes, 2000; Roulin, 2002). For example, prairie vole mothers interact differentially with weanlings but not newborns as a function of relatedness, and this result was interpreted as a function of costs of investment in young across development (Hayes, O'Bryan, Christiansen, & Solomon, 2004; see also Yu, Sun, & Fang, 2005). Yet a proximate explanation should be considered as well, and the development of odor production could provide a mechanistic explanation for the appearance of kin-differentiated behaviors as young mature (see also Paz y Miño & Tang-Martinez, 1999 for an example of how repeated exposures are necessary for the maintenance of sibling recognition in prairie voles). Paternal bluegill sunfish do not appear to discriminate between related and unrelated fertilized eggs, but do distinguish fry (newly hatched fish) based on kinship (Neff & Sherman, 2003), suggesting that recognition cues may not be produced at the egg stage. Finally, consider the paradox of parental investment by cuckolded males. We are often surprised that males apparently fail to recognize that young are not their own and continue to waste their parental investment (e.g., Bouwman et al., 2005; Edwards, Messenger, & Yasukawa, 1999; Kempenaers & Sheldon, 1996). If more were known about the cues used for recognizing offspring—whether they are visual, olfactory, auditory, or

vibrational—and the developmental timing of these cues, then this paradox may be resolved.

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 and when developing animals can be recognized accurately is not well understood. My results highlight the importance of determining when recognition cues are produced, which then influences whether or not young animals can be recognized and thus treated accordingly. In addition, my studies suggest we should re-consider results of studies which purportedly show a lack of recognition abilities, such as cases of indiscriminate parental investment, until it is known whether developing animals even produce recognition cues.

NOTES

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