How mothers influence the development of litter-mate preferences in Belding's ground squirrels

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Abstract. We performed three experiments to examine the role of mothers in the development of litter-mate preferences in captive juvenile Belding's ground squirrels, *Spermophilus beldingi*. First, when observed in the absence of mothers, juveniles did not play preferentially with litter-mates, which suggests that mothers somehow influence the ontogeny of litter-mate preferences. Second, when mothers were present but unable to intervene in social interactions, juveniles displayed litter-mate preferences, which suggests that mothers do not influence their offsprings' social development by directly intervening in social interactions. In another group, mothers were removed daily, a few hours before nocturnal immergence, and returned the following morning. Juveniles in this group did not display litter-mate preferences and at night they occupied burrows with many more non-litter-mates than litter-mates. These results suggest that associating with non-litter-mates can compromise the development of litter-mate preferences, and implies that mothers indirectly influence social development by affecting the identities of sleeping partners. Third, newly emergent juveniles that interacted only with litter-mates for 3 days in the absence of mothers subsequently preferred litter-mates over non-litter-mates as play partners. This result demonstrates that once litter-mate preferences are instilled, due in part to social experiences during juveniles' initial days above-ground, the preferences are expressed even in the absence of mothers. Collectively, the results demonstrate that the presence of *S. beldingi* mothers is important to juvenile social development, but that mothers do not actively direct the ontogeny of their offsprings' social relationships.

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Mammalian mothers play a prominent role in the early development of their offspring by providing young with nutrients, heat and protection, among other important resources (e.g. Gubernick & Klopfer 1981; Clutton Brock 1991). Besides affecting the physical development of their offspring, mothers can affect the acquisition of critical behavioural skills by a variety of learning processes (imitation, social facilitation, local enhancement; Galef 1988). Examples of such maternal effects are apparent in the development of hunting skills in felids (Caro 1994), anti-predator skills in rodents (Mateo & Holmes 1997) and locomotory skills in primates (Maestripieri 1995).

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Mammalian mothers can also influence the ontogeny of their offsprings' social relationships (e.g. Swartz & Rosenblum 1981; Chalmers 1983). Such effects are apparent, for example, in mother–infant separation studies (Harlow 1958), which show that separation for even brief periods can have measurable behavioural effects years after the separation (Hinde & Spencer-Booth 1971). In some species, mothers actively intervene in the social world of their developing young by allowing or preventing their offspring from interacting with various conspecifics (de Waal 1990; Drea et al. 1996). Interventions are regulatory processes, often behavioural in nature, by which one individual attempts to prevent, hinder or stop two other individuals from interacting (e.g. Schilder 1990). Interventions have proximate consequences (e.g. increasing or decreasing the likelihood that two individuals will interact) as well as functional consequences. In vervet monkeys, *Cercopithecus aethiops*, for instance, maternal intervention is

critical to the acquisition and maintenance of offsprings' dominance rank (reviewed in Chapais 1992), which later affects adult daughters' reproductive success (Fairbanks & McGuire 1986). Even if direct intervention by mothers is rare, a mother's choice of social companions can affect the spatial availability of potential social partners for her infants and thus the development of infants' social relationships (Berman et al. 1982).

Social relationships of adult female Belding's ground squirrels, *Spermophilus beldingi*, typically differ as a function of genetic relatedness (e.g. Sherman 1977, 1980, 1981a, b). For instance, adult female litter-mates cooperate more frequently and compete less frequently with each other in the context of territorial defence than do unrelated adult females (Sherman 1981a, b). That is, female litter-mates treat each other nepotistically as adults. (We use 'litter-mate' rather than 'sibling' because multiple paternity is the norm in *S. beldingi* litters; Hanken & Sherman 1981.) Kin favouritism is common, but not universal, in ground squirrels (genus *Spermophilus*), and is hypothesized to emerge from a socialization process that occurs in the first 4–6 weeks of life (Armitage 1981; Michener 1983). During this time, ground-squirrel mothers and their offspring live together and interact frequently (*S. richardsonii*, Michener 1973; *S. terecauditus*, Dunford 1977; *S. columbianus*, Wiggett & Boag 1992; *S. parryii*, McLean 1982; *S. tridecemlineatus*, Vestal & McCarley 1984), which affords mothers many opportunities to affect the social relationships that their offspring develop. In this study we examined how *S. beldingi* mothers influenced the social development of their young and thus the possible role of mothers in the ontogeny of adult nepotism.

Spermophilus beldingi mothers are important to the early ontogeny of their offspring in several ways. For example, mothers provide all parental care for pre-emergent young, including feeding and protecting them from infanticidal adults (Sherman 1981a). Following natal emergence, the first above-ground appearance of young from their natal burrow, juveniles and their mother continue to interact for at least 3 weeks, including occupying the same burrow each night (Morton et al. 1974; Holekamp 1984). To determine whether mothers prominently influence the development of their offsprings' early social relation-

ships, Holmes (1994) allowed mothers to rear their young to the age of natal emergence (see below) and then compared the social interactions of newly emergent, captive juveniles in two social environments: mothers present and mothers permanently absent. When mothers and their offspring continued to live together after natal emergence, juveniles displayed social preferences for their kin by playing more frequently with litter-mates than with non-litter-mates. (Social play is a common affiliative behaviour in juvenile ground squirrels; details below.) If juveniles were housed without their mothers, however they did not display social preferences for their litter-mates. These mother present–mother absent results suggest that the presence of adult females is important to the ontogeny of juveniles' social relationships, although how mothers might have influenced social development is unknown.

The earliest postnatal social interactions of *S. beldingi* are limited to those between offspring and their mother and between litter-mates because *S. beldingi* litters are reared in isolation, each in their own underground burrow, and because juveniles remain near their natal burrow during their first few days above-ground (Sherman 1976; Holekamp 1983). After natal emergence, juveniles' interactions with adults and age-mates vary as a function of genetic relatedness. For example, mothers are more cohesive and/or less agonistic towards their own young than towards alien young, and juveniles play more frequently with their litter-mates than with non-litter-mates (Waterman 1988; Holmes 1994). Thus, the behaviour of *S. beldingi* mothers and newly emergent juveniles is consistent with the hypothesized link between early socialization and adult nepotism, although the transition from juvenile to adult social relationships has not yet been investigated.

In this study, we sought (1) to verify that *S. beldingi* mothers had to be present following the natal emergence of their offspring for juveniles to display litter-mate preferences during their initial days above-ground, (2) to clarify the role of mothers in the development of their offsprings' social preferences by examining how mothers influenced their offsprings' choices of social partners after natal emergence and (3) to examine the proposition (Holmes 1994) that mothers influenced social development by how they affected the identities of juveniles'

Table I. Demographic characteristics and sample sizes for four groups of Belding's ground squirrels observed in outdoor enclosures to record juveniles' social interactions

	Groups observed in outdoor enclosures			
	1 Dams absent	2 Dams restricted	3 Dams removed and returned	4 Juveniles restricted
Age (days)*	27.0 ± 0.5	28.5 ± 0.2	27.1 ± 0.1	26.2 ± 0.2
Body weight (g)*	55.3 ± 1.4	61.3 ± 1.0	50.7 ± 1.8	58.4 ± 1.2
Days observed†	1–7	1–9	1–12	1–9
Total hours observed	12.9	14.5	27.2	12.8
Total play bouts observed	213	348	452	326
No. juvenile pairs observed	91	120	105	120
Litter-mate pairs	18	24	21	24
Non-litter-mate pairs	73	96	84	96

*Mean ± SE on the day juveniles were placed in an enclosure.
†Juveniles were placed in an enclosure on day 0 and behavioural observations began on day 1.

sleeping partners, that is, individuals that shared a burrow at night.

GENERAL METHODS

Study Location and Animals

Our study site was the Sierra Nevada Aquatic Research Laboratory (SNARL) in the east-central Sierra Nevada near Mammoth Lakes, California. Study animals were mothers live-trapped from four populations and the young they bore at SNARL. We housed each field-mated female in a nursery building in her own cage (61 × 45 × 35 cm), which included a nestbox (28 × 20 × 20 cm) in which young were born and reared (see also Holmes 1994). Mothers reared their litters in the nursery building until young reached about 4 weeks of age, after which we transferred them to outdoor enclosures where we observed them for 1–2 weeks.

Outdoor Enclosures

We and our three assistants observed animals in four 9.7 × 9.7 × 1.6 m outdoor enclosures during the 1990, 1992 and 1994 field seasons. Artificial burrows were located near each corner of an enclosure, which ground squirrels could access via 1.8-m tunnels of plastic pipe leading to each of the four underground nestboxes. We could cover the entrances to each of the four tunnels with wire-mesh gazebos measuring 76 × 61 × 46 cm, which allowed us to control animals' movements and to identify sleeping partners. Natural vegetation (1–3 cm in height) grew inside enclosures, and we provided food (Purina mouse chow No. 5015) and water in each enclosure in four feeding silos and four water bottles.

Behavioural Observations

Methods and schedules of observations

The day before we transferred animals to an outdoor enclosure, we weighed each individual and gave it a unique dye mark and/or coloured ear tags. We transferred animals when juveniles were about 27 days old (Table I), which approximates the age of natal emergence in nature (Morton et al. 1974). For enclosure-housed juveniles, we use 'natal emergence' to refer to the first above-ground appearance of juveniles, which always occurred on day 0, the day we transferred litters to an enclosure. We began behavioural observations on day 1 when, for the first time, all animals had unrestricted access to the entire enclosure.

We recorded social interactions on each of the 7–12 days that animals inhabited an enclosure. This period coincides with when free-living juveniles would first interact with various related and unrelated conspecifics and precedes the beginning of natal dispersal (Holekamp 1984). One person, who was not told the relatedness or sex of the animals, observed all animals in an enclosure between 0700 and 1100 hours when more than 90% of juveniles were continuously above-ground.

Social interactions recorded

We focused our attention on recording the frequency of play between juveniles for four reasons. First, because we sought to explain the development of social preferences, we concentrated on dyadic play, which ground-squirrel researchers have used to identify amicable or cohesive relationships between newly emergent juveniles (e.g. Yeaton 1972; Michener 1981; Waterman 1988). Second, agonistic interactions, which have been used to characterize social relations in several species of ground squirrels (Murie & Michener 1984), were rare between recently emergent juveniles (less than 3% of all interactions recorded), whereas play was quite common (more than 75% of all interactions recorded). Third, although the development of social relations between juvenile ground squirrels has been studied by assessing juveniles' patterns of spatial use (Michener 1981; Waterman 1986), neither nearest-neighbour distances nor the location of play bouts distinguishes litter-mate interactions from non-litter-mate interactions in captive *S. beldingi* juveniles (Holmes 1994). Finally, observers could easily identify social play (coefficients for inter-observer reliability were 0.85–0.95; Caro et al. 1979), and one observer watching one enclosure was able to record reliably on pre-constructed data sheets about 92% of all play bouts that occurred (Holmes 1994).

Spermophilus beldingi social play is composed of a series of motor patterns that may include (1) nudging with the nose, (2) rushing at, pouncing on or chasing, (3) mounting and (4) wrestling with the protagonists grasping or clinging to each other (see drawings of *S. columbianus* play in Steiner 1971). We observed these motor patterns in other social contexts, but during play they appeared exaggerated, they were often repetitious and they lacked an obvious goal such as acquiring food or entering a burrow. In some species of *Spermophilus*, play becomes more aggressive after juveniles have been above-ground several weeks (e.g. Yeaton 1972; Waterman 1986), but we limited our observations to the first 2 weeks after natal emergence and rarely detected clear aggression during play.

We recorded the occurrence of play bouts, which were composed of one or more of the motor patterns listed above, rather than the occurrence of individual play motor patterns, because statistical analyses of bout frequencies permitted us to distinguish reliably between pairs based on the relatedness and sex of the interactants. A bout started when one of the play motor patterns began, and it ended when the interactants had no contact with each other for more than 3 s and/or moved apart by more than 1 m. We counted a bout only if it lasted more than 3 s, and bout durations of 15–20 s were common. At least 60 s had to elapse between two bouts before we recorded them separately, if they involved the same two animals. For each bout we recorded the identities of the two interactants, but not initiators or recipients. We did not routinely record bout durations, because bout frequencies and bout durations are redundant for identifying preferred play partners (e.g. juvenile *S. columbianus*: Waterman 1988).

Besides play bouts, we recorded nose-to-body contact, which occurred when one (or both) juvenile approached another quadrupedally, extended its body and contacted with its nose the recipient's head (often its face, especially its nose or mouth), back, side or anal region (e.g. Steiner 1971, figures 1, 2). We used nose–body contact to assess kin discrimination (Holmes 1984) because kin that are recognizable are not always treated favourably (Gamboa et al. 1991), and we wanted to know whether the absence of a litter-mate preference, which we expected to find under certain rearing conditions, might be explained by juveniles' inability to discriminate between litter-mates and non-litter-mates. Because nose–body contact occurs so often in ground squirrel discrimination tests (Davis 1984; Hare 1992), we recorded such contact only if it lasted more than 2 s and if the recipient remained stationary when it was being investigated by the initiator. Using these criteria, we avoided recording incidental contact that occurred when two juveniles passed by one another.

Sleeping partners

Sleeping partners were individuals that spent the night in the same nestbox and we identified them each morning before gazebos were removed. To quantify sleeping-partner patterns, we calculated for each juvenile in an enclosure the percentage of its sleeping partners on day 1 that were the juvenile's litter-mates and repeated this procedure for each juvenile to establish a day-1 mean.

Similarly, we calculated means for all remaining days. Because each juvenile occupied an enclosure that included three litter-mates and 12 non-litter-mates, 80% of a juvenile's sleeping partners would be non-litter-mates if relatedness and sleeping partner were uncorrelated.

Groups Observed in Enclosures

We use 'group' to refer to a set of ground squirrels (juveniles and sometimes mothers) observed together in the *same* enclosure ($N = 4$ groups, Table I). Groups were composed of four litters, each of which included one mother and two male and two female juvenile per litter. In some groups, mothers were removed for experimental purposes. Factors used to assign animals to a group included juveniles' sex, minimal differences in body weight and relatedness (a mother and her offspring were unrelated to other animals in their group; Holmes 1994). Between-group differences in sample sizes (Table I) arose because we included a pair's data in our analyses only if both members were present throughout the period the group was observed, and we sometimes had to remove animals for health-related reasons (e.g. inadequate weight gain). It is not appropriate to make statistical comparisons between groups because groups were treated differently (e.g. mothers were present or absent) and observed under different weather conditions, which affected overall rates of social interactions (unpublished data).

Data Analysis and Statistics

For each group (Table I), we concentrated statistical analyses on the frequency of play bouts per juvenile pair, that is, the total number of times two juveniles played together during all days a group was observed. Because many pairs never played or did so infrequently, the distribution of pairs' play-bout frequencies in each group approximated a Poisson distribution. Therefore, we used log-linear models (e.g. Green 1988; Aitkin et al. 1989; McCullagh & Nelder 1989) and GLIM software (Crawley 1993) to analyse play-bout frequencies. Conceptually, log-linear modelling is similar to ANCOVA except frequency counts are analysed and the response variable (play-bout frequency) approximates a Poisson distribution.

We assessed the effects of three variables on the frequency of play per juvenile pair: (1) relatedness (litter-mates versus non-litter-mates); (2) sex-of-pair (male–male, male–female, female–female); and (3) weight difference (the absolute difference in body weight between two juveniles that played together). Log-linear modelling allows one to examine the independent effect of one variable while controlling for the effects of other variables. We concentrated on the relatedness variable, but we incorporated pairs' sex and weight difference in these models. Although play-bout frequencies routinely varied with pairs' sex, we rarely detected a sex-by-relatedness interaction; if litter-mates were preferred play partners, they were preferred in each sex-of-pair combination.

We modelled the frequency of play bouts per pair as a linear combination of the three variables of interest. We used a quasi-likelihood approach to log-linear modelling (McCullagh & Nelder 1989, page 333) because pairs were not independent, because a juvenile could be observed as a member of more than one pair. This approach helps correct the independence problem by calculating a constant scale factor that inflates the sample's variance. From log-linear models, we derived play ratios, which are conceptually similar to the regression coefficients in standard linear regression models.

The play ratio, derived from log-linear models, is the primary statistic we report. A play ratio ($\pm 95\%$ confidence interval) is the amount by which the play-bout frequency of one type of pair exceeds the play-bout frequency of another type of pair when the two types of pairs differed on a single variable. For instance, a litter-mate:non-litter-mate play ratio of 2.5 indicates that litter-mate pairs played 2.5 times as often as non-litter-mate pairs when pairs' sex and weight difference were controlled statistically (see details in Holmes 1994).

We also report mean $\pm$ SE play-bout frequencies for various types of pairs. We caution that these means must be viewed conservatively, however, because they were not used in inferential statistics, and because means based on a variable like relatedness do not control for the effect of another variable like pairs' sex. For interactions besides play (juvenile–juvenile nose-to-body contact and mother–juvenile agonism), we report descriptive statistics, because they occurred only infrequently.

Descriptive statistics are based on per-pair frequencies of interaction.

EXPERIMENT 1: ABSENT MOTHERS

During the first 2 weeks after juveniles' natal emergence, litter-mate play occurs two to three times more often than non-litter-mate play in captive *S. beldingi*, that is recently emergent juveniles have developed a social preference for their litter-mates, although mothers must be present for these preferences to be manifested (Holmes 1994). Before considering how mothers exerted their influence on social development, we examined four issues. First, we tested whether mothers really did have to be present for newly emergent juveniles to display litter-mate preferences because we were unaware of any evidence from field studies on *S. beldingi* (Sherman 1976; Holekamp 1983) or any other ground squirrel (Murie & Michener 1984) that juvenile–juvenile interactions varied as a function of the prolonged presence or absence of a third conspecific.

Second, we wanted to work with more age-appropriate juveniles than did Holmes (1994). To ensure that post-emergent juveniles would thrive without maternal care, Holmes did not remove mothers and did not allow juveniles to emerge until they were 37 days old, which is 10–12 days beyond the species-typical age of natal emergence (Holekamp et al. 1984). The age at which young rodents are weaned and/or separated from their mother can alter the species-typical development of social play (Bateson & Young 1981; Terranova & Laviola 1995). Perceptual development can also be altered significantly if young are exposed to more or less sensory stimulation than they would usually experience in a species-typical rearing environment (Radell & Gottlieb 1992). This work alerted us to the possibility that the protracted pre-emergent period created by Holmes (1994) may have altered the course of species-typical social development. Therefore, we studied a group of juveniles transferred without mothers to an enclosure at an age (about 27 days) closer to that at which free-living young would emerge.

Third, species-typical development can be studied profitably by creating atypical rearing conditions, but the degree to which manipulations deviate from species-typical conditions must be scrutinized when interpreting behavioural results (Miller 1981). Thus, we evaluated whether the atypical environment we created by removing mothers induced an abnormal process that had little relevance to species-typical development. We examined rates of total play (without regard to relatedness), the effect of pairs' sex on rates of play and rates of juvenile–juvenile agonism for differences in these measures as a function of the absence of mothers.

Finally, because kin preferences depend on an ability to discriminate between kin and non-kin (Holmes 1988), and because some classes of *S. beldingi* kin may not be afforded preferential treatment because they are not recognized as kin (Sherman 1981b), we tested whether we had disrupted the development of kin recognition by removing mothers from the post-emergent environment, which could explain why litter-mates were not preferred social partners. There are theoretical reasons for separating the perception component from the action component in kin-recognition research (Reeve 1989), and just because kin are recognized, it does not follow that they will be treated preferentially (Gamboa et al. 1991). We used rates of nose-to-body contact to assess whether juveniles could discriminate between litter-mates and non-litter-mates in the absence of mothers. We reasoned that if the frequencies of litter-mate and non-litter-mate play were similar, but if the frequencies of olfactory investigation differed for the two types of pairs, then we could infer that juveniles recognized their litter-mates even if they did not prefer them as social partners.

Methods

Mothers in group 1 reared their offspring from birth until about 27 days of age in the nursery (Table I). We then transferred juveniles, but not their mothers, to an enclosure and recorded juveniles' social interactions during their first week above-ground. We recorded all play bouts, all occurrences of juvenile–juvenile agonism (avoid, chase and fight combined; Holmes 1995), all occurrences of nose-to-body contact, and the identities of sleeping partners. Finally, we used a scan-sampling technique (with 2-min intervals) and a grid system of 1.2-m^2 squares to quantify nearest-neighbour distances for litter-mates and non-litter-mates (Holmes 1994) to
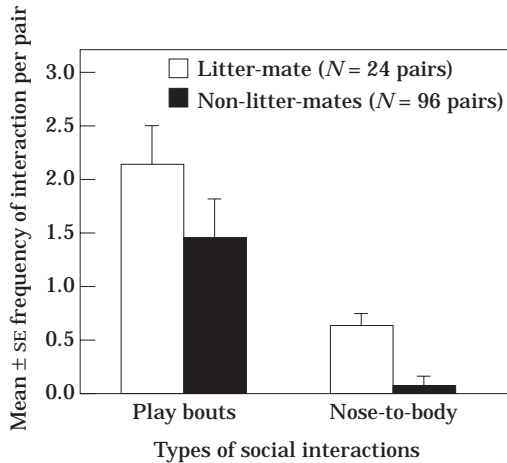
Figure 1. Mean ± SE frequencies of play bouts and of nose-to-body contact for pairs of litter-mates and non-litter-mates in group 1 observed during juveniles' first 7 days after natal emergence.

determine whether one type of juvenile might have been more available spatially for social interactions.

Results

The overall rate of play for group-1 juveniles observed in the permanent absence of mothers was 0.18 ± 0.06 bouts/pair/h. Based on the relatedness variable, the play ratio ($\pm 95\%$ confidence intervals) for group-1 juveniles was 1.25 (0.63, 2.25; $P \geq 0.1$); that is, the frequencies of litter-mate and non-litter-mate play were statistically indistinguishable when pairs' sex and weight difference was controlled (Fig. 1). In contrast, play ratios varied significantly with pairs' sex ($P<0.001$), ranging from 3.37 (1.79, 6.34) for male–male:female–female comparison to 1.59 (1.37, 1.84) for the male–male:male–female comparison. In the permanent absence of mothers, 3.9% of all juvenile interactions were agonistic (litter-mate and non-litter-mate agonism combined). Nose-to-body contact occurred about six times more often between litter-mates than non-litter-mates (Fig. 1).

Sleeping partners for group-1 juveniles were predominantly non-litter-mates, based on the mean derived from the 7 nights juveniles spent in the enclosure. For the average juvenile, $82.3 \pm 1.2\%$ of its sleeping partners were non-

litter-mates, which suggests that, in the absence of mothers, the identities of sleeping partners were independent of relatedness (General Methods). In contrast, when mothers are present, only about 15% of sleeping partners are non-litter-mates, which shows that litter-mates are preferred sleeping partners when mothers are present (Holmes 1994).

Mean nearest-neighbour distances for litter-mates (1.1 ± 0.3 m) and non-litter-mates (0.9 ± 0.2) were statistically indistinguishable ($P>0.1$); that is, both types of juveniles were equally available for social interactions.

Discussion

Both play-bout data and sleeping-partner data confirm that when mothers were removed at natal emergence, juveniles did not display social preferences for their litter-mates. Our results (Fig. 1) indicate that the lack of a litter-mate preference reported by Holmes (1994) was not due to the unusually long period of either exclusive mother–offspring pre-emergent association or development without exposure to non-litter-mates, both of which occurred in Holmes' (1994) study but not in the present study. The lack of an expressed litter-mate preference in experiment 1 was also not due to differences in nearest-neighbour distances for litter-mates and non-litter-mates, because both of these distances were about 1 m just as they were when mothers were present (Holmes 1994). Therefore, the spatial availability of a potential play partner cannot explain the presence or absence of a litter-mate preference.

Given the prominence of mothers in the lives of free-living juveniles (see Introduction), we considered whether litter-mate preferences failed to materialize because we created an abnormal environment by removing mothers. Four findings suggest that we did not induce abnormal development in captive juveniles. First, by the end of the 7-day observation period, mother-absent juveniles achieved about the same body weight (95.7 ± 4.8 g) as mother-present juveniles (99.1 ± 6.5 g, unpublished data), which suggests that the absence of mothers did not prevent normal juvenile growth. Second, mean rates of total play (litter-mate and non-litter-mate play combined) were unaffected by mothers' absence.

When mothers were present in enclosures, mean rates ranged from 0.15 to 0.27 bouts/pair/h (Holmes 1994), which includes the mean rate for group-1 juveniles observed without mothers (see Results). Third, although play bouts in experiment 1 were distributed randomly with respect to relatedness, they varied significantly with pairs' sex, as has been reported for both *S. beldingi* juveniles (Holmes 1994) and *S. lateralis* juveniles (Holmes 1995) studied in the presence of mothers, with male–male pairs playing the most and female–female pairs the least. Finally, the absence of mothers was not associated with increased juvenile aggression. Less than 5% of all juvenile–juvenile interactions are agonistic when mothers are present (Holmes 1994, 1997) and 3.9% of all juvenile interactions were agonistic in experiment 1.

In other species of mammals, there is little indication that the absence of mothers induces abnormal juvenile play (*Pan troglodytes*: Spijkerman et al. 1995; strains of *Mus*: Terranova & Laviola 1995). Even when differences in play do occur as a function of mothers' presence, the difference is often in the overall frequency of play rather than in its form (Bateson & Young 1981; see Pedersen et al. 1990 for a discussion of how social context affects mammalian play).

For kin to be preferred social partners they must be recognizable. Kin-recognition abilities are taxonomically widespread (Fletcher & Michener 1987), but there are also instances in which kin recognition would seem to be adaptive but apparently does not occur (Kempenaers & Sheldon 1996; Sherman et al. 1997). We do not think that *S. beldingi* juveniles failed to display a litter-mate preference because they could not discriminate between litter-mates and non-litter-mates. Kin recognition is inferred from the differential treatment of conspecifics based on correlates of genetic relatedness (Sherman et al. 1997) and the frequencies of nose-to-body contact (Fig. 1) suggest that juveniles living without mothers could distinguish between litter-mates and non-litter-mates. That juveniles recognized their litter-mates and yet did not prefer them as play partners or sleeping partners suggests that the development of kin recognition does not lead inevitably to the development of social preferences for kin. Thus, in *S. beldingi*, the developmental processes for kin recognition and kin preferences may not be the same.

EXPERIMENT 2: MOTHERS' AVAILABILITY

The most likely proximate explanation for the development of *S. beldingi* litter-mate preferences is learning through direct interactions with litter-mates, because litter-mates associate extensively with each other during early ontogeny but non-litter-mates do not (Holmes & Sherman 1982; Holmes 1997). We hypothesized that mothers might influence social development by affecting the opportunities of juveniles to associate with different types of social partners after natal emergence. Because juveniles encounter various age-mates during the day and associate with each other at night in burrows, we established two groups to examine how mothers influence the identities of social partners in each of these two contexts.

To examine how diurnal social experience might influence litter-mate preferences, we created a social environment similar to that used by Harlow & Harlow (1965) to investigate social development in rhesus macaques (*Macaca mulatta*). In this group, mothers were present in the enclosure, but were restricted to gazebos. If mothers influenced social development by preventing their offspring from interacting with non-litter-mates, for example, by herding them away from an alien juvenile or by attacking the alien, then we would not observe litter-mate preferences if mothers were present but restricted to gazebos and thus unable to intervene in juvenile–juvenile interactions.

In another group, mothers were not allowed to influence with whom their offspring shared a burrow at night, to test whether litter-mate preferences failed to develop in the absence of mothers because juveniles shared burrows with many more non-litter-mates than they would have if mothers were present (Holmes 1994). Therefore, we created a group in which mothers were present during most of the day, but they were removed daily before juveniles retired for the night.

Materials and Methods

In group 2 (Table I), we put mothers and their litters in an enclosure that included modified wire-mesh gazebos, placed over burrow entrances, with plastic tunnels (10 cm long × 2.5 cm in diameter) attached to each side of the gazebos. The size

of the tunnels restricted mothers to gazebos, but allowed juveniles to come and go. Mothers, therefore, could not intervene in social interactions that occurred outside gazebos or behave agonistically to alien young unless aliens entered gazebos. We observed group-2 juveniles during their first 9 days in the enclosure and recorded their social interactions during the day and their sleeping partners each night.

In group 3 (Table I), we removed mothers from the enclosure each afternoon (ca 1730 hours), about 2 h before juveniles' nocturnal immergence, and housed them individually overnight. Juveniles typically foraged before immergence and engaged in few social interactions. Each morning we reintroduced mothers, and they typically ran to their own burrow (the one into which they were placed on day 0), and used it during the day as an activity centre, as did mothers that were never removed from an enclosure. As a result of this schedule, mothers could intervene in juveniles' social interactions during the day, but they could not directly influence the identity of sleeping partners because mothers were removed before juveniles retired. We observed group-3 juveniles during their first 12 days in the enclosure, recording their social interactions during the day and their sleeping partners each night.

Results

For group 2, in which mothers were confined to gazebos, the litter-mate:non-litter-mate play ratio was 3.94 (2.94, 5.30; $P < 0.001$), that is, juveniles played with their litter-mates almost four times as often as with non-litter-mates on a per pair basis (Fig. 2). Thus, group-2 juveniles displayed a clear litter-mate preference. To determine whether we unduly affected juveniles' social interactions by confining mothers to gazebos, we compared rates of play, agonism (see experiment 1) and total social interactions of group-2 juveniles with the same measures from groups in which mothers were not confined to gazebos. For group-2 juveniles, the mean rates of play (0.20 bouts/pair/h), agonism (0.009 interactions/pair/h) and all social interactions combined (0.29 interactions/pair/h) were indistinguishable from those observed when mothers were not confined (Holmes 1994). Thus, restricting mothers to gazebos did not interfere with the ontogeny of litter-mate preferences nor did it produce atypical juvenile behaviour.
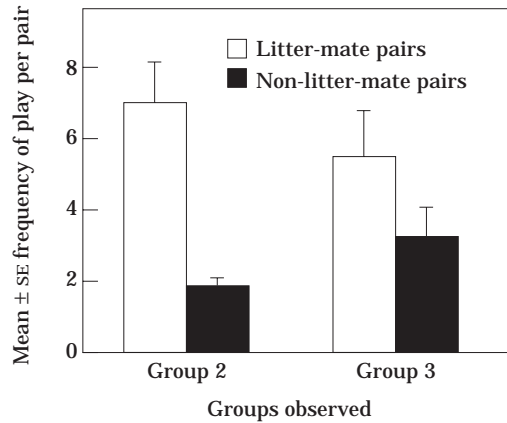

Figure 2. Mean ± SE frequencies of play bouts for pairs of litter-mates and non-litter-mates observed during juveniles' first 9 days (group 2) or first 12 days (group 3) after natal emergence. See Table I for sample sizes.

Sleeping partners in group 2 were predominantly litter-mates. Each night three or four juveniles (and one mother) occupied a burrow and for the average group-2 juvenile, more than 75% of its juvenile sleeping partners were litter-mates on each of its first 7 nights in the enclosure (Fig. 3).

For group 3, in which mothers were removed from the enclosure at the end of each day and returned the next morning, the litter-mate:non-litter-mate play ratio was 1.61 (1.00, 2.58; $P \geq 0.05$). Thus, although litter-mate play was more common than non-litter-mate play, juveniles did not display a statistically significant preference to play with their litter-mates.

Sleeping partners in group 3 were much more likely to be non-litter-mates than litter-mates. Although juveniles slept primarily with litter-mates during their first few nights in the enclosure, non-litter-mates soon became the most common sleeping partners; from day 4 on, about 80% of sleeping partners were non-litter-mates (Fig. 3). By day 4, 7–10 juveniles slept in each of two burrows at night and left two burrows unoccupied. To summarize, when mothers were present during the day and absent at night, juveniles did not display play-partner or sleeping-partner preferences for litter-mates.

Discussion

Our results (Fig. 2) suggest that *S. beldingi* mothers do not actively direct the development of
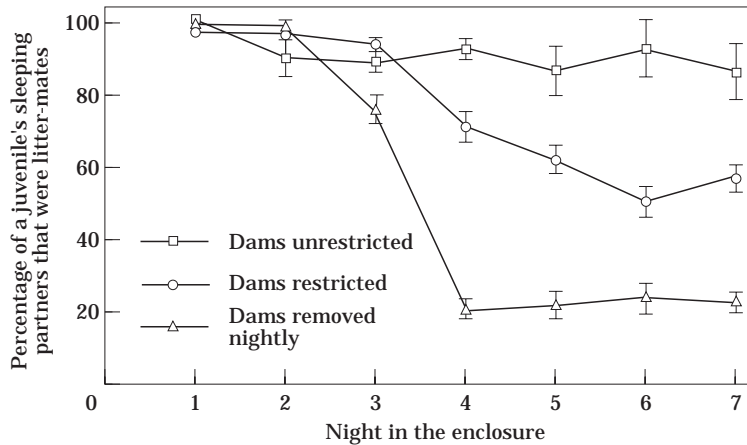
Figure 3. Mean $\pm$ SE percentages of juveniles' sleeping partners (juveniles in the same nestbox at night) that were litter-mates rather than non-litter-mates during the first 7 days juveniles were in an enclosure. Data for 'Dams unrestricted' are from Holmes (1994, figure 5), and data for 'Dams restricted' and 'Dams removed nightly' are from groups 2 and 3, respectively. If sleeping partners were chosen independently of relatedness, on average, 20% of sleeping partners would be litter-mates.

their offsprings' litter-mate preferences, even though mothers must be present after natal emergence for their offspring to express litter-mate preferences (experiment 1). First, we still observed litter-mate preferences even when group-2 mothers could not intervene in juveniles' above-ground social interactions (Fig. 2, group 2). Second, the distances between a juvenile and its nearest litter-mate and non-litter-mate neighbours did not differ whether mothers were present or absent, which means that mothers did not affect the spatial availability of potential play partners (Holmes 1994). These two results would not have been obtained if litter-mate preferences depended on mothers that could actively manage or control the above-ground interactions or movements of their offspring.

The presence or absence of mothers was associated with the relatedness of juveniles' sleeping partners. When mothers were restricted to gazebos, juveniles spent the night together with their litter-mates (Fig. 3, group 2) and preferred litter-mates as social partners (Fig. 2, group 2). In contrast, when mothers were present during most of the day but removed daily before juveniles retired for the night, sleeping partners were predominantly non-litter-mates (Fig. 3, group 3) and litter-mate preferences were not displayed (Fig. 2, group 3). The combined results from groups 2 and 3 suggest that the mother's presence influ-

enced the development of litter-mate preferences by affecting juveniles' opportunities to associate with classes of kin and non-kin at night, rather than by regulating juveniles' social partners during the day.

We do not know what motivates or controls juveniles' choices of sleeping burrows and/or sleeping partners. Three points, however, suggest that the presence of mothers can influence juveniles' nocturnal immergence, but that mothers do not actively dictate who sleeps where and with whom. First, mothers often behave agonistically to alien juveniles that approach them, which reduces the likelihood that a juvenile would enter an alien mother's burrow. Second, earlier observations (group 3 in Holmes 1994) revealed that juveniles occupied a burrow with their own mother rather than an alien mother on 81.3% of the nights juveniles were in an enclosure. If a mother had already retired for the night, however, and an alien juvenile entered her burrow, there was an 83.0% chance (93 of 112 instances) that the alien would remain overnight rather than be evicted. Thus, even though juveniles spent the night with their mother over three times as often as expected by chance (25%), mothers that were already below ground were tolerant of aliens that entered their burrow and spent the night. Finally, observers never saw mothers act as gatekeepers during nocturnal immergence by staying near

their burrow and inspecting each juvenile that approached. We believe that where and with whom an enclosure-housed juvenile spends the night depends on multiple factors (e.g. the burrow into which the juveniles was first placed, the presence/absence of related and unrelated age-mates in the burrow, the presence/absence of the juvenile's mother), and we found no indication that mothers actively determined the identity of their offsprings' sleeping partners.

EXPERIMENT 3: EARLY JUVENILE INTERACTIONS

Spermophilus beldingi juveniles use their mother's burrow system as an activity centre during the day (Holekamp 1984) and spend nights in the natal burrow with their mother and litter-mates (Sherman 1980) for their first few weeks above-ground. During juveniles' first 3–5 days above-ground, natal-burrow fidelity provides juveniles with many opportunities to interact with their litter-mates and reduces the likelihood of meeting non-litter-mates (Holekamp 1984). Social inter-actions during the peri-emergence period, the few days before and after natal emergence, are crucial to the ontogeny of litter-mate preferences (Holmes 1997), and the results of experiment 2 suggest that the mother's presence influenced post-emergent social development, specifically juveniles' opportunities to associate with related and unrelated age-mates. If so, then even in the absence of mothers we should be able to instill litter-mate preferences by limiting juveniles' social associations shortly after natal emergence. To test this prediction, we removed mothers at natal emergence and housed juveniles so that they could interact only with their litter-mates for a few days. We then gave juveniles access to both litter-mates and non-litter-mates in the continued absence of mothers to assess juveniles' social preferences. We also recorded juveniles' sleeping partners to pur-sue the association between play-partner prefer-ences and sleeping-partner preferences found in experiment 2.

Methods

We transferred group-4 juveniles (Table I) with-out their mothers to an enclosure on day 0 and placed one litter in each of four nestboxes. We covered burrow entrances with gazebos (see General Methods), which restricted juveniles' social partners to litter-mates, and left gazebos in place until the morning of day 3. We then removed the gazebos for the first time, and recorded social interactions and sleeping partners for 7 days (days 3–9). We left gazebos in place on days 1–3 because this period falls within the time window during which above-ground interactions influence the development of *S. beldingi* social preferences (Holmes 1997) and free-living juve-niles start venturing from their natal burrow (unpublished data).

Results and Discussion

The litter-mate:non-litter-mate play ratio for group-4 juveniles was 1.54 (1.11, 2.12; $P \leq 0.02$). Although this play ratio was not as great as the one found in group 2 (3.94; see experiment 2), it was significant, indicating that litter-mate play occurred about 1.5 times as often as non-litter-mate play after gazebos were removed. For the average juvenile on nights 3–9, $36.2 \pm 4.0\%$ of its sleeping partners were litter-mates (Fig. 4). Thus, in the absence of mothers, group-4 juveniles dis-played a play-partner preference for litter-mates, unlike group-1 juveniles which displayed no such preference in mothers' absence, but group-4 juve-niles did not display a sleeping-partner preference for litter-mates (Fig. 4). That is, play-partner preferences and sleeping-partner preferences were disassociated with respect to juvenile relatedness.

We suggest that, by restricting newly emergent juveniles to gazebos for 3 days, we mimicked part of what happens when mothers are present at natal emergence: juveniles associate exclusively with litter-mates, both during the day and night, which facilitates the developmental process that generates litter-mate preferences. The display of litter-mate preferences in the absence of mothers (Fig. 4) supports our proposition that mothers do not actively direct the ontogeny of litter-mate preferences. The results demonstrate that once litter-mate preferences are instilled, in part as a result of social experience on juveniles' first few days above-ground, they remain intact even though juveniles' night-time associates are much more likely to be non-litter-mates than litter-mates in mothers' absence. Hence, whatever the
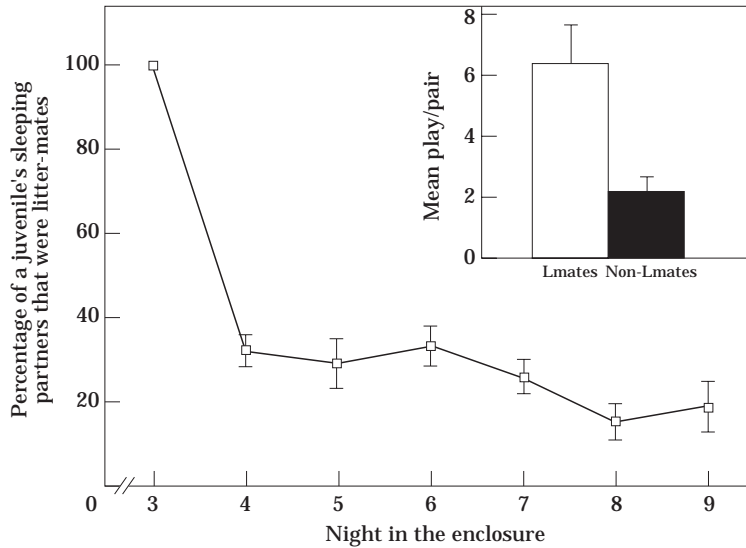
Figure 4. Mean ± SE percentages of juveniles' sleeping partners in group 4 that were litter-mates rather than non-litter-mates during nights 3–9 when juveniles were in an enclosure. The insert shows mean ± SE frequencies of play bouts for litter-mates (Lmates) and non-litter-mates (Non-Lmates) in group-4 juveniles.

effect mothers have on the ontogeny of their offsprings' social preferences, it seems to operate for only the first few days after natal emergence, and the results of experiment 2 suggest that even this effect is indirect.

GENERAL DISCUSSION

Maternal effects, those that result when a mother's phenotype directly influences the phenotype of her developing young (Mather & Jinks 1971, page 293), have been investigated in several vertebrates (reviewed in Bernardo 1996). The development of long-term affiliative relationships (Chalmers 1983; Hinde 1983) and of social networks (Berman et al. 1997) can have important fitness consequences for group-living organisms (e.g. Fairbanks & McGuire 1986), and in some species maternal effects are apparent in the developmental processes that generate such relationships (Chalmers 1983; Pereira & Altmann 1985; de Waal 1996). In ground-dwelling squirrels (*Cynomys*, *Marmota* and *Spermophilus*), adult social relationships are hypothesized to emerge from experiences that young have during their first 2 months of postnatal life (Armitage 1981; Michener 1983), and the mother–infant dyad

seems to be the most fundamental unit from which other relationships derive (e.g. Rayor & Armitage 1991).

For Belding's ground squirrels, a maternal effect on social development was apparent when, in the absence of mothers, juveniles failed to display social preferences for their litter-mates (experiment 1), preferences they express under a variety of rearing regimens when mothers are present (Holmes 1997). Rhesus macaque mothers affect the development of their offsprings' social networks by actively and selectively preventing or allowing other conspecifics to interact with their offspring and vice versa (de Waal 1990; Berman et al. 1997), whereas spotted hyaena, *Crocuta crocuta*, mothers affect social development by sometimes interrupting intensely aggressive interactions in which their offspring are involved (Jenks et al. 1995). We sought evidence for similar patterns of active maternal intervention in *S. beldingi*, but found none. In over 300 h of observations on 18 enclosure-housed groups, we never saw an unequivocal example of an adult female intervening in a juvenile–juvenile social interaction (Holmes 1994, 1997; unpublished data). Lacking evidence for direct maternal intervention, combined with the results of experiment 2, we propose that the mother's presence

indirectly influences post-emergent juvenile social development by affecting nocturnal burrow use, and thus the degree to which juveniles associate with non-litter-mates after natal emergence.

Even when mammalian mothers do influence the development of their offsprings' social relationships, it may be difficult to detect a maternal effect because there are so many ways in which such effects could be mediated (Bernardo 1996). For instance, maternal intervention may be one proximate mechanism by which juvenile spotted hyaenas establish dominance over other juveniles (Holekamp & Smale 1991). Despite the appeal of this hypothesis, maternal interventions in both free-living (Holekamp & Smale 1993) and captive (Drea et al. 1996) spotted hyaenas are rare, even though mothers are frequently present when their offspring interact with other juveniles in circumstances that are important to survival. A host of factors contribute to the ontogeny of dominance relationships in juvenile spotted hyaenas (Jenks et al. 1995), making it difficult to detect and study a maternal effect on social development independently of other factors. Indeed, maternal effects may be the rule rather than the exception in species with maternal care, and some of these effects may have been overlooked because of their subtle nature. For example, maternal style and the degree to which maternal care influences the development of infant rhesus macaques' social networks depend on the demographic make-up of the infants' social group (Berman et al. 1997).

In free-living Belding's ground squirrels, we suggest that, after juveniles have come above-ground, their social development proceeds with little direct input from mothers. For instance, mothers cease territorial defence within 1–2 days of the above-ground appearance of their offspring, which allows unrelated adults to visit the resident mother's former territory (Sherman 1976, 1980). Mothers give alarm calls that warn their offspring and other kin of danger (Sherman 1977, 1985), but mothers do not try to herd or lead their offspring to safety when they hear an alarm call (Mateo 1996; Mateo & Holmes, 1997). Finally, because mothers routinely forage over 15 m from their offspring during juveniles' first 5 days above-ground (unpublished field data), mothers have few opportunities to intervene in juveniles' social interactions even if they were motivated to do so. We hypothesize that litter-mate preferences

develop in free-living juveniles for three proximate reasons. First, juveniles are biased to interact with their litter-mates coincident with natal emergence as a result of having shared a burrow with them (Holmes 1997). Second, newly emergent juveniles remain near their natal burrow after emergence, interacting frequently with litter-mates, which helps to consolidate the litter-mate bias with which juveniles emerge. Finally, the chances of encountering non-litter-mates are slim during juveniles' first few days above-ground because of the distances between natal burrows.

If free-living mothers are as uninvolved in their offsprings' post-emergent social development as we suggest, then what is the relevance of our captive-animal experiments to the role of mothers in the ontogeny of litter-mate preferences in nature? First, litter-mate preferences are not fully formed when juveniles first appear above-ground because, if they were, we should have observed preferences even if mothers were absent. Had we not removed mothers, we might have concluded that preferences were fully formed at natal emergence, because litter-mate play is more common that non-litter-mate play on day 1 above-ground when mothers are present (unpublished data). Second, because mother–juvenile distances were much reduced in enclosures compared with in the field (Holmes 1994), we discovered that even when captive mothers were consistently near juveniles, they still did not intervene directly in juveniles' social interactions. In nature, mothers might not intervene because they lack opportunities to do so due to the spatial distribution of juveniles. Such an argument, however, could not be made for enclosure-housed mothers.

Finally, our results suggest that free-living juveniles' preferred social partners are those with whom they associated directly, independently of relatedness, and that sharing a burrow at night, after natal emergence, provides the kind of association that can influence social development. This direct-association effect would have been difficult to examine in the field because juveniles in their first week above ground rarely sleep in a burrow other than their natal burrow (Sherman 1980); thus, by default the night-time associates of juveniles are almost exclusively litter-mates. In contrast, we discovered in our mother-removal experiments that the night-time associates of captive juveniles were primarily non-litter-mates (Fig. 3), and that play-partner preferences for

litter-mates failed to materialize when juveniles routinely shared burrows with non-litter-mates (Fig. 2, group 3). This result suggests that, for free-living ground squirrels, an important consequence of natal-burrow fidelity is that it affords juveniles the experience they need with related age-mates to complete the development of litter-mate preferences. It remains to be seen whether the ontogeny of litter-mate favouritism in other species of polytocus mammals requires the presence of mothers and/or opportunities for litter-mates to interact outside the natal environment they first occupied and before they begin to encounter non-kin age-mates.

ACKNOWLEDGMENTS

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