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ORIGINAL ARTICLE

Alloparental behaviour in Sinai spiny mice *Acomys dimidiatus*: a case of misdirected parental care?

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Abstract Communal breeding, where reproducing females share a nest and the care of their pups, occurs in many animal species. According to kin selection theory, alloparental behaviour should occur predominantly among closely related conspecifics. However, familiarity between females, a prerequisite for reciprocal altruism, may also play a role. The aim of our study was to analyse the effect of kinship and familiarity on the occurrence of two types of alloparental care—nursing and the retrieval of pups wandering from the nest—in a communally breeding rodent, the Sinai spiny mice *Acomys dimidiatus*. In addition, the effects of other factors that may also have an impact on alloparental care were tested; these included age difference between litters, pup age, maternal experience, pup sex ratio, litter size, group age, and mother's weight. We found that kinship and familiarity had no effect on alloparental care. The nursing of alien pups depended on the maternal reproductive experience measured as the number of weaned litters and also on the age difference between the litters of both females. Less experienced females nursed alien pups more often than experienced ones. With increasing age difference between litters, females preferentially nursed their own pups. Similarly, the retrieval of alien pups was affected by the age disparity between the litters; with increased age difference, the females more readily retrieved their own pups. These results indicate that the occurrence of alloparental care in the Sinai spiny mouse may be more related to misdirected parental care than to kin selection.

Keywords Alloparental behaviour · Communal breeding · Spiny mice · Cross-fostering · Kin selection · Misdirected care

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Significance statement

Despite the widespread interest in kin selection theory, which was considered to be most appropriate explanation of alloparental behaviour in the past, little is known about other social factors that affect this behaviour, especially about those connected with pup recognition. The aim of our study was to analyse the effect of kinship and familiarity together with other social factors regarding two types of alloparental care in cooperatively breeding Sinai spiny mouse (*Acomys dimidiatus*) to test kin selection and/or reciprocal altruism theory. 85 family groups differing in kinship and/or familiarity between co-nesting females using cross-fostering method were tested in the experiments. Our results demonstrate that alloparenting in this species is rather related to misdirected parental care than kin selection and/or reciprocal altruism strategy. Pup discrimination in Sinai spiny mouse seems to be probably more costly issue than providing alloparental behaviour.

Introduction

Among several group-living animals, some individuals take care of infants that are not their own—a behaviour named alloparenting (e.g. Bourke and Heinze 1994; Dugatkin 1997; Scott 1998; Hayes 2000; Balshine et al. 2001; Clutton-Brock 2002; Roulin 2002; Koenig and Dickinson 2004; Pluháček

et al. 2011). Alloparenting species in which breeding adults share a nest are denoted as communal breeders. Foster caregiving individuals exhibit various forms of alloparental care including grooming, huddling, defence against predators, retrieval of offspring and even nursing (König 1997). Among these forms of parental behaviour in mammals, lactation is especially energetically costly; it requires increased food intake and can negatively affect females' future reproductive success (Clutton-Brock et al. 1989; Rogowitz 1996; Liu et al. 2003; Bårdsen et al. 2009). Similarly, the retrieval of pups that have strayed from the nest is a display of protective behaviour that may increase the risk of predation, and it limits the locomotive ability of the carrier (Price 1992; Schradin and Anzengerger 2001; Noren 2008). As a result of high parental investment, females should preferentially care for their own offspring instead of providing such valuable resources as milk and protection to alien young (König 1994a).

The potential costs associated with communal breeding may be partially offset if aid is given to relatives and thus enhances indirect fitness (Hamilton 1964). Therefore, taking mutual care of a close kin's pups should be adaptive (Cockburn 1998; Russell and Hatchwell 2001; Rusu and Krackow 2004; Eberle and Kappeler 2006; Hatchwell 2009). For instance, in the colonial breeding mammal tuco-tuco (*Ctenomys sociabilis*), groups consist predominantly of closely related females (Lacey and Wieczorek, 2004). Similarly, in laboratory house mice (*Mus musculus domesticus*) and bank voles (*Myodes glareolus*), communally breeding sisters breed more often and wean more offspring than unrelated females (König 1993, 1994a; Mappes et al. 1995; Rusu and Krackow 2004).

However, in several other rodent species that communally breed, such as the degu (*Octodon degus*) or the wood mouse (*Apodemus sylvaticus*), alloparental behaviour among individuals is based on familiarity, not the relatedness (Gerlach and Bartmann 2002; Epensperger et al. 2006). Familiarity between unrelated partners is a basic requisite for reciprocal altruism (Fletcher and Zwick 2006), where the helping behaviour of two or more individuals is mutual (Trivers 1971). According to this theory of reciprocal altruism, one individual could increase the fitness of another individual on the basis of previous interaction, and the potential costs of helping are offset by expected future help (Rutte and Taborsky 2008). Thus, communal breeding may be beneficial in terms of increased reproductive success for both familiar co-nesting females and related ones. Several studies of house mice confirm this assumption (König 1994b; Rusu et al. 2004; Weidt et al. 2008).

On the other hand, some authors consider alloparenting to be misdirected parental care that results from group living and communal nesting (Riedman 1982; Price et al. 1983; Wisenden 1999; Strickler 2013). Thus, the nursing of alien pups may be a consequence of a reduced ability to recognize own pups because of similar age of non-sibling littermates (Manning et al. 1995), low breeding experience of primiparous females (Maniscalco et al. 2007) or large litters (Roulin 2002). There are also some other factors potentially influencing alloparental behaviour such as a pup's age or the age of the breeding group (Porter and Doane 1978; Lambin and Mathers 1997; Hayes 2000). The participation of females in communal care may also be influenced by their physical condition (König 1994b) or by the sex ratio of the pups (Lacey 2004).

Sinai spiny mice (*Acomys dimidiatus*, Rodentia) breed communally, at least in laboratory conditions (Čížková et al. 2011). Previous behavioural research regarding spiny mice, especially Cairo spiny mouse (*Acomys cahirinus*), was predominantly focused on sibling recognition and huddling preferences (e.g. Porter 1988). Huddling among siblings in spiny mice is largely affected by familiarity and kinship (Porter et al. 1982; Porter 1986). However, relatedness and familiarity were not studied in the case of alloparental care. Previous studies concerning alloparental behaviour have focused mainly on the dominance hierarchy of co-nesting females, their actual reproductive state, and the age difference between the litters of co-nesting females (Porter and Doane 1978; Porter et al. 1980).

The aim of our study was to test several hypotheses about the occurrence and function of alloparental care in Sinai spiny mice during nursing and pup retrieval tests. First, we expected that nursing and retrieval are kin-selected. Due to the costs associated with these two types of behaviour (energy expenditure connected with lactation and decreased locomotive abilities associated with retrieval in addition to increased risk of predation), we expected that alloparenting in kin would be more common than in non-kin females. Secondly, we tested that alloparental behaviour would be supported by familiarity irrespective of relatedness. In this case, we predicted that alloparenting would be more prevalent in familiar than in unfamiliar females. Finally, we tested the misdirected parental care hypothesis, whereby if alloparental behaviour is a result of misdirected care, it should be more frequent in cases where conditions for correct pup recognition are difficult (e.g. low breeding maternal experience, large litters or litters with same-aged pups) (c.f. Porter 1986; Maniscalco et al. 2007). We also included other factors (pup age, pup sex ratio, group age and mother's weight—see Table 1) that might also contribute to the occurrence of nursing and the retrieval of alien pups (König 1997). For our experiments, we used the cross-fostering approach. Moreover, in part of the retrieval experiment, we simulated the more difficult conditions of a physical barrier, over which a female carrying a pup had to climb back to the nest. This setup allowed us to differentiate between accidental and directed alloparenting. Due to the fact that some species indiscriminately nurse alien pups but do not retrieve them so often (Eberle and Kappeler 2006), we also expected differences in the incidences of these two forms of alloparental care with higher proportion of allocare during nursing.

Table 1 The list of variables included in the full GLMM model assessing the potential influence on the nursing and/or retrieval of alien pups of both co-nesting females of the Sinai spiny mouse

Variable	Description
Relationship between females	Kinship and/or familiarity of co-nesting females
Maternal experience	Measured by the number of the weaned litters
Weight of female	In grams
Age disparity between litters	Age disparity between the last litters of both breeding females (in days)
Litter size	Number of pups in the litter of the nursing or retrieving female
Age of pup(s)	In days
Sex of the pup(s)	Sex ratio in allonursing (number of nursed male pups/number of all nursed pups) or sex of retrieved pup respectively
Group age	Age when the family group of the given female was established (in days)
Barrier	The presence or absence of a barrier (only for retrieval tests)

Material and methods

Study species

Spiny mice of the genus *Acomys* (Acomyinae, Muridae) are small rodents native to Africa and the Middle East (Nowak 1999; Dewey 2003). The Sinai spiny mouse was previously considered to be a subspecies of the Cairo spiny mouse (*Acomys cahirinus*), but is now regarded as a distinct species according to Musser and Carleton (2005) and Volobouev et al. (2007). Despite extensive knowledge on the physiology and recognition capabilities of the genus *Acomys* (predominantly Cairo spiny mice) (Porter 1988), studies on social and maternal behaviour of spiny mice are rare (for an exception, see, e.g. Dieterlen 1962). Further, studies on Sinai spiny mice from nature are lacking completely; the only information regarding the biology and social behaviour that is available is from captive animals (Čížková et al. 2011; Frynta et al. 2011). Sinai spiny mice live in small family groups consisting of an adult male, several breeding females and their offspring. According to our observations, this species usually nests communally with the pups in one nest. Communally nesting Sinai spiny mice females cooperate in nursing and retrieving alien pups, and even males display huddling and paternal care of pups (BC and RS, unpublished data). Breeding in the Sinai spiny mouse in captivity is continual and females have postpartum oestrus. If fertilization is not successful, copulation re-occurs within 9 to 11 days (BC, unpublished data); these characteristics are similar to those in the Cairo spiny mouse (Peitz 1981). After a gestation period of 38–39 days, Sinai spiny mice produce an average of three precocial pups (range 1–6; Frynta et al. 2011). When separated from pups, spiny mice mothers retrieve them (BC, unpublished data). Pups are weaned at 3–4 weeks of age and reach sexual maturity at about 2 months of age (Peitz 1981; VT, unpublished data).

The breeding stock of Sinai spiny mice in our study came from Prague Zoo, via the Bronx Zoo. The mitochondrial control region haplotype indicates a probable origin in Israel, Sinai or Jordan (Frynta et al. 2010). Our studied spiny mice were descendants of animals living in captivity for many years, i.e. unknown number of generations.

Animal housing

The animals were kept in plastic rodent cages T4 VELAZ (55 × 32 × 18 cm) under standard laboratory conditions (14L/10D; temperature between 20 and 23 °C) in the animal facilities at the Faculty of Science, University of South Bohemia, in České Budějovice. Food (commercial rodent pellets ST1) and water were provided ad libitum. Sawdust was used as bedding and flowerpot halves were provided as shelter or nests (Libhaber and Eilam 2004). When females delivered pups on the same day, they were observed to give birth in different places in the cage. Within a few hours after parturition, females brought both litters together in one nest, usually under the clay flowerpot. The animals also had access to sources of environmental enrichment (tree branches, rolls of paper, coconuts) and supplemental food such as bread crusts and mealworms.

Observation and experiments

The experiments were performed in accordance with all Czech laws and in compliance with all corresponding EU regulations. All of the experiments were conducted during year-round breeding under lab conditions. Eighty-five family groups of Sinai spiny mouse were divided into four categories (see below). We did not use blinded methods for establishing the family groups, i.e. the experimenter in all cases knew to which family groups tested females belonged. Each group initially consisted of two adult nulliparous females and an

unrelated adult male of the same age. Older offspring were regularly removed from the groups to avoid inbreeding and overcrowding. Breeding females were individually marked by cutting off small patches of fur. Marks were redone every 2 months. Pups were marked with a black felt-tip pen and re-marked every third day during weighing. These ink marks were usually ignored by other cage mates and were rarely sniffed; no aggressive behaviour towards marked pups due to the procedure was observed. Marking rodent pups with felt-tip pens is an acceptable method for individual identification (e.g. Cavigelli et al. 2010). Breeding females were weighed once a week (Čížková et al. 2011). The health of each animal was monitored, usually during weighing or regular daily care.

The groups were divided into four categories according to their kinship and familiarity of co-nesting females: kin familiar (26 groups)—sisters that grew up together from birth; kin unfamiliar (18 groups)—sisters that were separated after birth and grew up in separate families, one in its own and another in a foster family; non-kin familiar (16 groups)—unrelated females, which grew up together from birth, but one of them was born in another family group; and non-kin unfamiliar (25 groups)—unrelated females, which did not grow up together from birth. Cross-fostering was started within 24 h after birth (see Mateo and Holmes 2004; Porter et al. 1981). One newborn female pup was removed from its biological mother, scented carefully with the bedding material from the foster family's cage and placed among pups of the foster litter. The age of the cross-fostered pups was within 24 h of the age with the foster litter. These pups grew in foster families until sexual maturity and along with their biological sisters were used as founders of new groups in the kin non-familiar category or with their foster siblings in the non-kin familiar category. From the 47 female pups that were moved into foster families, 42 of them were successfully weaned (89 % survival). Five pups (11 %) subsequently died, probably due to natural mortality as we did not observe any infanticide during the cross-fostering procedure.

All family groups were checked daily for newborn pups. For all litters, the number of pups in the litter, the sex of each pup based on anogenital distance and the identity of their mother was recorded. If both co-nesting females gave birth at the same time, identification of the mother was determined by site of delivery (see above) and by the behaviour of the female towards the pups (each female was more attached to its own pups). Litters that were not distinguishable from each other were not included in the analysis.

Experiment I: nursing

Nursing mothers were monitored once per check day. Check day means that females were controlled for potential occurrence of allonursing behaviour. Each female was lifted by her tail and the suckling pups remained attached to the female's nipples. The identity of nursed pups was assessed and the relationship between the mother and infant recorded (own or alien pup). During the entire study, every group and female was examined an average of 30 times and each litter was checked an average of seven times. Checks were conducted about two or three times per week, evenly distributed throughout the breeding period and based on actual litter production. A total of 1682 checks of nursing were done.

Experiment II: retrieval

The retrieval test was conducted on pups within 2 weeks of birth. After 2 weeks of age, pups were agile enough to move back to the nest and were rarely retrieved by females. This experiment was based on the observation that Sinai spiny mice pups which are separated from their nest and mothers are retrieved (BC and VT, unpublished data). Every family (i.e. pair of females) was tested an average of 16 times and every litter about five times. The test was carried out in the home cage with both mothers at the same time and had two options. In the first option, all pups in the cage were removed from the nest and placed on the opposite side of the cage at 30-cm distance from the nest. The experiment ended when one of the females retrieved the first pup. Our preliminary observations showed that while one female carried a pup to the nest, the other pups would start to crawl back to the nest. If no pup was retrieved, the experiment was stopped after 5 min (Manning et al. 1995). The retrieving female and the first retrieved pup were identified, and the latency time to retrieval was recorded, i.e. the duration from placing the pups in the opposite side of the cage to the beginning of retrieval.

The second option of the retrieval test was carried out 1 h later with the same experimental protocol as the first but with a barrier in the middle of the cage that separated the females and the pups (see Porter and Doane 1978). It was a 6-cm-high paper carton barrier and its length corresponded to the width of the cage. The pups could not pass the barrier and the females could climb over only with some effort. Thus, the barrier simulated more difficult conditions than in the first option. The experiment was finished when the first pup was retrieved or when the 5-min limit had elapsed.

Statistical analyses

Generalized linear mixed effect models (GLMM) in R 2.13.0 (R-project 2011, GLMER lme4 package) were used to assess the effect of the factors (see below) on the nursing and retrieval of alien pups. Each type of alloparental behaviour was evaluated separately. The relationship between female and nursed/retrieved pup(s) (own versus alien) was a dependent variable with a binomial distribution in both GLMM analyses. The complete list of all independent variables tested in the full

model is included in Table 1. In order to assess the best model, we started with the full model including all of the tested variables in both analyses and then we performed backward stepwise regression using AIC-IT approach for model variable selection (Symonds and Moussalli 2011). The final model was the one with the lowest value of AIC. Additionally, because of non-linearity of the effect of some variables, we used second-order polynomial approximation of the given variable(s) in the final model in order to better describe the slope of dependency. The second-order polynomial model was then compared with a linear effect of the given variable, and suitability of both models was based on the lower value of AIC.

In addition to the analyses using absolute values of the age difference between litters (see Table 1) in days, separate analyses were performed to assess the effect of the litter order on the differences in display of alloparental behaviour in females. The relationship between female and nursed/retrieved pup(s) (own versus alien) was a dependent variable with a binomial distribution in both GLMM analyses. The independent variables included in the full model were the same as in the above model except for the age difference between litters in days which was replaced by litter order to acquire information on whether the female's own litter was younger or older than the alien litter. The cases where both litters were delivered on the same day were not included in this analysis.

The GLMM model was also used to compare the proportion of two alloparental activities, i.e. whether alloparenting occurs more often during nursing or retrieval. For this analysis, we use the proportion of instances of allonursing in the total number of nursing events versus the proportion of instances of alloretrieval in the total number of retrievals (independent variable activity), with relationship between the female and the pup(s) (own versus alien) as the dependent variable with binomial distribution. A linear mixed effect model (LMM) was used to determine the difference in latency between the retrieval of own and alien pups, with latency as a dependent variable with normal distribution. Individual female identity was included as a random effect in all of the performed analysis to avoid pseudoreplication.

Results

We observed 447 cases of pup nursing out of 1682 checks. Females were nursing only their own pups in 311 instances (69.6 %), and at least one alien pup (alone or together with the female's own pup) was being nursed in 136 cases (30.4 %). 34.2 % of the females never nursed alien pups. The GLMM model (Table 2) revealed significant effects for maternal experience and age disparity between litters in relation to the occurrence of allonursing. The nursing of alien pups decreased with the greater reproductive experience of the female, i.e. females with more litters were more likely to nurse their own pups rather than alien ones (GLMM: estimate 0.304, SE = 0.07, df = 1, $z = 4.41$, $p < 0.0001$; Fig. 1). Females also preferentially nursed their own pups when the difference in age between their own and the alien pups increased (GLMM: estimate 0.05, SE = 0.02, df = 1, $z = 2.33$, $p = 0.0197$; Fig. 2). After exclusion of the cases where females delivered litters on the same day, litter order had a significant effect on the occurrence of allonursing again together with maternal experience (GLMM: estimate 0.36, SE = 0.08, df = 1, $z = 4.7$, $p < 0.0001$). Females nursed alien pups more often if their own litter was older than the alien (GLMM: estimate −0.95, SE = 0.24, df = 1, $z = -3.91$, $p < 0.0001$; Fig. 3). Other factors including relationship between females (kinship and/or familiarity) had no effect on the occurrence of allonursing in both analyses (Table 2).

Table 2 Effect of particular variables on the occurrence of allonursing (GLMM)

Variable	Estimates	SE	df	z	p
Relationship between females	−0.52	0.58	3	−0.89	0.3716
Experience of female	0.53	0.16	1	3.40	0.0007
Weight of female	−0.004	0.02	1	−0.31	0.7532
Age variation between litters	0.05	0.02	1	2.40	0.0162
Size of litter	−0.006	0.17	1	−0.04	0.9707
Number of pups	−0.008	0.16	1	−0.05	0.9614
Age of pups	−0.019	0.02	1	−1.01	0.3150
Gender of pups	−0.34	0.32	1	−1.06	0.2904
Age of group	−0.006	0.004	1	−1.54	0.1231

Out of 907 retrieval tests, 626 instances of pup retrieval were observed during the 5-min tests. Females were observed retrieving their own pup in 514 instances (82.1 %) and an alien pup in 112 cases (17.9 %); 54.2 % of females never retrieved alien pups. The GLMM model (Table 3) revealed a significant effect for age disparity between litters. The retrieval of alien pup(s) decreased with increasing age difference between litters. With a greater age difference between pups, females predominantly retrieved their own pup (polynomial-GLMM, estimate 19.72, SE = 4.79, df = 1, $z = 4.11$, $p < 0.0001$; Fig. 4). After we excluded cases where females delivered litters on the same day, litter order had a significant effect on the occurrence of retrieval of the alien pups. Females retrieved alien pups more often if their own litter was older than the alien litter (GLMM: estimate −1.82, SE = 0.35, df = 1, $z = -5.15$, $p < 0.0001$; Fig. 5). Other factors, including the relationship between females (i.e. kinship and/or familiarity), had no significant effect on the incidence of retrieval of alien pups in both analyses (Table 3). The presence of a barrier had no significant effect on the number of occurrences of retrieval of own/alien pups. Females tended to retrieve their own pups more quickly (latency was shorter) than the alien pups (LMM: estimate −0.28, SE = 0.15, df = 1, 526, $t = -1.86$, $p = 0.064$).

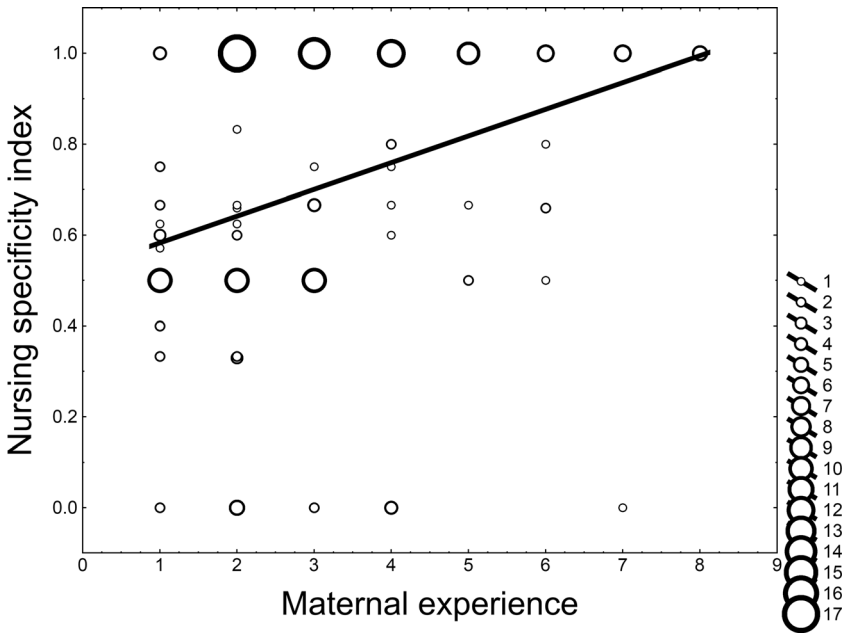

Fig. 1 Effect of maternal breeding experience on the occurrence of allonursing in the Sinai spiny mouse. The *point size* indicates the number of females in a particular sample; maternal breeding experience is measured by the number of weaned litters and nursing specificity index—instances of exclusively nursing own pups/total instances of nursing. Females with greater reproductive experience were more likely to nurse their own pups rather than alien ones

The proportion of allocare in the total number of nursing events significantly differed from the proportion of allocare in all retrieval events. The nursing of alien pups occurred more often than retrieval, i.e. females would rather nurse alien pups than retrieve them (GLMM: estimate 0.66, SE = 0.16, df = 1, $z = 4.11$, $p < 0.0001$) (Fig. 6).

Discussion

The aim of our study was to test several hypotheses about the occurrence and function of alloparental care in a social rodent, the Sinai spiny mice, related to nursing of pups and during their retrieval to the nest. Although we expected an effect of the relatedness and/or familiarity between co-nesting females, our results demonstrated that kinship and familiarity had no significant effect on the occurrence of either of these behaviours. Nursing and the retrieval of an alien pup were more likely exhibited in reproductively less experienced females and among mothers with litters of similar age.

We found that maternal reproductive experience had an influence on the occurrence of allocare in Sinai spiny mice. Less experienced mothers, i.e. females with a low number of weaned litters, nursed alien pups more often than more

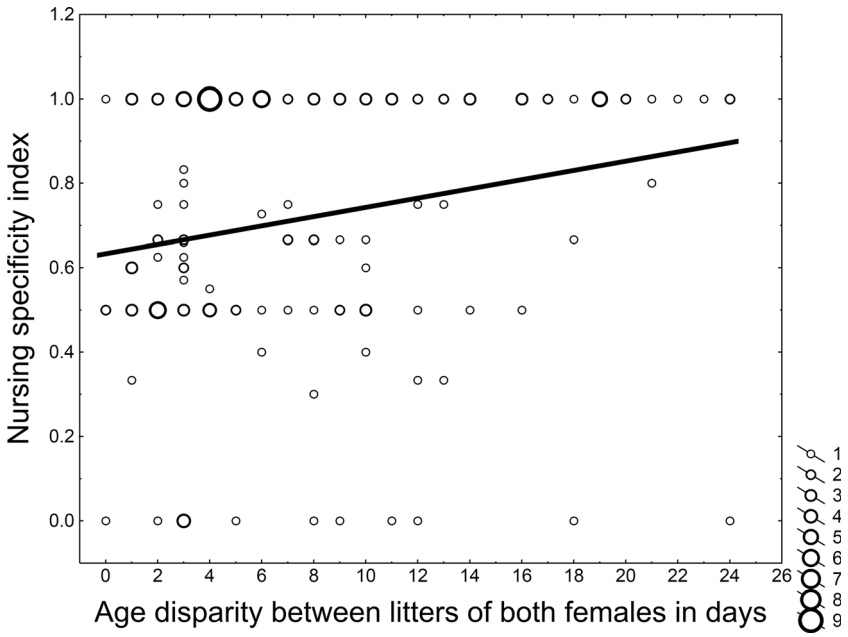

Fig. 2 Effect of the age disparity between litters of two co-nesting females on the occurrence of allonursing in the Sinai spiny mouse. The *point size* indicates the number of females in a particular sample; nursing specificity index—instances of exclusively nursing own pups/total instances of nursing. Females preferentially nursed own pups when the difference in age between own and alien pups increased

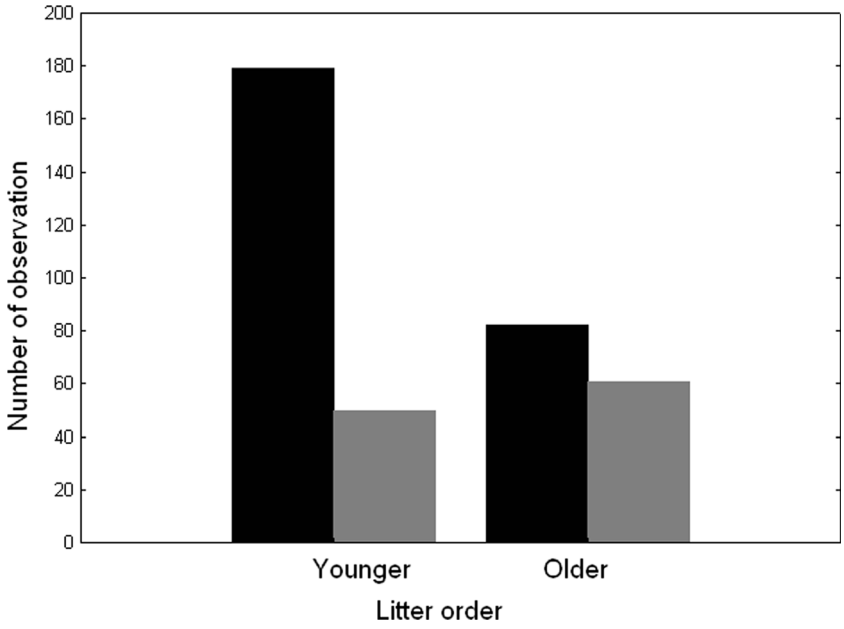

Fig. 3 Effect of the litter order of two co-nesting females on the occurrence of allonursing in the Sinai spiny mouse. Litter order means whether the female's own litter was younger or older than the alien litter of the co-nesting female—we omitted cases where females delivered on the same day in this analysis (*black columns* own pups, *grey columns* alien pups)

experienced ones. Maternal reproductive experience is probably important for the recognition of one's own pups, a skill which helps to avoid misdirected parental care (e.g. Roulin 2002). For example, Maniscalco et al. (2007) reported that more experienced females of the Steller sea lion (*Eumetopias jubatus*) are better able to discriminate between aliens and their own pups than inexperienced females. As a consequence, allonursing in this species was observed mainly in inexperienced mothers, probably as a result of the misdirected parental care. Theoretically, such behaviour could still have some adaptive value. For example, it might be useful as training for future successful breeding of inexperienced females. If it is true, this alloparental training behaviour should be observed mainly in nulliparous females. However, we did not see such behaviour in these females during our experiments.

We also found that allonursing decreases with increasing age disparity between both litters, indicating again that the nursing of alien pups in Sinai spiny mice is caused by misdirected parental care. This corresponds to the results of studies regarding several other rodent species, where allonursing was also more frequent between females with age-matched litters. In those litters, pups might easily suckle from females other than mothers because females are not able to quickly identify alien pups and to chase them away immediately (e.g. Sayler and Salmon 1971; Porter et al. 1980; Packer et al. 1992). In house mice, it was found that as age disparity between litters increased, females were more aggressive towards alien pups and communal nursing was not as frequent (Sayler and Salmon 1971; Manning et al. 1995). Hayes (2000) also hypothesized that competition between the pups of two litters is less costly in age-matched litters than in pups with a greater age disparity. Older pups may be more successful in competing for nursing access to either female (e.g. Mennella et al. 1990). Interestingly, if we excluded females that delivered litters on the same day, we found that Sinai spiny mouse nursed alien pups more often if their own litter was older than the alien litter. The fact that females found small non-offspring attractive may be related to the presence of newborn pups. For example, in Cairo spiny mice, females with their own litter of 8-day-old pups nursed 1-day-old alien pups more frequently than vice versa (Porter et al. 1980).

The retrieval of alien pups in Sinai spiny mice was also affected by a small disparity in age between the litters of the co-nesting females. Generally, separation of pups from their mother is a stressful situation and females try to recover the pups quickly (Porter and Doane 1978; Patris and Baudoin 2000). Such stressful conditions may also result in misdirected parental care. For example, females of the Norway rat (*Rattus norvegicus*), if stressed by separation from their pups, retrieved a wide variety of objects by mistake (Spencer-Booth

Table 3 Effect of particular variables on the occurrence of alien pup retrieval (GLMM)

Variable	Estimates	SE	df	*z*	*p*
Relationship between females	−1.04	0.73	3	−1.42	0.1561
Experience of female	0.19	0.16	1	1.14	0.2547
Weight of female	−0.03	0.02	1	−1.56	0.1190
Age variation between litters	0.13	0.03	1	4.05	<0.0001
Size of litter	0.07	0.14	1	0.54	0.5891
Age of pup	−0.006	0.004	1	−1.58	0.1136
Gender of pups	−0.07	0.26	1	−0.26	0.7920
Barrier	0.03	0.24	1	0.11	0.9155
Age of group	−0.007	0.004	1	−1.58	0.1136

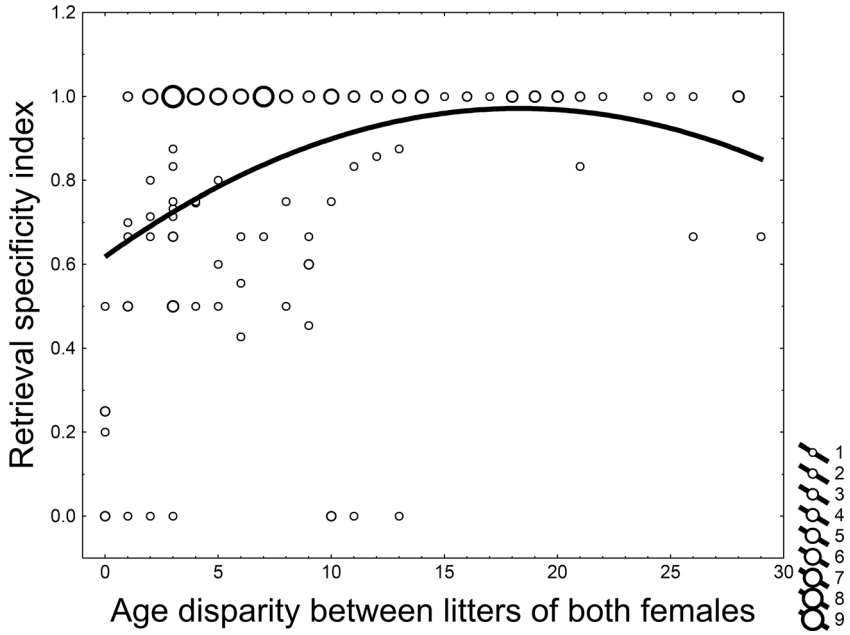

Fig. 4 Effect of the age disparity between litters of two co-nesting females on the occurrence of allocare during pup retrieval in the Sinai spiny mouse. The *point size* indicates the number of females in a particular sample; retrieval specificity index—instances of retrieval of own pups/total instances of retrieval. With greater age disparity between pups, females retrieved predominantly their own pups

1971). This behaviour was sometimes observed in our study. Age difference between litters may help mothers to better recognize their own pups vs. pups from different litters and decrease the probability of misdirected parental care. A similar pattern was observed in house mice, where females also discriminated between pups that differed in age but not between age-matched littermates in retrieval tests (Manning et al. 1995). Thus, our study supports previous research on discrimination abilities of spiny mice in which pup recognition was related mainly to the age difference between pups (Porter 1986, 1988).

Similar to nursing, females retrieved alien pups more often if their own litter was older than the alien litter. It seems that the retrieval of smaller alien pups may be dependent on physiological stage of females combined with a higher attractiveness of newborn pups. For example, Porter and Doane (1978) found that in Cairo spiny mice alien neonates (1 day old) were retrieved only by lactating females while nulliparous females or those with weaned pups did not retrieve them.

We also found that in Sinai spiny mice retrieval of alien pups occurred less frequently than allonursing. These results may indicate that the retrieval of alien pups is a more risk-laden form of allocare probably due to limited mobility of the carrier and the potential increased risk of predation (Price 1992; Schradin and Anzengerger 2001; Noren 2008). An analogous pattern was also found in the grey mouse lemur

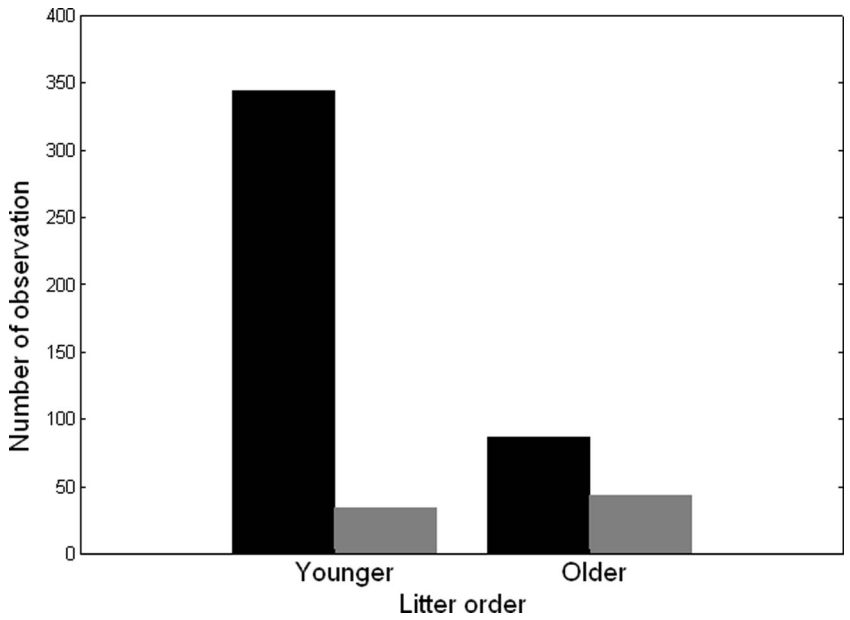

Fig. 5 Effect of the litter order of two co-nesting females on the occurrence of allocare during retrieval in the Sinai spiny mouse; litter order means whether the female's own litter was younger or older than the alien litter of the co-nesting female. We omitted cases where females delivered on the same day in this analysis (*black columns* own pups, *grey columns* alien pups)

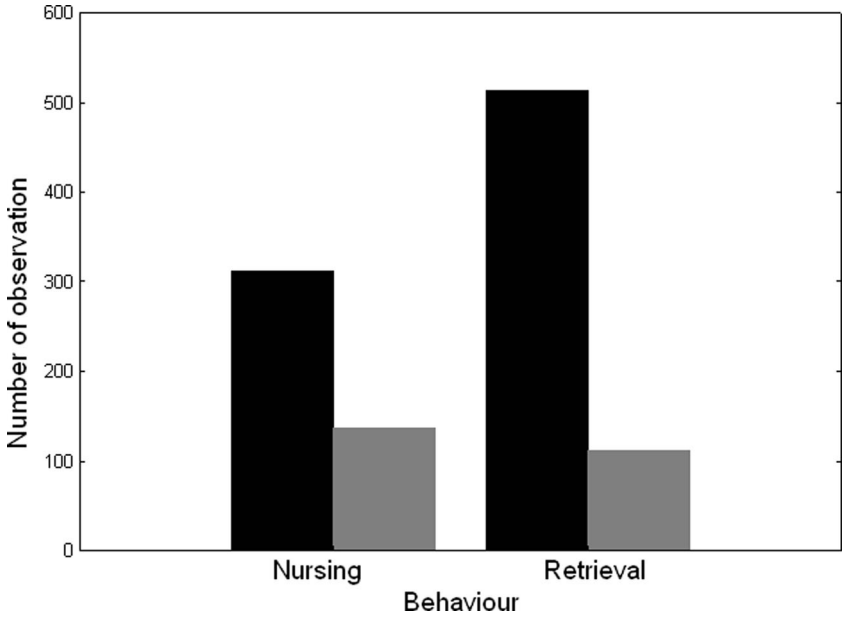

Fig. 6 Comparison of the occurrence of alloparenting during two types of maternal behaviour—pup nursing and retrieval by two co-nesting females in Sinai spiny mice (*black columns* own pups, *grey columns* alien pup)

(*Microcebus murinus*), where helpers nursed the alien infant regularly but preferentially retrieved their own infant (Eberle and Kappeler 2006). We also observed that females tended to retrieve their own pups quicker than an alien pup. In this context, it could be mentioned that several rodent species do not display pup discrimination during communal care. If the cost associated with alloparental behaviour (nursing, retrieval) is not very high, they usually take care of pups indiscriminately although they are able to recognize their own/alien pups in discriminative tests (e.g. Pereira, 2006; Jesseau et al. 2008).

Some authors consider alloparental care to be an artefact of reproduction in captivity because of crowding (Sayler and Salmon 1971; Manning et al. 1995; König 1997). Although living space used in our study was limited, we do not believe that it had a significant influence on the occurrence and frequency of alloparental behaviour in the spiny mouse. Limited nesting space is probably also common in nature, because spiny mice live frequently in harsh arid conditions (Nowak 1999; Dewey 2003). Restricted living conditions also may be associated with low food availability and suitable nesting sites such as holes and crevices which may lead to philopatry, resulting in the sharing of a communal nest, as observed in other rodent species (Jannett 1982; Lambin and Krebs 1997; Wollf 1994; Marin and Pilsatro 1994; Lacey and Wieczorek 2004; Randall et al. 2005). Unfortunately, there are no field studies on communal nesting of the Sinai spiny mouse.

Contrary to some previous studies on rodents (e.g. König 1993, 1994b; Marin and Pilsatro 1994; Mappes et al. 1995; Dobson et al. 2000), our results did not demonstrate that familiarity and/or kinship between females was the primary cause of communal breeding in Sinai spiny mice. We discovered that alloparenting could be more affected by other factors, primarily age difference between own and alien pups, and the maternal reproductive experience, suggesting a low ability to discriminate pups in some situations. Kin discrimination in this species may be more costly than providing alloparental behaviour. Nevertheless, spiny mice females may invest more in pup recognition if the costs associated with a particular behaviour (retrieval) outweigh the costs spent on pup discrimination (e.g. risk of mistaken identification of own pup). Further studies regarding pup recognition as well as social structure and dominance hierarchy are necessary to explain why females of the Sinai spiny mouse share their nests and breed communally.

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Compliance with ethical standards This study was funded by GAJU 39_2007_P-PŘF. The authors declare that they have no conflict of interest. All applicable international, national and/or institutional guidelines for the care and use of animals were followed. The experimental animals suffered no harm, and the experiments were performed in accordance with all Czech laws and implemented all corresponding EU regulations. All procedures performed in the study involving animals were in accordance with the ethical standards of the Animal Ethic Committee of the Faculty of Science, University of South Bohemia, and Ministry of Education, Youth and Sport of the Czech Republic (26300/2007-30). This article does not contain any studies with human participants by any of the authors.

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