



Nest attendance of lactating females in a wild house mouse population: benefits associated with communal nesting



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Among species providing uniparental care, the caring parent faces time constraints and may have to compromise offspring care/protection for self-maintenance. In most mammalian species females raise their offspring without receiving help from males. Communal nesting, when multiple females share a single nest where they rear their pups together, may have evolved as a mutually beneficial cooperative behaviour to reduce mothers' nest attendance without increasing the time their offspring are left alone. We tested this hypothesis using data collected in a free-living house mouse, *Mus musculus domesticus*, population in which reproduction occurred in nestboxes and was closely monitored. Individuals were fitted with transponders allowing automatic recording of their location, and a genetic parentage analysis confirmed maternal identity. Compared with mothers raising their pups solitarily, communally nesting mothers spent less time inside their nest. Their pups, however, were left alone for a similar amount of time as solitarily raised pups. The time communal litters were left alone did not covary with the kinship of communally nesting females. These results indicate that communally nesting mothers can allocate more time to foraging or territorial defence without impairing the amount of maternal attention received by their offspring. Nevertheless, communally nesting mothers showed some overlap in their stays at the nest. Offspring may benefit from more regular meals while mothers may gain information on the partner's contribution to combined maternal care which could potentially prevent cheating.

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As altricial offspring are nonmobile and can neither forage nor thermoregulate at birth, extensive parental care is essential to ensure their survival to weaning (Clutton-Brock, 1991; Galef, 1981). Parents usually keep their offspring inside a protected shelter or nest in which they can influence the inside temperature and avoid access by predators and/or infanticidal individuals (Montgomerie & Weatherhead, 1988; vom Saal, Franks, Boechler, Palanza, & Parmigiani, 1995; Wolff & Peterson, 1998). Offspring, however, remain highly vulnerable as they may suffer starvation, low body temperature, infanticide or predation whenever their parents leave the shelter to satisfy their physiological and/or social needs (e.g. feeding, territory defence; Galef, 1981; Hoogland, 1985). How parents respond to these time constraints and allocate their time therefore influences their current and future reproductive success (Stearns, 1992).

Although males and females can share parental duties in species providing biparental care, the caring parent in uniparental species may have to compromise offspring care and protection for self-maintenance. Consequently, such species may evolve cooperative strategies in which same-sex individuals associate with each other and share offspring care and defence (West, Griffin, & Gardner, 2007a). Parental care could be reduced by sharing the parental load with others so that the amount of parental care received by the offspring could remain the same or increase as more individuals care for them (Gittleman, 1985; König, 1997; Solomon, 1991). For instance, if a mother alone cannot attend her nest more than 30% of a day, a perfect alternation and share of the nest attendance with two other mothers could lead to a maternal presence of 90% of a day. Such a mechanism has been suggested to improve offspring survival in communally nesting species (Hayes, 2000; König, 1997; Wolff & Peterson, 1998). Even though kin selection is not necessary for the evolution of such mutually beneficial behaviours (Bshary & Bergmüller, 2008; Clutton-Brock, 2002), kinship can help in stabilizing the relationship between cooperative partners and thus improves their performance (Holmes & Sherman, 1982). Hamilton's rule of inclusive fitness suggests that relatedness between the individuals involved can compensate for the extra costs incurred by

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an individual who has invested in an altruistic behaviour (Hamilton, 1964a, 1964b).

Communal nesting, when females rear their offspring in the same nest or shelter, is observed in 15% of mammalian species, a taxon in which parental care consists almost exclusively of maternal care since only the dams contribute to the nutrition of the young to weaning (Hayes, 2000; Packer, Lewis, & Pusey, 1992). Lactating females have to bear high energetic costs that increase with offspring age to reach a lactation peak just before weaning, a situation that increases a mother's need for foraging (Clutton-Brock, Albon, & Guinness, 1989; Hammond & Diamond, 1992). Although communal care can raise the risks of pathogen transmission (Roulin & Heeb, 1999) or infanticide (Hager & Johnstone, 2004), offspring raised under these conditions can benefit from enhanced thermoregulation (Hayes & Solomon, 2006), feeding (Jacquot & Vessey, 1994; Mennella, Blumberg, McClintock, & Moltz, 1990), growth rate (Sayler & Salmon, 1969, 1971), immunocompetence (Boulinier & Staszewski, 2008) and nest defence (Manning, Dewsbury, Wakeland, & Potts, 1995). Furthermore, nursing indiscriminately their own and other females' offspring when litters are of different ages may help females to reduce peak energy demand by spacing lactation peaks just before weaning (Godbole, Grundleger, Pasquine, & Thenen, 1981; König, 2006).

In house mice, *Mus musculus domesticus*, laboratory experiments have shown that communally nesting females cannot discriminate their own offspring from other females' offspring (König, 1989a, 1989b; König, 1993; Manning et al., 1995). They also seem unable to control the pups' access to their nipples to prevent milk theft (Packer et al., 1992). Consequently, pups raised in communal nests receive milk from all females (König, 2006) which can result in a faster growth rate (Heiderstadt & Blizard, 2011; Sayler & Salmon, 1969). Communally nesting females, on the other hand, benefit from improved lifetime reproductive success owing to higher offspring survival until weaning (König, 1994a). Another laboratory study associated communal nesting with a lower risk of infanticide to explain the better offspring survival observed within communally raised litters (Manning et al., 1995). The influence of communal nesting on nest attendance, however, has received very little attention (Hayes & Solomon, 2006; Izquierdo & Lacey, 2008) despite its potential benefits in improving pup survival.

Data from laboratory experiments may not allow generalization of any benefit of nest attendance, as the laboratory is a rather luxurious environment (controlled temperature, food and water easily available, rarely if ever any territorial competition, etc.) compared with a natural situation. Using data collected from a wild house mouse population we analysed mothers' nest attendance to test whether communal nesting could benefit mothers and/or their pups. Accounting for litter size and pup age, we tested whether communal nesting influenced the amount of time mothers spent in the nest with their litters and the amount of time pups were left alone in the nest by their mother (or mothers for pups raised in communal nests). Furthermore, we looked at whether the number of caring mothers and their kinship, as reflected by their coefficient of coancestry, influenced the time offspring were left without maternal attention in communal nests.

METHODS

Study Species

The house mouse, a small rodent living in socially complex groups, is useful for testing the link between communal nesting and nest attendance (König & Lindholm, 2012). Female house mice give birth to altricial pups kept in a nest until weaning and which

receive maternal care only (König & Markl, 1987; Latham & Mason, 2004). Females are regularly observed sharing a nest with one or more other mothers even though they can rear their pups solitarily (König, 1994a; Latham & Mason, 2004; Weidt, Lindholm, & König, 2014). Familiarity between females has been reported to be as important as genetic relatedness for social partner choice (König, 1994b; Weidt, Hofmann, & König, 2008). Competition over reproduction is high in this plurally breeding species (König & Lindholm, 2012) and both sexes can be infanticidal (McCarthy & vom Saal, 1985; vom Saal & Howard, 1982). Nest attendance could therefore play an important role in reproductive success through an increase in the amount of care the offspring receive or through better protection of the nest against intruders (Lewis & Pusey, 1997).

Study Population

Data were collected from an open free-living house mouse population in a 70 m² building, open to dispersal but closed to predators, in the vicinity of Zurich, Switzerland. Numerous wooden and plastic materials structured the inside of the building to provide territories or shelters to the mice. Food (a 50/50 mixture of oats and hamster food, Landi AG, Switzerland) and water were provided ad libitum in 10 feeding trays and 15 water dispensers.

Every 7 weeks, all individuals of the population (during the 2-year study period: 146 ± 7 adult mice and 57 ± 11 subadults; mean ± SE) were captured within a day between 1000 and 1800 hours. To that end, experimenters encouraged mice previously spotted in shelters or refuges to leave their hiding place (by blowing air, making some noise or gentle shakes when necessary) and head towards a glass jar in which they were captured and weighed. As mice prefer walking along edges and cover their territory following the same routes, it is possible to predict their preferred paths in a structured area like the inside of the building. A mouse moving from a shelter to another will therefore enter a glass jar placed on one of these well-used runs.

Every individual weighing at least 18 g was implanted with a subcutaneous transponder (RFID tag; Trovan ID-100A implantable microtransponder: 0.1 g weight, 11.5 mm length, 2.1 mm diameter; implanter Trovan IID100E; Euro ID Identifikationssysteme GmbH & Co, Germany) in the scruff of its neck and had an ear tissue sample collected (ear puncher Napox KN-293: 1.5 mm diameter) while being handled with a one-hand restraining technique. Each transponder gave a unique identification number to every mouse and allowed a noninvasive recording of their location (König & Lindholm, 2012; Perony, Tessone, König, & Schweitzer, 2012; Weidt et al., 2008). No obvious adverse effects of these transponders on the behaviour or physiology of the mice have ever been observed in this population or reported in the literature. Ear tissue samples were used as genetic material as recommended by the Swiss Federal Law on Animal Protection.

The whole procedure was performed by a trained and licensed animal care technician (FELASA-Category A) and lasted no longer than 3 min per mouse before being released. Neither analgesic nor anaesthetic were used as they would prolong the duration of this rapid procedure and induce more stress. No bleeding or infection of the transponder implantation site has been observed and there was no evidence that transponders migrated around the body. In the meantime, litters were processed by Y.A., B.K. or A.K.L. (FELASA-Category C; see [Reproductive Activity](#) section) so that they were not at risk of infanticide while mothers were handled. More information about the set-up and population can be found in König and Lindholm (2012). Data collection was approved by the Veterinary Office Zurich, Switzerland (Kantonales Veterinäramt Zürich, no. 215/2006).

Reproductive Activity

Forty nestboxes distributed in the entire building allowed a close monitoring of reproductive activity. Mice could enter nestboxes through a tube (one per box). Two antennas installed on the entrance tube of all nestboxes continuously recorded the identity of the mice that entered and left a nestbox, allowing calculation of the duration (s) of their stays. Experimenters could open the nests from the top, so that litters could be observed, and pups could be counted and aged. We searched for new litters approximately every 10 days, and all litters born between January 2008 and December 2009 were documented. Litter size was recorded and pup age was estimated based on morphological development. Pigmentation of the skin, development of the ears, fur growth, teeth eruption and eye development give reliable cues about the age of the pups (± 1 day). Every documented litter was searched for to collect an ear tissue sample when pups were forecast to be 13 days old. We consider day 13 as the closest age to weaning that data can be collected because pups start to open their eyes and are mobile at day 14 so they can mix with other litters (weaning begins at 17 days and is terminated at 21–23 days old; König & Markl, 1987).

Genetic and Maternity Analyses

We extracted DNA from the ear tissue samples collected on all adults captured and all pups sampled on their 13th day to determine maternity. We isolated DNA using salt–chloroform extraction (Müllenbach, Lagoda, & Welter, 1989). Twenty-five microsatellite loci were amplified in four multiplex PCR reactions (Chr1_20, D2Mit145, D3Mit278, D4Mit227, Chr5_20, D5Mit122, D5Mit352, D6Mit139, D6Mit390, D7Mit17, D7Mit319, Chr8_3, D8Mit115, D9Mit201, Chr10_11, D10Mit230, D11Mit150, D11Mit90, Chr12_2, D12Mit91, D13Mit88, D14Mit44, D16Mit139, D18Mit194 and Chr19_17). Marker information is available in Schimenti and Hammer (1990), Meagher and Potts (1997), Bult et al. (2008), Teschke, Mukabayire, Wiehe, & Tautz (2008) and Hardouin et al. (2010). PCR reactions used the Qiagen Multiplex PCR Kit or AmpliTaq Gold DNA Polymerase (Applied Biosystems Inc., Foster City, CA, U.S.A.) and a final concentration of 0.075–0.4 μM primer for 28–31 cycles using a 60 °C annealing temperature. We analysed PCR products using a 3730xl DNA Analyzer (Applied Biosystems) and Genemapper software (Applied Biosystems). There were no significant deviations from Hardy–Weinberg equilibrium ($\chi^2_{50} = 62.77$, $P > 0.160$) for the 25 loci in testing all adult and subadult mice ($N = 55$) that were present in the barn at a reference time point, using Genepop on the Web (Raymond & Rousset, 1995; Rousset, 2008).

Maternity analyses were conducted for pups born in 2008–2009 using CERVUS 3.0 (Kalinowski, Taper, & Marshall, 2007). For each pup, candidate mothers were considered to be those females that were present in the barn within 2 days of the estimated pup birth date. The list of candidate mothers per pup included on average 78 females for 2008 and 103 females for 2009. We used an error rate of 0.01 in CERVUS analyses based on the frequency of alleles scored differently between PCR amplifications of 100 individuals on average per locus, which was 0.006. The proportion of loci typed was 0.99. We considered 100 000 offspring and a sampling rate of 90% of mothers for simulations to generate critical delta values. Maternity assignments were accepted at a 95% level of confidence and only when no more than one mismatching allele occurred between putative mother and offspring. Over the 2 years, success at assigning mothers was 87–88%. However, as a 95% level of confidence populationwide can still sometimes lead to assignment errors (Walling, Pemberton, Hadfield, & Kruuk, 2010), we adopted a conservative approach and excluded from the data set

any litters of one as they may not provide enough information to ensure a reliable maternity assignment. In this population the average litter size at birth is 5.5 whereas litter size at 13 days of age is four giving an average loss of 0.14 pups per day (Manser, Lindholm, König, & Bagheri, 2011).

Kinship between Communally Nesting Mothers

Kinship between communally nesting mothers was assessed by the coefficient of coancestry, which is the probability that an allele randomly chosen from one individual is identical by descent to an allele randomly drawn from the same locus of another individual (Malécot, 1948). We assessed kinship between two mothers nesting communally by the Malécot coancestry coefficient using the software Pedigree Viewer (version 6.5b, <http://www-personal.une.edu.au/~bkinghor/>). Whenever a communal nest involved more than two mothers we averaged the different pairwise coancestry coefficients. The average kinship between communally nesting females was 0.16 ± 0.03 and ranged from 0 to 0.54.

Communal versus Solitary Nesting

Communal nests were defined as those containing litters produced by more than one mother. As communal nests are easy to identify only when they contain litters of different age, genetic analyses confirmed maternity of each pup. Note that our study was based on an observational design so that females were not manipulated and free to choose whether to breed communally or solitarily.

Variables Measured

For every documented litter, presence of adults in the nest was recorded by the antenna system for a tracking period starting from the first time the litter was found and ending when pups were 13 days old. During this period the antenna data allowed us to measure the cumulated time a mother spent with her litter as well as the frequency of her visits. We divided the cumulated time spent in the nest by the total number of visits to calculate the average duration of a visit to the nest. Moreover, we calculated the cumulated time a litter was neither with its mother nor with the mother of its littermates when raised in a communal nest.

Data Refinement

One hundred and fourteen litters in which there was no change in rearing conditions (communal or solitary nesting) were used in the analyses. Of these, 42 litters were excluded since only 1 day of tracking was available (otherwise, tracking period ranged from 3 to 13 days). Tracking is imprecise if females move their litter to another nestbox. Since females sometimes move litters between nestboxes after disturbances, we refrained from inspecting nests before litters were 13 days old. Nevertheless, to make sure that we only considered litters that remained in the same nestbox during the tracking period, we excluded litters for which the proportion of time the mothers spent in the nest with their offspring in relation to the total time they spent in all nestboxes during the tracking period was lower than an arbitrary cutoff of 30%. In the laboratory, females spend more than half of their time in the same cage as their offspring (König & Markl, 1987). After this refinement which excluded another 21 litters, the final range of the time females spent in the same box as their pups was 47.4–100.0% ($N = 51$ litters).

This study presents data from 24 communal litters and 27 solitary litters, produced by 51 mothers between January 2008 and

December 2009. Communal litters were older (average pup age over the tracking period; $t_{49} = 2.32$, $P = 0.025$) and smaller ($t_{49} = -4.26$, $P < 0.001$) than solitary litters (Table 1). Both communal and solitary litters were tracked for a similar period ($t_{49} = -1.68$, $P = 0.099$; communal: 7.9 ± 0.5 days, solitary: 9.1 ± 0.5 days). The whole antenna data set is available to download in open access format as supplementary material in Perony et al. (2012).

Statistical Analyses

Statistical tests were carried out using R 2.15.0 (R Development Core Team, 2012). We followed a proportion data analysis procedure to analyse the cumulated time (s) the mothers spent in their nest and the cumulated time (s) the pups were left alone by the mothers in their nest, using independent generalized linear models fitted by a quasibinomial error distribution (Crawley, 2007). Pup age, litter size, communal nesting (yes or no) and their second-degree interactions were used as predictors. Using the same effects structure, we analysed the frequency of mothers' visits (log-transformed to satisfy linearity) and their average duration with two independent linear models. We also used a generalized linear model fitted by a quasibinomial error distribution to test the influence of the number of mothers, their kinship, pup age, number of pups in the nest and their second-degree interactions on the time spent alone by pups raised in communal nests. The significance of the predictor variables in the models was assessed using F tests.

RESULTS

Lactating female house mice spent a considerable amount of their time in the nest with their pups (36% when rearing litters solitarily and 29% when rearing litters communally; Table 1). The frequency of a mother's visit to her litter was not influenced by pup age, litter size, communal nesting or any of their interactions (Table 2). Furthermore, communally nesting mothers made significantly shorter visits to their litters than solitarily nesting mothers (Table 2, Fig. 1a). The duration of a mother's visit was not influenced by pup age, litter size or any of the interactions involving pup age, litter size and communal nesting (Table 2).

Although the cumulated time a mother attended her nest was not significantly influenced by pup age or litter size, solitarily nesting mothers spent significantly more time inside the nest with their litters than communally nesting mothers (Table 2, Fig. 1b). None of the interactions between pup age, litter size and communal nesting had a significant influence on a mother's nest attendance (Table 2).

The amount of time litters were left alone by their mother, and the mothers of the other litters for those raised in communal nests, was not influenced by litter size, communal nesting or their

Table 1
Summary of the raw data observed for communally and solitarily nesting mothers

	Solitarily nesting mother		Communally nesting mother	
	Mean	SE	Mean	SE
Number of mothers	1.0	0.0	2.2	0.1
Litter size	5.5	0.3	3.7	0.3
Litter age (averaged over the tracking period in days)	8.8	0.3	10.0	0.4
Cumulated time in the nest (s/day)	31343.9	2400.9	25160.4	2809.2
Number of visits to the nest (per day)	15.2	2.6	12.3	1.8
Duration of a visit to the nest (s)	3251.9	463.6	2508.4	239.2
Time spent alone by the litters (s/day)	55056.1	2400.9	42400.6	4095.8

Table 2

Results from multivariate linear or generalized linear models (when appropriate) explaining variation in the frequency and duration of a mother's visit to her litter as well as in a mother's cumulated time in her nest and the cumulated time litters were left alone

	Frequency of a mother's visit		Duration of a mother's visit		Mother's cumulated time in nest		Cumulated time litters were alone	
	$F_{1,50}$	P	$F_{1,50}$	P	$F_{1,50}$	P	$F_{1,50}$	P
Pup age	0.03	0.862	0.33	0.570	0.45	0.503	17.03	<0.001
Litter size	0.84	0.363	2.11	0.153	0.21	0.651	1.63	0.209
Communal nesting	0.01	0.976	5.28	0.026	8.04	0.007	1.40	0.242
Litter size: Pup age	1.01	0.320	2.46	0.124	0.94	0.338	0.01	0.990
Communal nesting: Pup age	1.71	0.197	0.02	0.886	2.99	0.091	21.51	<0.001
Communal nesting: Litter size	0.65	0.426	1.53	0.223	0.15	0.698	1.63	0.208

Significant P values are in bold.

interaction (Table 2). However, older litters spent less time alone in their nest than younger ones; the negative relationship between pup age and the time left alone was stronger for litters raised in communal nests than for those raised in solitary nests (Table 2, Fig. 2). The interaction between pup age and litter size had no significant effect on the amount of time litters were left alone (Table 2).

Within communal nests, the time litters were left alone was not significantly influenced by the number of caring mothers ($F_{1,21} = 0.17$, $P = 0.687$), their kinship ($F_{1,21} = 0.52$, $P = 0.479$), pup age ($F_{1,21} = 3.42$, $P = 0.082$) or the number of pups ($F_{1,21} = 0.11$, $P = 0.748$). None of the second-degree interactions were significant ($P > 0.05$). Moreover, the cumulated time per day communally nesting females spent in the nest was not related to the ratio of their own offspring to the total offspring in a communal nest (Pearson correlation: $r_{22} = 0.11$, $P = 0.617$).

DISCUSSION

The present study shows that communally nesting mothers spent less time attending their litters than solitarily nesting mothers in a wild population. Although communally nesting mothers visited their nest as often as solitarily nesting mothers, they made shorter visits to them. This saving in time at the nest indicates that mothers may mutually benefit from communal nesting. A reduced nest attendance gives lactating mothers the opportunity to spend more time foraging which is necessary to increase milk yield or quality (Kretzmann, Costa, Higgins, & Needham, 1991; Mann, Miele, Kinsley, & Svare, 1983; Myrcha, Ryszkowski, & Walkowa, 1969), or to reduce opportunity costs by engaging in other activities such as patrolling the territory to refresh urine markings or repel potentially infanticidal individuals (Hurst, 1990; Latham & Mason, 2004). To analyse the foraging hypothesis further it would be interesting to equip access to feeding trays with antennas and thus quantify time spent feeding. Such a method should allow testing of whether foraging behaviour covaries with nest attendance.

Since our study is based on an observational design, the differences in nest attendance observed among communally nesting females could be confounded by other factors. House mice descended from the same population have been shown to express consistent interindividual differences in their behaviour (Auclair, König, & Lindholm, 2013). The differences in nest attendance between solitarily and communally nesting females might thus be driven by their predisposition to associate with individuals of similar behavioural profiles. Such a scenario, however, is not very

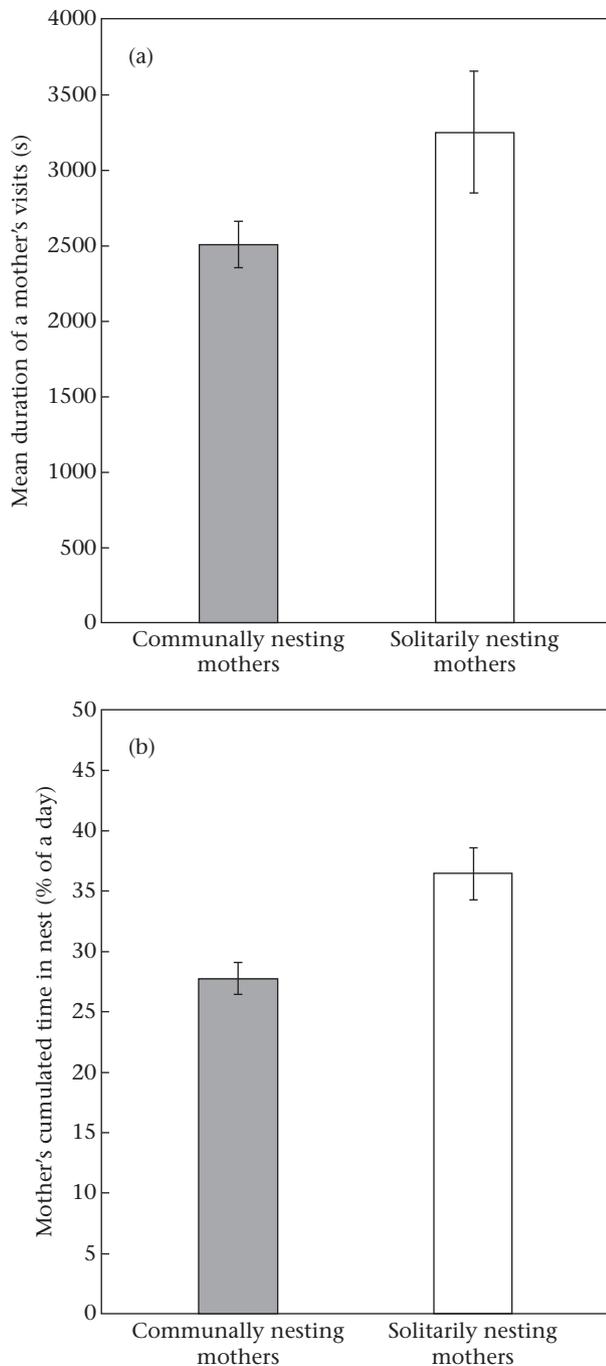


Figure 1. Mother's nest attendance represented as (a) the average duration of her visits and (b) the cumulated time she spent in her nest over a day. Figure shows model predictions $\pm 95\%$ CI.

likely as a recent study reported that female house mice do not follow a unique reproductive strategy, solitary or communal nesting, over their lifetime but can switch between reproductive events (Weidt et al., 2014).

Mothers increased the time spent in the nest with increasing age of their offspring. Because offspring have higher energetic requirements when approaching weaning age, increasing time in the nest may reflect increasing maternal care. This effect was more pronounced in communally nursed litters. Nevertheless, as mentioned before, mothers raising offspring communally were generally more often absent from their nest (on average 71% of a day; Table 1) than solitarily nesting mothers (64%), suggesting that

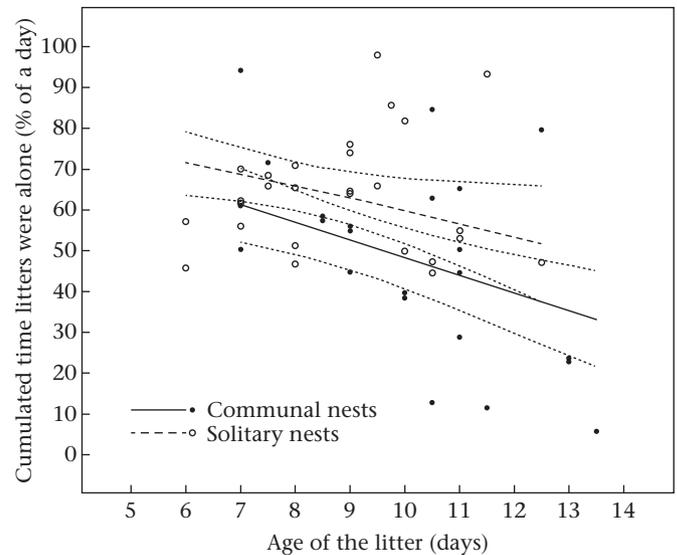


Figure 2. Percentage of a day litters were left alone with regard to their age and solitary or communal nesting. Figure shows model predictions $\pm 95\%$ CI.

solitarily nursing mothers are constrained in efficient milk investment or in gaining benefits from spending time outside of the nest (Kenagy, Masman, Sharbaugh, & Nagy, 1990; König & Markl, 1987; König, Riester, & Markl, 1988; Millar, 1977; Priestnall, 1972). Furthermore, in agreement with previous reports of the inability of females to recognize their own offspring (König, 1989a, 1989b; König, 1993; Manning et al., 1995), the nest attendance of communally nesting females did not covary with their relative contribution to the number of pups pooled in communal nests.

As females nesting communally spent 29% of a day in their nest (Table 1), one could predict that if two females sharing a communal nest (which was the case in the majority of the communal nests observed, Table 1) alternate their stays at the nest, and never meet, their litters should be attended for a total of 58% of a day. Communally raised litters were, however, attended for 51% of a day (litters were left alone for 49% of a day; Table 1). As a consequence, communally nesting females do show some overlap, since each mother stays in the nest for longer than 50% of the time the pups were attended. Overlap in the presence of mothers at the nest has been reported in two cases of communally nesting meadow voles, *Microtus pennsylvanicus* (McShea & Madison, 1984). Further studies will have to reveal whether communally nesting females influence each other's presence in the nest or whether they overlap according to random expectation.

Our observation that communally nursing females made shorter visits to their litters suggests that they can leave the nest earlier than solitarily nursing females after a nursing bout. In the laboratory, a nursing bout lasts approximately 20 min and does not differ between communally and solitarily nursing females (König, 1993; König & Markl, 1987). Solitary females in the wild population may have to stay in the nest to warm the litters after a nursing bout. In communally nesting females, in contrast, the short overlaps in their stays may allow them to leave the nest shortly after the completion of a nursing bout as their cooperative partner can ensure the warming of the litters and even initiate another nursing bout. Offspring may thus further benefit from shortened meal intervals (Caraco & Brown, 1986).

For the mothers, on the other hand, such overlap could provide information on the partner's contribution to combined maternal care which could potentially prevent cheating. The presence of an audience or cues suggesting their presence is known to encourage cooperation (Bateson, Nettle, & Roberts, 2006; Pinto, Oates, Grutter,

& Bshary, 2011). Information on the partner's investment in the combined litters may also be communicated by the sucking behaviour of pups, reflecting whether they had been nursed during a female's absence from the nest. Cooperation and competition are often closely linked, and cheaters can greatly improve their immediate payoff by cooperating less than a fair share with their partners (West, Griffin, & Gardner, 2007b). Individuals initiating cooperative behaviours are always susceptible to exploitation by others, as shown in a wide range of taxa from bacteria to fish, birds and mammals (Andersson & Eriksson, 1982; Bshary & Grutter, 2002; Nowak, 2006; Velicer & Vos, 2009). A lower than proportional share of nursing would allow a female to lower the large energy expenditure usually associated with lactation (Hammond & Diamond, 1992). Furthermore, it has been shown that the litter of the first female to give birth in communal nests is more susceptible to infanticide (Andersson & Eriksson, 1982; Koenig, Mumme, Stanback, & Pitelka, 1995; König, 1994a). An infanticidal second female would increase the ratio of her own to the total offspring in the communal nest. Such conflicts are likely to occur between females initiating a communal nest right after litters are born which may explain why communally raised litters were smaller than those raised solitarily when we found them.

The time communal litters were left alone was apparently not influenced by their kinship. Mutually beneficial behaviours can occur without kinship (Bshary & Bergmüller, 2008; Clutton-Brock, 2002). Unrelated females have been reported to protect other females' offspring in other mammalian species such as sperm whales, *Physeter macrocephalus*, and African elephants, *Loxodonta africana* (Lee, 1987; Whitehead, 1996). Female wild house mice also successfully communally nurse with unrelated females under laboratory conditions, when given the opportunity to choose among social partners (Weidt et al., 2008).

Our study reports that communally nesting mothers reduce their nest attendance compared with solitarily nesting females. This suggests that communally nesting mothers can allocate more time to foraging to face the energetic burden of lactation, or to protect the territory and nest against intraspecific competitors. Moreover, the amount of maternal attention received by offspring raised in communal nests was even higher, at least for older pups, than that of offspring raised in solitary nests. Nevertheless, communally nesting mothers showed some overlap in nest attendance. Such behaviour may perhaps prevent a reduction in contribution to maternal care by nesting partners. The extent to which communally nesting females exploit each other remains unknown and requires more investigation.

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References

Andersson, M., & Eriksson, M. O. G. (1982). Nest parasitism in goldeneyes *Bucephala clangula*: some evolutionary aspects. *The American Naturalist*, *120*, 1–16.
 Auclair, Y., König, B., & Lindholm, A. K. (2013). A selfish genetic element influencing longevity correlates with reactive behavioural traits in female house mice (*Mus domesticus*). *PLoS One*, *8*(6), e67130.

Bateson, M., Nettle, D., & Roberts, G. (2006). Cues of being watched enhance cooperation in a real-world setting. *Biology Letters*, *2*, 412–414.
 Boulunier, T., & Staszewski, V. (2008). Maternal transfer of antibodies: raising immuno-ecology issues. *Trends in Ecology & Evolution*, *23*, 282–288.
 Bshary, R., & Bergmüller, R. (2008). Distinguishing four fundamental approaches to the evolution of helping. *Journal of Evolutionary Biology*, *21*, 405–420.
 Bshary, R., & Grutter, A. S. (2002). Asymmetric cheating opportunities and partner control in a cleaner fish mutualism. *Animal Behaviour*, *63*, 547–555.
 Bult, C. J., Eppig, J. T., Kadin, J. A., Richardson, J. E., Blake, J. A., & the Mouse Genome Database Group. (2008). The mouse genome database (MGD): mouse biology and model systems. *Nucleic Acids Research*, *36*, D724–D728.
 Caraco, T., & Brown, J. L. (1986). A game between communal breeders: when is food-sharing stable? *Journal of Theoretical Biology*, *118*, 379–393.
 Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton, NJ: Princeton University Press.
 Clutton-Brock, T. H. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, *296*, 69–72.
 Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature*, *337*, 260–262.
 Crawley, M. J. (2007). *The R book*. Chichester, U.K.: Wiley.
 Galef, B. G. (1981). The ecology of weaning. Parasitism and the achievement of independence by altricial mammals. In D. J. Gubernick, & P. H. Klopfer (Eds.), *Parental care in mammals* (pp. 211–241). New York: Plenum Press.
 Gittleman, J. L. (1985). Functions of communal care in mammals. In P. J. Greenwood, P. H. Harvey, & M. Slatkin (Eds.), *Evolution. Essays in honour of John Maynard Smith* (pp. 187–205). Cambridge, U.K.: Cambridge University Press.
 Godbole, V. Y., Grundleiger, M. L., Pasquine, T. A., & Thenen, S. W. (1981). Composition of rat milk from day 5 to 20 of lactation and milk intake of lean and preobese Zucker pups. *Journal of Nutrition*, *111*, 480–487.
 Hager, R., & Johnstone, R. A. (2004). Infanticide and control of reproduction in cooperative and communal breeders. *Animal Behaviour*, *67*, 941–949.
 Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*, 1–16.
 Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, *7*, 17–52.
 Hammond, K. A., & Diamond, J. (1992). An experimental test for a ceiling on sustained metabolic rate in lactating mice. *Physiological Zoology*, *65*, 952–977.
 Hardouin, E. A., Chapuis, J.-L., Stevens, M. I., van Vuuren, J. B., Quillfeldt, P., Scavetta, R. J., et al. (2010). House mouse colonization patterns on the sub-Antarctic Kerguelen Archipelago suggest singular primary invasions and resilience against re-invasion. *BMC Evolutionary Biology*, *10*, 325.
 Hayes, L. D. (2000). To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Animal Behaviour*, *59*, 677–688.
 Hayes, L. D., & Solomon, N. G. (2006). Mechanisms of maternal investment by communal prairie voles, *Microtus ochrogaster*. *Animal Behaviour*, *72*, 1069–1080.
 Heiderstadt, K. M., & Blizard, D. A. (2011). Increased juvenile and adult body weights in BALB/cByJ mice reared in a communal nest. *Journal of the American Association for Laboratory Animal Science*, *50*, 484–487.
 Holmes, W. G., & Sherman, P. W. (1982). The ontogeny of kin recognition in two species of ground squirrels. *American Zoologist*, *22*, 491–517.
 Hoogland, J. L. (1985). Infanticide in prairie dogs: lactating females kill offspring of close kin. *Science*, *230*, 1037–1040.
 Hurst, J. L. (1990). Urine marking in populations of wild house mice *Mus domesticus* Ratty. II. Communication between females. *Animal Behaviour*, *40*, 223–232.
 Izquierdo, G., & Lacey, E. A. (2008). Effects of group size on nest attendance in the communally breeding colonial tuco-tuco. *Mammalian Biology*, *73*, 438–443.
 Jacquot, J. J., & Vessey, S. H. (1994). Non-offspring nursing in the white-footed mouse, *Peromyscus leucopus*. *Animal Behaviour*, *48*, 1238–1240.
 Kalinowski, S. T., Taper, M. L., & Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, *16*, 1099–1106.
 Kenagy, G. J., Masman, D., Sharbaugh, S. M., & Nagy, K. A. (1990). Energy expenditure during lactation in relation to litter size in free-living golden-mantled ground squirrels. *Journal of Animal Ecology*, *59*, 73–88.
 Koenig, W. D., Mumme, R. L., Stanback, M. T., & Pitelka, F. A. (1995). Patterns and consequences of egg destruction among joint-nesting acorn woodpeckers. *Animal Behaviour*, *50*, 607–621.
 König, B. (1989a). Behavioural ecology of kin recognition in house mice. *Ethology Ecology & Evolution*, *1*, 99–110.
 König, B. (1989b). Kin recognition and maternal care under restricted feeding in house mice (*Mus domesticus*). *Ethology*, *82*, 328–343.
 König, B. (1993). Maternal investment of communally nursing female house mice (*Mus musculus domesticus*). *Behavioural Processes*, *30*, 61–74.
 König, B. (1994a). Components of lifetime reproductive success in communally and solitarily nursing house mice: a laboratory study. *Behavioral Ecology and Sociobiology*, *34*, 275–283.
 König, B. (1994b). Fitness effects of communal rearing in house mice: the role of relatedness versus familiarity. *Animal Behaviour*, *48*, 1449–1457.
 König, B. (1997). Cooperative care of young in mammals. *Naturwissenschaften*, *84*, 95–104.
 König, B. (2006). Non-offspring nursing in mammals: general implications from a case study on house mice. In *Cooperation in primates and humans. Mechanisms and evolution* (pp. 191–205). Berlin, Germany: Springer-Verlag.
 König, B., & Lindholm, A. (2012). The complex social environment of female house mice (*Mus domesticus*). In M. Macholán, S. J. E. Baird, P. Munclinger, & J. Piálek

- (Eds.), *Evolution of the house mouse* (pp. 114–134). Cambridge, U.K.: Cambridge University Press.
- König, B., & Markl, H. (1987). Maternal care in house mice. *Behavioral Ecology and Sociobiology*, 20, 1–9.
- König, B., Riester, J., & Markl, H. (1988). Maternal care in house mice (*Mus musculus*): II. The energy cost of lactation as a function of litter size. *Journal of Zoology*, 216, 195–210.
- Kretzmann, M. B., Costa, D. P., Higgins, L. V., & Needham, D. J. (1991). Milk composition of Australian sea lions, *Neophoca cinerea*: variability in lipid content. *Canadian Journal of Zoology*, 69, 2556–2561.
- Latham, N., & Mason, G. (2004). From house mouse to mouse house: the behavioural biology of free-living *Mus musculus* and its implications in the laboratory. *Applied Animal Behaviour Science*, 86, 261–289.
- Lee, P. C. (1987). Allomothering among African elephants. *Animal Behaviour*, 35, 278–291.
- Lewis, S. E., & Pusey, A. (1997). Factors influencing the occurrence of communal care in plural breeding mammals. In N. G. Solomon, & J. A. French (Eds.), *Cooperative breeding in mammals* (pp. 335–363). Cambridge, U.K.: Cambridge University Press.
- Malécot, G. (1948). *Les mathématiques de l'hérédité*. Paris: Masson & Cie.
- Mann, M. A., Miele, J. L., Kinsley, C. H., & Svare, B. (1983). Postpartum behavior in the mouse: the contribution of suckling stimulation to water intake, food intake and body weight regulation. *Physiology & Behavior*, 31, 633–638.
- Manning, C. J., Dewsbury, D. A., Wakeland, E. K., & Potts, W. K. (1995). Communal nesting and communal nursing in house mice, *Mus musculus domesticus*. *Animal Behaviour*, 50, 741–751.
- Manser, A., Lindholm, A., König, B., & Bagheri, H. (2011). Polyandry and the decrease of a selfish genetic element in a wild house mouse population. *Evolution*, 65, 2435–2447.
- McCarthy, M. M., & vom Saal, F. S. (1985). The influence of reproductive state on infanticide by wild female house mice (*Mus domesticus*). *Physiology & Behavior*, 35, 843–849.
- McShea, W. J., & Madison, D. M. (1984). Communal nesting between reproductively active females in a spring population of *Microtus pennsylvanicus*. *Canadian Journal of Zoology*, 62, 344–346.
- Meagher, S., & Potts, W. K. (1997). A microsatellite-based MHC genotyping system for house mice (*Mus domesticus*). *Hereditas*, 127, 75–82.
- Mennella, J. A., Blumberg, M. S., McClintock, M. K., & Moltz, H. (1990). Inter-litter competition and communal nursing among Norway rats: advantages of birth synchrony. *Behavioral Ecology and Sociobiology*, 27, 183–190.
- Millar, J. S. (1977). Adaptive features of mammalian reproduction. *Evolution*, 31, 370–386.
- Montgomery, R. D., & Weatherhead, P. J. (1988). Risks and rewards of nest defence by parent birds. *The Quarterly Review of Biology*, 63, 167–187.
- Müllenbach, R., Lagoda, P. J. L., & Welter, C. (1989). An efficient salt-chloroform extraction of DNA from blood and tissues. *Trends in Genetics*, 5, 391.
- Myrcha, A., Ryszkowski, L., & Walkowa, W. (1969). Bioenergetics of pregnancy and lactation in the white mouse. *Acta Theriologica*, 12, 161–166.
- Nowak, M. A. (2006). Five rules for the evolution of cooperation. *Science*, 314, 1560–1563.
- Packer, C., Lewis, S., & Pusey, A. (1992). A comparative analysis of non-offspring nursing. *Animal Behaviour*, 43, 265–281.
- Perony, N., Tessone, C. J., König, B., & Schweitzer, F. (2012). How random is social behaviour? Disentangling social complexity through the study of a wild house mouse population. *PLoS Computational Biology*, 8, e1002786.
- Pinto, A., Oates, J., Grutter, A., & Bshary, R. (2011). Cleaner wrasses *Labroides dimidiatus* are more cooperative in the presence of an audience. *Current Biology*, 21, 1140–1144.
- Priestnall, R. (1972). Effects of litter size on the behaviour of lactating female mice (*Mus musculus*). *Animal Behaviour*, 20, 386–394.
- R Development Core Team. (2012). *R: A language and environment for statistical computing*. <http://www.R-project.org>.
- Raymond, M., & Rousset, F. (1995). GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, 86, 248–249.
- Roulin, A., & Heeb, P. (1999). The immunological function of allosuckling. *Ecology Letters*, 2, 319–324.
- Rousset, F. (2008). Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. *Molecular Ecology Resources*, 8, 103–106.
- vom Saal, F. S., Franks, P., Boechler, M., Palanza, P., & Parmigiani, S. (1995). Nest defense and survival of offspring in highly aggressive wild Canadian female house mice. *Physiology & Behavior*, 58, 669–678.
- vom Saal, F. S., & Howard, L. S. (1982). The regulation of infanticide and parental behavior: implications for reproductive success in male mice. *Science*, 215, 1270–1272.
- Sayler, A., & Salmon, M. (1969). Communal nursing in mice: influence of multiple mothers on the growth of the young. *Science*, 164, 1309–1310.
- Sayler, A., & Salmon, M. (1971). An ethological analysis of communal nursing by the house mouse (*Mus musculus*). *Behaviour*, 40, 62–85.
- Schimenti, J., & Hammer, M. F. (1990). Rapid identification of mouse t haplotypes by PCR polymorphism (PCR). *Mouse Genome*, 87, 108.
- Solomon, N. G. (1991). Current indirect fitness benefits associated with philopatry in juvenile prairie voles. *Behavioral Ecology and Sociobiology*, 29, 277–282.
- Stearns, S. C. (1992). *The evolution of life histories*. New York: Oxford University Press.
- Teschke, M., Mukabayire, O., Wiehe, T., & Tautz, D. (2008). Identification of selective sweeps in closely related populations of the house mouse based on microsatellite scans. *Genetics*, 180, 1537–1545.
- Velicer, G. J., & Vos, M. (2009). Sociobiology of the myxobacteria. *Annual Review of Microbiology*, 63, 599–623.
- Walling, C. A., Pemberton, J. M., Hadfield, J. D., & Kruuk, L. E. B. (2010). Comparing parentage inference software: reanalysis of a red deer pedigree. *Molecular Ecology*, 19, 1914–1928.
- Weidt, A., Hofmann, S. E., & König, B. (2008). Not only mate choice matters: fitness consequences of social partner choice in female house mice. *Animal Behaviour*, 75, 801–808.
- Weidt, A., Lindholm, A. K., & König, B. (2014). Communal nursing in wild house mice is not a by-product of group living: females choose. *Naturwissenschaften*, 101, 73–76.
- West, S. A., Griffin, A. S., & Gardner, A. (2007a). Evolutionary explanations for cooperation. *Current Biology*, 17, 661–672.
- West, S. A., Griffin, A. S., & Gardner, A. (2007b). Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20, 415–432.
- Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology*, 38, 237–244.
- Wolff, J. O., & Peterson, J. A. (1998). An offspring-defence hypothesis for territoriality in female mammals. *Ethology Ecology & Evolution*, 10, 227–239.