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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.

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 m^2 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 $\pm$ 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).