



The risk of exploitation during communal nursing in house mice, *Mus musculus domesticus*



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Parental care is associated with costs. Communal offspring care in species with altricial young may reduce the costs for a parent, but it comes with a risk of exploitation, jeopardizing the evolution of stable cooperation. Female house mice can either rear their young alone or communally with one or several other females. In the latter case, females pool litters and do not discriminate in their maternal behaviour between their own and alien offspring. Differences in litter size between females, or differences in the amount of investment they provide, might therefore result in one female exploiting another. To analyse the potential for conflict during cooperation, we compared under laboratory conditions the maternal investment (milk quantity and quality at peak lactation, when a female's own offspring were 15 days old) of wild-bred females nursing communally with one partner with that of females nursing solitarily. To increase the probability of asymmetry in litter sizes between communally nursing females, we used a genetic tool to reduce in utero litter size for one of the two partners. Communally nursing females invested according to the total number of pups in the joint nest and not according to their own litter size, making them vulnerable to exploitation. Females that gave birth to the smaller litter consequently overinvested; they had a higher investment per weaned offspring than females that gave birth to larger litters in communal nests or solitarily nursing females. Communal nursing in house mice thus represents a public good situation. Both partners invest according to the combined litter size, but they differ in the benefit they gain, which is the number of weaned offspring.

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Parental care improves offspring survival, typically at a cost for the investing parent in terms of decreased future reproduction or survival (Clutton-Brock, 1991). It is often associated with high energetic and opportunity costs, especially in species that produce altricial offspring, which initially fully depend on care or protection provided by adults (Bennett, 1981; Clutton-Brock, 1991). Communal offspring care may present an opportunity to reduce the costs of parental care and has been described for about 15% of mammals (Bronson, 1989; Gittleman, 1985; König, 1997) and 2.5% of birds (Brown, 1987).

Communal offspring care can be expressed in two ways. First, nonreproducing individuals help to raise the offspring of other individuals. Second, several reproducing individuals share parental load by pooling their clutches or litters in one nest. The main difference between these types of communal offspring care is the

degree of reproductive skew between females in a group. The skew can range from despotic, with one dominant breeder as in bird species with helpers-at-the-nest (Koenig & Dickinson, 2004) and in cooperatively breeding mammals (Clutton-Brock, 2002), to egalitarian reproduction among the females in a group as in communally (plurally) breeding species (Hayes, 2000; Koford, Bowen, & Vehrencamp, 1990). Although egalitarian groups may also experience reproductive skew, it will be less pronounced than in despotic groups. Lower potential for conflict is thus expected in communally breeding species, since all group members gain direct fitness benefits. If individual investment (cost), however, corresponds to the total number of offspring in the communal or joint nest and not a female's own offspring only, the potential for exploitation, and thus conflict, is raised also among communally breeding species.

Whenever we observe regular and indiscriminate provisioning of a female's own and alien offspring we have to analyse the underlying potential for conflict among the partners involved to understand the factors stabilizing cooperation during communal offspring care. Indiscriminate care or the lack of discrimination between a female's own and alien young in species with altricial

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offspring is rather common and has been described for a number of communally nursing mammals (bats: [Watkins & Shump, 1981](#); rodents: [Holmes & Sherman, 1982](#)), communally feeding birds ([Koford et al., 1990](#)) and invertebrates ([Samuk & Avilés, 2013](#)).

Mammals provide interesting case studies for the potential for exploitation in communal offspring care. Females predominantly or exclusively provide parental care and lactation comes at a high cost ([Bateman, 1957](#); [Clutton-Brock, Albon, & Guinness, 1989](#)). Lactation increases a mother's daily caloric intake by 66 up to 180% in comparison to the nonreproducing period ([Gittleman & Thompson, 1988](#); [König, Riester, & Markl, 1988](#)), and increased investment in the present offspring delays the birth of the next litter ([Clutton-Brock et al., 1989](#)). Regular and indiscriminate provisioning of milk to a female's own and alien offspring, as observed in communally nursing species, thus requires an adaptive explanation ([König, 2006](#); [Roulin, 2002](#)).

In house mice, allonursing of pups by communally breeding females has been observed both in the wild and under laboratory conditions ([Sayler & Salmon, 1971](#); [Schmidt et al., 2015](#); [Weidt, Lindholm, & König, 2014](#); [Wilkinson & Baker, 1988](#)). Communal nursing with a familiar partner improves a female's lifetime reproductive success analysed for wild house mice under laboratory conditions ([König, 1994](#)). However, communal nursing in mice is facultative. Even during periods of high population density females nurse litters solitarily. When nursing communally they are selective, with clear evidence for social partner choice both in a free-living population and under standardized laboratory conditions ([Weidt, Hofmann, & König, 2008](#); [Weidt et al., 2014](#)). In a laboratory experiment, such social partner choice improved female lifetime reproductive success ([Weidt et al., 2008](#)).

Since litters in communal nests vary in age and in size, indiscriminate nursing has the potential for exploitation or free riding (when one partner benefits more than it invests, or even benefits without investing at all). If one female has a larger litter than her nursing partner(s), but all females invest equally in the combined nest, she will exploit the other(s). The benefit (number of offspring weaned) will vary for the different females contributing to the communal nest, while all partners share the costs (energy invested) equally. The risk of exploitation is even higher, as female infanticide occurs regularly among communally nursing females. The female that gives birth second may kill one or more of the other female's pups before she gives birth herself, therefore biasing the relative contribution to the communal litter in her favour ([König, 1994](#); [Palanza, Della Seta, Ferrari, & Parmigiani, 2005](#)).

Females could avoid being exploited by preferentially nursing their own young. Contrasting results have been found as to whether female house mice are able to discriminate between their own and alien pups in a communal nest, with overall only weak evidence indicating the ability to recognize their own offspring ([Auclair, König, Ferrari, Perony, & Lindholm, 2014](#); [Chantrey & Jenkins, 1982](#); [Hager & Johnstone, 2005](#); [König, 1989b](#); [Manning, Dewsbury, Wakeland, & Potts, 1995](#); [Yamazaki, Beauchamp, Curran, Bard, & Boyse, 2000](#)). Still, even an ability to discriminate between her own and alien young on the mother's side would not guarantee selective nursing. Females may be unable to fend off alien offspring in the confined environment of a communal nest (milk theft). To our knowledge, it has not yet been demonstrated or tested whether wild house mice are able to transfer more milk to their own than alien offspring, for example by allowing their own young access to teats with higher milk let-down. Furthermore, females in a laboratory study were not found to spend more time nursing their own versus alien young ([König, 1989a](#)). If females indeed selectively nurse their own young, we expect their milk production to correlate with their own litter size at the time of measuring milk production.

Alternatively, females could avoid exploitation by adjusting their milk production to the litter size to which they gave birth. However, female house mice adjust their investment to postpartum changes in litter size ([Knight, 1982](#); [König et al., 1988](#)), very likely directly influenced through the number of suckling young. It has been observed in many mammals that milk yield increases with the number of sucklings (sheep, *Ovis aries*: [Alexander & Davies, 1959](#); goats, *Capra aegagrus hircus*: [Hayden, Thomas, & Forsyth, 1979](#); rats, *Rattus norvegicus*: [Morag, Popliker, & Yagil, 1975](#); mice, *Mus musculus*: [Knight, 1982](#); [König et al., 1988](#)). If the suckling stimulus determines milk production, and if females are unable to prevent alien young from accessing their teats, we expect females to invest according to the joint litter size in the nest, irrespective of a female's ability to recognize her own offspring. Such indiscriminate nursing would make them highly vulnerable to exploitation, as soon as communally nursing females differ in litter size.

In a laboratory setting we analysed female investment during peak lactation (milk quantity and quality) in wild house mice to assess, first, whether communally nursing females invest according to their own litter size or the joint litter size in the nest. To increase the probability of asymmetry in litter sizes between communally nursing females, we used a genetic tool to reduce in utero litter size for one of the two partners and thus avoided the disadvantages of manipulating litters shortly after birth ([Ferrari, Lindholm, & König, 2014](#)). In a second step we compared the lactation performance of communally and solitarily nursing females to analyse whether females use different investment strategies under these different breeding conditions. Information about the potential of conflict among partners will be a prerequisite for understanding the factors stabilizing cooperation.

METHODS

Animals and Husbandry

Experimental animals were F1 to F3 descendants of wild house mice from a population near Zurich, Switzerland (for more information see [König & Lindholm, 2012](#)). Mice were kept in the laboratory at a temperature of 22–24 °C under a constant light:dark cycle of 14:10 h (light on at 0530 hours CET). Food (laboratory animal diet for mice and rats, no. 3430, Kliba) and water were provided ad libitum, as well as paper towels and cardboard that served as nest-building material. Experimental animals originated from monogamous breeding pairs and stayed in their parents' cages until the age of 28 days, when a tissue sample (small ear punch) was taken for genotyping and individual identification. Subadults were afterwards kept in same-sex sibling groups in Macrolon Type III cages (23.5 × 39 cm and 15 cm high) until the beginning of the experiment.

The population of origin contained a selfish genetic element, the *t* haplotype ([Lindholm, Musolf, Weidt, & König, 2013](#)). This haplotype is characterized by drive in males (90% of offspring sired by a *t* heterozygous male inherit the *t*) and is associated with a recessive lethal, as has been described for other populations ([Silver, 1993](#)). Embryos that are *t* heterozygous die in utero, so that a mating between two *t* heterozygous individuals results in 40% smaller birth litter sizes ([Lindholm et al., 2013](#)). Genotyping experimental mice for the presence of the *t* haplotype (*t* heterozygous, *+/t*) or for its absence (*+/+*), and afterwards using a carefully designed mating scheme, allowed us to manipulate whether females gave birth to a normally sized or to a smaller litter (for a detailed description of the method see [Ferrari et al., 2014](#)). This method enabled us to increase the variation in litter size differences between communally nursing females, while remaining in the natural range.

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