Chapter 11

Non-offspring nursing in mammals: general implications from a case study on house mice

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11.1
Introduction

Reproduction in female mammals is associated with lactation, which involves relatively high energetic costs and influences a mother's future reproduction (Fuchs 1981, Bronson 1989, Clutton-Brock 1991). Because of these high costs, we do not expect females to provide milk to non-offspring. Hence, if they engage in such potentially altruistic or mutualistic behavior, careful study of its evolutionary causes and mechanisms is warranted.

Non-offspring nursing (also communal nursing or allonursing) is known from both breeding and non-breeding individuals, most probably exclusively done by females (to my knowledge, there has been only one rather anecdotal documentation of lactating males in free living Dayak fruit bats, *Dyacopterus spadiceus*; Francis et al. 1994).

Among species with some kind of communal care of young, singular breeders (i.e. typically one breeding female per social unit) form the majority in most mammalian taxa, as they do in social birds and insects. Singular breeders are species with high reproductive skew, and frequently with helpers-at-the-nest (non-breeding individuals that help caring for the dominant's offspring). Sometimes, a subordinate female can also produce pups, as in suricates, dwarf mongooses, callitrichids or wild dogs. For recent reviews, see Stacey (1990), Emlen (1991), Jennions (1994), Creel (1997) and Solomon (1997).

Plural breeders, instead, are species with several breeding females per group and more egalitarian reproduction among females, as in lions, house mice, most bats, most primates and most ungulates. Females in some of these species cooperate in some kind of communal care, as for example babysitting, social thermoregulation, communal defence of young, provisioning of food to pups, or non-offspring nursing (Packer et al. 1992, Jennions & Macdonald 1994, König 1997, Solomon & French 1997).

Nevertheless, there are principal differences between singular breeders with helpers-at-the-nest and cooperating plural breeders. As Lewis & Pusey (1997) have emphasized, non-breeding helpers sacrifice their direct reproductive effort in the short term, whereas cooperation among breeders does not necessarily imply a loss of current direct fitness. In singular breeders, the focus of interest is primarily on the following questions addressing non-breeding subordinates: (i) Why not disperse? (ii) Why delay breeding? (ii) Why help? In plural breeders, instead, questions regarding the value of breeding in groups rather than alone are most important: (i) Why live and breed in groups? (ii) Why help or nurse non-offspring?

Cooperative care of young has mainly been studied in singular breeders, and relatively fewer studies analyze species with shared reproduction among breeding group members. Here, I will focus on communal nursing as an example of a specific cooperative behavior, and I will discuss for a species with plural breeders why lactating females nurse non-offspring. I will summarize our understanding of the ultimate causation of non-offspring nursing, and will present experiments analyzing its proximate mechanisms. Furthermore, I will suggest a novel hypothesis for why it occurs, and speculate on its distribution among mammals.

11.2
Non-offspring nursing in mammals

Non-offspring nursing has been described for approximately 70 species in 12 orders. Field observations indicate that it is more common in pigs than in other Artiodactyls, and that it is more common among rodents and carnivores than in primates and bats. In carnivores, non-offspring nursing is ubiquitous in canids, but also occurs in felids like lions and domestic cats. Furthermore, it has been observed in otters, coatis and some populations of Eurasian badgers. In primates, it has been documented in the field among marmosets (*Callithrix*), in *Alouatta*, *Cebus*, *Erythrocebus*, *Homo sapiens*, *Lemur*, *Microcebus*, *Miopithecus*, *Presbytis*, *Varecia*, and maybe in Goeldi's monkeys (*Callimico*). In rodents, non-offspring nursing has been documented for members of the Cricetidae, Gliridae, Muridae, Sciuridae, Cavidae and Hydrochoeridae. However, in only 10% of all species in which non-offspring nursing is recorded were non-offspring nursed as much as one's own young (for recent reviews, see Packer et al. 1992, König 1997, Lewis & Pusey 1997, Solomon & French 1997, Hayes 2000).

11.2.1
Why do females nurse non-offspring?

Several hypotheses have been suggested to explain the phenomenon of non-offspring nursing, and there is some controversy as to whether communal nursing confers a reproductive advantage or not.

11.2.1.1 Non-adaptive hypotheses

Two non-adaptive hypotheses have been proposed. First, some authors consider non-offspring nursing to be milk theft by other females' young, making it obviously non-adaptive for the donor (McCracken 1984, Boness 1990). The second hypothesis is that it represents a byproduct of providing parental care in a group-living context. Jamieson & Craig (Jamieson 1989, Jamieson & Craig 1987) suggested that alloparental behavior occurs simply because the social structure of those species in which it is found provides an opportunity for parent-like behavior. A similar explanation was offered by Pusey & Packer (1994) for non-offspring nursing in lions. Female lions live in groups and raise their young in crèches because of the advantages of defense against infanticidal males. Non-offspring nursing then occurs as an inevitable consequence of group rearing, with the costs of rejecting non-offspring being higher than the costs of allowing some nursing by non-offspring.

11.2.1.2 Adaptive hypotheses

Adaptive explanations, on the other hand, include kin selection, or direct benefits. Such direct benefits can accrue due to improved survival, growth, or future reproduction of own offspring, or due to improved breeding success of mothers in the presence of lactating peers. I will discuss later which mechanisms can result in direct benefits for either mothers or pups.

11.3

Non-offspring nursing in house mice: a case study

In order to assess which of these hypotheses best account for non-offspring nursing, we study this phenomenon in house mice. We are interested in non-offspring nursing at both the ultimate and proximate level, to complement evolutionary approaches with mechanistic ones.

House mice (*Mus domesticus*) are short-lived rodents with a high reproductive output. They have a rather flexible social structure, but most typically they live in small groups that consist of a dominant male, one or several adult females with their litters and several subordinate animals (DeLong 1967, Lidicker 1976, Bronson 1979, Berry 1981a, Singleton 1983, Gray et al. 2000). Litter size of wild house mice increases from the first to the second lactation, and decreases again after the fifth lactation (Pelikán 1981, König & Markl 1987). Fifty years ago, Southwick (1955) published for the first time that females of the same reproductive group can pool their litters in communal nests. Since then, this behavior has been documented both in the field and in captivity (Sayler & Salmon 1969, Wilkinson & Baker 1988, König 1993, Manning et al. 1995).

To analyze whether non-offspring nursing in house mice is adaptive, we quantified the fitness consequences of communal rearing of young under laboratory conditions. Experimental animals were first- to third-generation wild-caught house mice, born and reared in the lab. Under otherwise standardized conditions, we simulated different social structures that are known to occur in feral or commensal house mice, and measured the females' lifetime reproductive success. We defined lifetime reproductive success as the number of offspring weaned during an experimental lifespan of six months (for a detailed description of the methods used see König 1993, 1994b). Although average life expectancy of newborn house mice is only 100-150 days, an experimental lifespan of six months is realistic for females that survived at least until maturity (Berry 1971, Berry 1981b, Pennycuik et al. 1986).

In all experiments, females always reared litters in a communal nest as soon as more than one female in a group gave birth to pups. Moreover, nursing of pups within a communal nest was indiscriminate (König 1989, 1993).

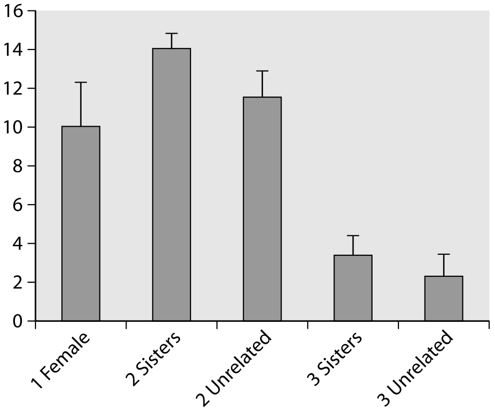

Fig. 11.1. Number of offspring weaned during an experimental lifespan of six months (median ± SE) of female house mice as a function of group size (number of females per group ranged between one and three) and of genetic relatedness. Sisters were familiar full-sibs that grew up together; unrelated females were previously unfamiliar and genetically unrelated females. An unrelated adult male was always present. Independent sample sizes (number of groups per treatment): 1 Female: n = 21; 2 Sisters: n = 21; 2 Unrelated: n = 24; 3 Sisters: n = 10; 3 Unrelated: n = 10. Data modified from König (1994a).

We manipulated group size (the number of adult females per group) and relatedness among females. At the age of 7-8 weeks, females were mated with an adult, unrelated male and during the following four months lived either monogamously (one female plus one male) or in polygynous groups (for further details see König 1993, 1994a, 1994b). In polygynous groups, females were either two or three genetically full-sibs, reared together (simulating the situation of sisters staying together), or two or three genetically unrelated and previously unfamiliar females (simulating the situation of females immigrating into a group).

Lifetime reproductive success of individual females differed significantly as a function of both group size and relatedness among the females, and reached a peak for females living with one sister (Fig. 11.1). In a group of three females, however, individual lifetime reproductive success was lower than in a monogamous situation, irrespective of the females' relatedness. Offspring weight at weaning did not differ significantly among the groups (König 1993, 1994b).

The reason why females differed in individual reproductive success as a function of group size and relatedness is that females varied in the probability of reproduction and of successfully weaning young within the experimental lifespan. Not all females weaned young, due to competition over reproduction despite communal nesting. The extent of this competition is illustrated by the index of reproductive skew for the females involved (Fig. 11.2; index of reproductive skew according to Reeve & Keller 1995; data on house mice from König 1994a).

This index varies between zero and one. When a single individual produces all the offspring, the skew is one, reflecting a despotic society; when reproduction is perfectly equitable among all group members, the skew is zero, indicating egalitarian reproduction among females.

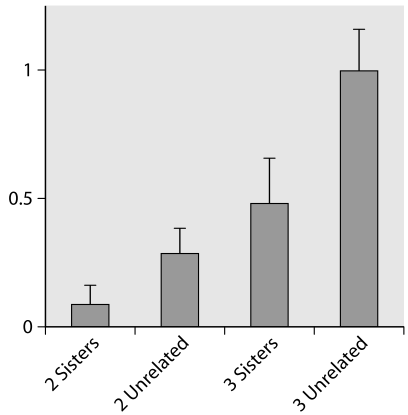

Fig. 11.2. Index of reproductive skew (median ± SE) among female house mice as a function of group size (two or three females) and relatedness. The index was calculated according to Reeve & Keller (1995), for all groups in which at least one female produced a litter and in which individual reproductive success was known (groups in which females gave birth to litters on the same day were excluded, because of lack of information about maternity). Independent sample sizes: 2 Sisters: n = 20; 2 Unrelated: n = 20; 3 Sisters: n = 6; 3 Unrelated: n = 7. Data on individual lifetime reproductive success is from König (1994a).

The lowest index was found for pairs of sisters. In such units, females are not only egalitarian in terms of the probability of reproduction but also in terms of the number of offspring weaned. The median degree of reproductive skew increased significantly towards despotic relationships with decreasing relatedness among the females within a group, and with increasing group size.

These findings permit two conclusions. First, non-offspring nursing is an integral part of the reproductive behavior of female house mice in egalitarian groups. Thus, the non-adaptive hypothesis that it is milk theft by young can be rejected in this case. The milk theft hypothesis should result in more variable occurrences of non-offspring nursing, with an increase with increasing age and mobility of young. Furthermore, female house mice have the option to breed solitarily even when another female reproduces within their territory (Weidt & König, unpublished observations from a population of wild house mice in a barn), which allows us to exclude the hypotheses of misdirected maternal care, and of a byproduct of group living.

Second, where a female established an egalitarian reproductive relationship, communal nursing increased her individual lifetime reproductive success, irrespective of the degree of relatedness or familiarity to the female partner (König 1994c). However, the probability for such mutualistic cooperation was highest when a female shared a nest with a familiar sister to form a low-skew society. As a consequence, non-offspring nursing of female house mice in pairs with egalitarian reproduction proved to be adaptive, and involved mutualistic, direct fitness benefits for both partners. The fact that communal nursing was most efficient among familiar relatives may indicate that kin selection played a role during the evolution of communal nursing. However, because neither familiarity during juvenile development nor high relatedness are necessary pre-requisites, direct benefits of cooperation seem to stabilize non-offspring nursing among female house mice.

11.4
Direct benefits of allomaternal care

The experiment demonstrated that female mice gained a direct mutualistic benefit from forming a communal unit characterized by allonursing. Several hypotheses have been suggested to explain why female mammals or their offspring gain direct benefits when mothers exhibit allomaternal care (licking, huddling over, or carrying non-offspring) or nursing non-offspring (for previous reviews see Packer et al. 1992, Lewis & Pusey 1997, Hayes 2000, Hayes & Solomon 2004).

11.4.1
Improved survival of pups

Communal nursing can reduce pup predation either by the dilution effect (Hoogland 1989; in analogy to communal care of eggs in birds as in ostriches, Bertram 1992), or due to improved protection against infanticide committed by non-group members, as suggested by Manning et al. (1992). When females alternate nursing pups in a communal nest, offspring are left alone less often and thus have a lower probability to be killed by unfamiliar conspecifics compared with pups reared by a single female.

11.4.2
Improved future reproduction of pups

Packer and co-workers further raised the idea of improved cooperation, based on their long-term observations of lions. Group size is critical for reproductive success in both male and female lions (Packer et al. 1990, 1991, Pusey & Packer 1997). Thus, communal care would result in their own young having more potential allies later in life, even if no full-sib survived.

Nevertheless, both hypotheses mentioned so far cannot explain why communally nursing female house mice weaned more offspring within their lifespan in our experiments under rather luxurious environmental conditions, with unlimited food, in a favorable climate, and in the absence of predators or cannibalistic non-group members.

11.4.3
Improved growth of pups

According to Caraco & Brown (1986), allomaternal (pluriparental) care may reduce starvation of young if at least one of the participating parents finds sufficient food to allow for lactation. When there is a cost of starvation, cooperative provisioning of young might evolve through reciprocity given that breeders feed the young asynchronously. The authors further suggest that even when food is plentiful, offspring may benefit because of reduced time between meals. In house mice, communally nesting females do not nurse simultaneously so that pups are almost always cared for by one lactating female (unpubl. pers. obs.). Litters that grew up in a communal nest have a relatively high weaning weight compared to same-sized litters from solitarily nursed mothers (König 1993; see also Table 11.1). It is not known, however, whether shorter time intervals between meals cause this effect, or whether other energetic benefits of communal nesting are involved, as suggested by the following hypotheses.

11.4.4
Immunological benefits for pups

As an alternative hypothesis to explain intra- and inter-specific variation in allosuckling frequency, Roulin & Heeb (1999) suggested immunological benefits (the immunological function of the allosuckling hypothesis). We modified the authors' hypothesis and tested the prediction that house mouse pups gain a more variable immunocompetence through milk provided by several females (Ramsauer & König, submitted).

Newborn mammals do not yet have a functioning immune system and are dependent on immune factors received through maternal milk. During the first two weeks of lactation in house mice, immunoglobulin and lymphocytes reach the pups' intestines through the milk, and then are passed on into the blood (Janeway & Travers 1997). Due to indiscriminate nursing of own and alien young in communal nests, pups might benefit by acquiring a broader immunocompetence when reared communally in comparison to pups raised by just one female. The major histocompatibility complex (MHC) is crucial for the production of immunocomponents and plays an important role in pathogen recognition. Receiving variable MHC products through maternal milk supplied by both the mother and another lactating female might thus allow for a better defense of pups against pathogens and be of importance for the growth and viability of offspring.

Immunocompetence typically is a matter of genetics and experience. The social behavior of female house mice, however, might offer a non-genetic tool to influence offspring immunocompetence through cooperative nursing. We therefore predicted improved growth and/or earlier weaning of pups reared by females of different MHC, and differences in the immunocompetence of subadult house mice that have been nursed by two mothers compared to those receiving milk from one mother. We tested these predictions by cross-fostering newborn house mouse pups from our population of wild-caught animals to a communal nest of two lactating foster mothers either of the same or of different MHC types (Ramsauer & König, submitted).

Foster mothers were from two congenic strains differing in the MHC ('A' = B10BR/OlaHsd and 'B' = C57BL/10ScSnOlaHsd). Each replicate consisted of three newborn full-sisters: one reared by 'AA'-foster mothers, one by 'BB'-females, and the third by one 'A'- and one 'B'-female. Litter size of communal nests was always standardized and consisted of 13 congenic offspring, with a sex ratio of seven males and six females, plus one wild female pup; independent sample size was 12.

Growth and weaning weight did not differ significantly for females reared by two foster mothers of either the same or different MHC. In collaboration with Andrew MacPherson from the Institute of Immunology at Zürich University, we measured immunocomponents in the pups' blood. Our treatment did not significantly influence immunoglobulin concentrations (IgA, IgM and IgG) of young at day 15 (before the immune system of pups is fully functional). Lymphocyte concentrations (B220 representing B-cells, and CD4 representing T-cells), however, differed significantly at day 28, with intermediate values in females raised by 'AB'-foster mothers (at the age of four weeks, subadult house mice are already immunocompetent). 'A'-females had rather high concentrations of CD4 lymphocytes in their milk which is reflected in high concentrations in pups that had been nursed by 'AA'-foster mothers; 'B'-females, on the other hand, had rather high concentrations of B220 lymphocytes resulting in similarly high values in their offspring (Ramsauer & König, submitted).

Immunological components that are transferred via milk influence the immunocompetence of wild-type house mouse pups irrespective of their own genotype. Such influence on immunocompetence, however, did not result in energetic benefits of young as reflected in improved growth or earlier weaning under our experimental conditions. Nevertheless, a female house mouse that chooses a partner for communal nursing according to MHC characteristics might be able to influence her offspring's future survival and reproduction. Under more natural conditions, when offspring encounter a variety of pathogens, we therefore may expect that MHC characteristics contribute to structuring among females within social groups in house mice. Even if the influence of maternal milk on offspring immunocompetence cannot explain our observation of improved reproductive success of communally nursing females, it might influence a female's choice of a social partner, which remains to be tested.

11.4.5

Physiological benefits for the mother

Wilkinson (1992) suggested that female evening bats, *Nycticeius humeralis*, nurse non-offspring to dump excess milk prior to the next feeding trip, thereby obtaining immediate energetic benefits and maintaining maximum milk production. House mouse pups, however, are limited in their growth by the milk available from the mother (König et al. 1988), and especially in communal nests with many pups, it is not plausible that females have to face the problem of getting rid of excess milk before they leave for a foraging trip.

For relatively small mammals such as rodents, communal care might involve direct energetic or metabolic benefits as improved thermoregulation or improved milk production, and thus allow for a higher weaning success of females that nurse non-offspring (Sayler & Salmon 1969, Boyce & Boyce 1988, Hayes & Solomon 2004).

To test whether females are more efficient in converting solid food into offspring body mass during cooperative care of young, we measured the energy costs of lactation of females rearing litters either solitarily or communally with a familiar sister. Litter size of experienced females (rearing at least the second litter) was standardized to 6–7 pups directly after birth, and litters of communally nursing sisters did not differ by more than six days in age. The animals had *ad libitum* access to food and water, but were kept in a climatic chamber at an ambient temperature of 15°C. This should reflect rather natural conditions for house mice and avoid missing an effect due to climate conditions that are too luxurious (Barnett 1965, DeLong 1967, Berry 1981a; for detailed methods, see Diedrichsen 1993).

Daily food consumption of females was measured from day 2 until day 13 of lactation with the help of an automatic feeding device (Neuhäusser-Wespy & König 2000). This device allows measuring individual food consumption of group-living animals without any disturbance. At day 14, we milked females with a milking device (König et al. 1988) and measured the amount of milk produced (after four hours of separation from the litters), and its energy content from lipids and total solids.

Neither litter weight at birth and weaning, nor the individual female's food consumption or milk production differed significantly for solitarily or communally nursing females (Table 11.1).

To quantify the females' allocation of energy into lactation versus maintenance, we calculated Calow's index of reproduction (Calow 1979). This index (I) was analyzed for day 14 of lactation, by using the following equation:

$$I = 1 - \frac{(\text{Energy consumed}) - (\text{Energy invested})}{(\text{Energy consumed when non-reproducing})}$$

Energy consumed = energy equivalents of maternal food consumption at day 14 of lactation; Energy invested = total energy of milk produced at day 14; Energy consumed when non-reproducing = energy equivalents of daily amount of food eaten (averaged over five consecutive days) when the adult females were non-pregnant and non-lactating. Energy equivalents of food pellets (Altromin rat and mouse) were 12.5 kJ/g (information according to the producer).

The index, I, relates a female's energy investment during lactation to her maintenance metabolism. A value equal or less than zero indicates that females compensate the energetic demand of reproduction (or lactation) through increased food consumption. For a value larger than zero, females meet the energetic costs of lactation at the expense of their maintenance metabolism, or by using lipid stores or other reserves that they accumulated before reproduction.

Energy allocation during reproduction did not differ significantly in both social groups (Table 11.1). Females did not allocate more energy to milk production, and did not lactate more efficiently, when nursing communally compared to mothers nursing solitarily.

Table 11.1. Energy allocation during lactation of female house mice rearing litters solitarily or communally with a familiar sister. Litter size was standardized at birth to six pups.

	Females rearing litters			
	Solitarily (n = 7)	Communally (n = 11 pairs)	z (U-test)	
Female weight day 1 (g)	30.1 ± 5.5	31.3 ± 3.0	−0.498	ns
Female weight day 23 (g)	30.9 ± 5.6	31.3 ± 3.0	−0.045	ns
Offspring weight day 1 (g)	1.6 ± 0.1	1.5 ± 0.1	−0.126	ns
Offspring weight day 23 (g)	8.5 ± 1.4	9.2 ± 1.4	−1.907	$p < 0.10$
Maternal food consumption (days 2-13; kJ)	1971 ± 98.9	2002 ± 113.8	−0.226	ns
Milk production at day 14 (g)	1.0 ± 0.3	1.0 ± 0.3	−0.317	ns
Energy provided through milk (at day 14; kJ/day)	63.7 ± 29.1	67.1 ± 24.9	−0.402	ns
Calow's index I (see text for explanation)	−0.7 ± 0.3	−1.1±0.6	−1.407	ns

11.4.6
Metabolic peak load reduction

In the experiment described before, both solitarily and communally nursing females met the energy need for lactation through increased food consumption from days 1–4 until days 13–16 (see also König et al. 1988). Lactating house mice were able to rear a growing litter both by increasing the amount of milk produced and by improving the quality through an increase in total solid and fat concentrations until day 16 of lactation. At the age of 17 days, offspring shift to solid food and are fully weaned when they are 23-days-old (König & Markl 1987). As a consequence, females go through a period of peak energy demand during lactation that is reflected in a drastic increase in daily food consumption, by over 200% in comparison to the non-reproducing state. This energetic demand can be further increased by simultaneous pregnancy during lactation. Conception during the postpartum estrus results in the birth of one litter every 28 days, on average. Nevertheless, female house mice are limited in their maximal (or peak) sustainable metabolism especially when nursing a large litter (Hammond & Diamond 1992). This effect is called 'metabolic ceiling'.

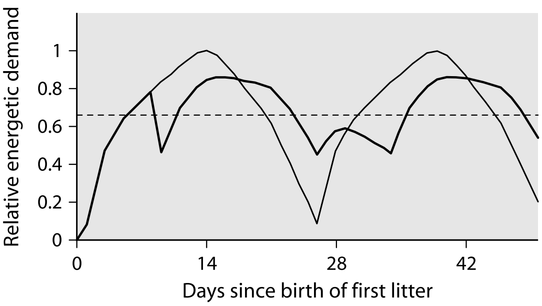

Fig. 11.3. Model of the relative energetic demand during lactation of a female house mouse over two consecutive litters. Thin line: female rearing litters solitarily. Bold line: female rearing litters communally with a female conspecific, the two litters differing in age by eight days. Dotted line: average demand in both situations. Maximum demand is set to one. The curves were derived from data of laboratory mice rearing a medium-sized litter (König et al. 1988), calculated as daily amount of milk produced times the proportion of dry weight. For the communal situation, we assumed equal contributions of both females to both litters.

In our population of house mice kept in polygynous groups over an extended period, litters in communal nests showed an average age difference of eight days (König 1994b). Due to indiscriminate care of young, females in such a situation are nursing more or less continuously. Based on these observations, we assumed that the energy budget of communally nursing females remains at a rather constant and medium level because both litters do not simultaneously reach the period of highest energy need (Fig. 11.3). We therefore formulated the hypothesis of benefits due to peak load reduction (Müller & König, submitted). By nursing litters communally, lactating females avoid peak energy demand. Because peak energy demands at the metabolic ceiling are especially costly, females that avoid such peaks will benefit by improved reproductive success.

To test this hypothesis, we manipulated the energy demand of females rearing litters alone, so that other possible benefits of communal breeding were absent. We analyzed the energy output of two groups of lactating females in which the total amount of energy spent on rearing a litter was the same, but energy allocation was timed differently.

In the manipulated group, we simulated a constant, medium-level energy output for lactating females by cross-fostering two older pups against younger ones every 2–3 days, beginning at day 8 of the first lactation, and continuing during the females' second lactation. As a control, we used females in which handling was done in the same way, but without cross-fostering. Manipulated and control females reared similar-sized litters (litter size was standardized at day 1 of lactation: six pups for the first litters, and seven for the second ones). Energetic demand of the manipulated females during lactation was assumed to have the same mean but lower variance as that of the control females, without a prominent peak two weeks after giving birth (for further details see Müller & König, submitted).

To quantify energy output, we measured the females' food consumption and resting metabolic rate. As fitness correlates, we analyzed the interbirth intervals and the size and weight of the females' second and third litters.

In accordance with our assumption, total energy output was similar for manipulated and control females that consumed similar amounts of food when rearing both the first and the second litters (there was a tendency for higher total food consumption in manipulated females during the first lactation). Daily food consumption of control females increased significantly from day 9 until day 15 of lactation and significantly decreased afterwards. No such variation was observed in manipulated females, with significantly lower food consumption at peak lactation, and higher food consumption during day 28 than in control animals, both during then first and the second litter.

Resting metabolic rates (RMR) of manipulated and control females were measured twice during each lactation period (at day 14 and at day 28), which allows further examination of the assumption of a rather constant energetic burden throughout lactation in manipulated females. RMR of control females decreased significantly, as expected, from peak lactation to weaning in both lactation periods. The RMR of manipulated females, however, did not change significantly.

Given that the assumptions of our model were fulfilled, we tested the prediction that females not experiencing peak loads had lower reproductive costs than control females, reflected in shorter interbirth intervals and/or larger litter sizes of manipulated females on the next reproductive occasion.

Neither the number of young at birth of the second and third litters, nor the proportion of females that mated *post partum* differed significantly between manipulated and control females (Müller & König, submitted). These observations support data from a former study on house mice by Fuchs (1981, 1982), who found an effect of the burden of lactation on the interval to the following litter, but not on its size.

As predicted, intervals between the first and second litters were shorter in manipulated than in control females. This effect, however, was only significant for those females where standardization of litter size directly after birth resulted in an experimentally increased litter (manipulated females gave birth to the second litter two days earlier than control ones, on average). Females, whose litters had been decreased in size at day 1 of lactation, might not have been confronted with an energy demand at their metabolic ceiling.

These data suggest that peak load reduction results in lower future reproductive costs at least for females that suffer an energetic burden near or at their maximum metabolic capacity.

Intervals between the second and the third litters, however, did not differ significantly between the two groups (Müller & König, submitted). Recent work by Johnson et al. (2001) has shown that the metabolic ceiling does not remain constant throughout the life of a house mouse but that it increases from the first to the second litter. Presumably, with a litter size of seven young, females were not forced to invest at their metabolic ceiling during the second lactation, and peak load reduction therefore did not result in lowered reproductive costs.

Nevertheless, the experiment suggests that communal nursing can modify a female's energy output, and can reduce peak energy demand of lactating females if litters differ in age by several days. Peak load reduction may thus affect fitness parameters of lactating house mice, and we further suggest that this effect is most pronounced if the peak forces them to approach their metabolic ceiling. However, it remains to be shown that this is not only the case in the rather artificial setting used during the experiments, but also under conditions of communal nursing.

11.5

Can peak load reduction explain non-offspring nursing in mammals?

Metabolic benefits due to peak load reduction are a prime candidate for explaining the observed higher reproductive output of communally versus solitarily nursing females. It is therefore tempting to speculate that such energetic benefits can also underlie other cases of non-offspring nursing, including those that have been interpreted as non-adaptive.

Packer et al.'s (1992) investigation of the effects of a variety of factors on the frequency of non-offspring nursing (excluding data from captive studies!) revealed three significant findings. First, non-offspring nursing increases with litter size across taxa. Second, non-offspring nursing is more common and better tolerated in polytocous (average litter size larger than one) than in monotocous species. In species that typically nurse only one pup, non-offspring nursing is more likely to be classified as milk theft (as for example in Mexican free-tailed bats, or Northern elephant seals). In contrast, in polytocous species, non-offspring nursing is less likely to be classified as milk theft, and also occurs in species where females can discriminate their own from foreign young, as in African lions (Pusey & Packer 1994). In both situations, non-offspring nursing correlates with increased energetic costs of lactation that peak shortly before weaning (Oftedal 1984, Oftedal & Gittleman 1989), increasing the probability that females invest at their metabolic ceiling. These two findings are consistent with the peak load reduction hypothesis; females are not expected to carry such a heavy energetic burden when litters are small and their life history is not as fast-paced.

Their third finding was that non-offspring nursing is most common in polytocous species when group size is small, and decreases significantly as group size increases. This observation is also in accordance with the hypothesis of peak load reduction if the probability of avoiding simultaneous peaks during lactation decreases with increasing number of breeding females in a group. Furthermore, the risk of exploitation by non-mutualistic individuals increases with group size and thus will hinder the evolution of stable cooperation.

The hypothesis of peak load reduction requires that females increase energy allocation during lactation up to their metabolic ceiling. Furthermore, females within a group have to be synchronized in reproduction, so that there is considerable overlap in lactation (perfect synchrony, however, that is giving birth on the same day, should not occur). Such constraints might explain why non-offspring nursing, although not very rare, nevertheless is limited to rather few taxa.

11.6
Concluding remarks

During communal nursing, female house mice do not discriminate between own and non-offspring, and gain direct, mutualistic benefits. Non-offspring nursing therefore is a cooperative behavior that allows females to improve weaning success of pups in a reciprocal manner, even among unrelated partners, once they have established an egalitarian relationship.

Such cooperation, however, may run the risk of being exploited. The most extreme case would be a highly pregnant female that drops her litter into another lactating female's nest and deserts. The benefits of such free-riding behavior are high. A non-lactating female will give birth to her next litter on average six days earlier than a female simultaneously being pregnant and lactating (König & Markl 1987). The deserted female, on the other hand, has to invest into non-offspring because she cannot tell them apart from own young (König 1989, 1993). It is not known whether such brood parasitism exists in house mice, but some aspects of the females' social behavior suggest protection against exploitation by non-cooperative partners.

First, female aggression is rather rare within groups and among relatives. Females, however, are very aggressive towards foreign females, not belonging to the same group, and especially so, when they are lactating (Crowcroft & Rowe 1963, Haug 1978, Kareem & Barnard 1982). Second, females preferentially share nests with a familiar relative (Manning et al. 1992, Dobson et al. 2000). Interestingly, familiarity during juvenile development is of paramount importance for improved reproductive success of females in egalitarian pairs, and overrides the effect of genetic relatedness (König 1994c), despite the fact that house mice of both sexes use genetic cues to discriminate against unfamiliar kin during mate choice (for a recent review, see Penn 2002). The importance of familiarity may suggest either that a physiological mechanism is involved which requires some period of adaptation to or synchronization with a partner, or that information about the partner is of significance for successful cooperation. The rather simple rules of thumb to communally nurse with a familiar group member and to aggressively keep away strangers might prevent females from being exploited by the opportunistic free-riding of other females.

Nevertheless, even during communal nursing females might benefit when reducing their investment, given that the partner will do more. In rodents, lactation performance is influenced by litter size *in utero*, which determines *pre partum* mammary growth (Jameson 1998), but more so by the number of sucking pups (Mann et al. 1983). Due to indiscriminate nursing, we assume that lactating females do not adjust milk production according to their own litter size but that energetic investment is shared equally among the members of a communal nest (we are currently testing this assumption). Such equalized investment therefore might be a prerequisite for stable cooperation among female house mice.

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