

## Components of lifetime reproductive success in communally and solitarily nursing house mice – a laboratory study

Barbara König

Theodor-Boveri-Institut, Zoologie III, Biozentrum, Am Hubland, Würzburg, Germany

**Abstract.** Under laboratory conditions, communal nursing among familiar and closely related female house mice (*Mus domesticus*) improved lifetime reproductive success compared to females rearing litters alone or females living with a previously unfamiliar, unrelated partner (reproductive success was measured within an experimental “lifespan” of 6 months, standardized as 120 days after mating at the age of about 2 months). An analysis of the contribution of three multiplicatively combined components to variation in reproductive success among breeding females revealed that, in all three social groups, survival of young until weaning contributed most to differences in lifetime reproduction (46–64% of the total variance). Females living with a sister had a significantly higher probability of reproducing successfully than females in the other groups, and also reared significantly more litters communally than females sharing nests with an unrelated partner. Weaning probabilities of young were highest in litters cared for by sisters and lowest in nests of unrelated females. Young were found dead either directly after birth (within the first 2 days of lactation) or after they had been cared for and nursed for at least 1 day. The loss of an entire litter typically occurred directly after birth. In monogamous females rearing litters alone the death of almost all young coincided with such early entire-litter mortality. In polygynous groups, however, offspring died at an older age and more litters suffered the loss of some young. Still, rearing young with a sister improved survival directly after birth and fewer litters were lost entirely in comparison with females in the other groups. In polygynous groups, pregnant females were observed to kill some of their partner’s dependent young shortly before they gave birth themselves. As a consequence, individual young had reduced survival when they were firstborn in a communal nest (another litter was born within 16 days). Analyzed over a lifetime, communal care among familiar and closely related female house mice seems to be an adaptation to maximize the survival of offspring until weaning.

**Key words:** Communal nursing – Cooperation – Fitness components – House mouse – Reproductive success

### Introduction

For many organisms conspecifics are a major environmental factor not only as mating partners but also because they are partners in cooperative and competitive interactions (for recent work on benefits and costs of group living see e.g. Møller 1987; Mumme et al. 1988; Packer et al. 1990; Creel and Creel 1991; Wilkinson 1992). Competition for limited resources among conspecifics living in the same group is thought to oppose the evolution of cooperative behaviour, especially if fitness costs are involved for the cooperating individual (in terms of reduced future reproduction; see Hamilton 1964).

Communal nursing in house mice (*Mus domesticus*) is a prominent example of cooperative behaviour in mammals. House mice live in small reproductive units, consisting of a dominant male and one or several adult females with their offspring (Crowcroft and Rowe 1963; Reimer and Petras 1967; Selander 1970; Lidicker 1976; Mackintosh 1981). Females that share nest sites are likely to be related because daughters often stay and reproduce in their parental territory (Petras 1967; Pennycuik et al. 1986), but immigration of young, presumably unrelated, females into established groups has also been observed (Anderson 1965; Reimer and Petras 1967; Selander 1970; Baker 1981; Bronson 1983). Within the same breeding group females often rear their litters in communal nests (Southwick 1955; Crowcroft and Rowe 1963; Sayler and Salmon 1969; Gandelman et al. 1970; Werboff et al. 1970; Baker 1981) and indiscriminately nurse both their own and alien young if litters are less than 10 days apart in age (König 1989).

The energy cost of lactation in house mice is high. To wean a litter of seven to eight young, a female has to produce approximately 100 g of milk of an energy equiv-

alent of 1100 KJ over a lactation period of 22 days (König et al. 1988). The amount of investment through milk influences the future reproduction of both a female and her young. The larger the litter size and the longer the lactation period, the more delayed is the next reproduction event (Fuchs 1981, 1982). For the offspring, on the other hand, weaning weight increases with the amount of milk received which improves future reproduction (DeFries and McClearn 1970; Fuchs 1981; Singleton and Hay 1983). Because of such high parental investment, females should preferentially invest in their own offspring and not provide milk to other young at a cost to their own offspring.

As a first step in determining why female house mice cooperate during provisioning of young, the fitness consequences of nursing litters alone and communally with a female partner of a different degree of relatedness and familiarity were analyzed under laboratory conditions (a male was always present in each breeding group; König 1989, 1993). Females nursing communally with a familiar sister weaned significantly more young within a standardized "lifespan" of 6 months than females rearing litters alone. Females sharing a nest with a previously unfamiliar, unrelated female weaned an intermediate number of offspring. These data predict that female house mice should preferentially cooperate with a (familiar) relative, which is supported by the observation of genetic assortment among reproducing, communally nesting females in a field study (Wilkinson and Baker 1988). Furthermore, Manning et al. (1992) observed that female house mice under semi-natural conditions showed preferences for MHC-similar partners for communal nursing (similarity in the MHC correlates with genetic relatedness; Beauchamp et al. 1986).

The problem of separating between effects due to genetic relatedness and due to familiarity during juvenile development on a female's reproductive success in polygynous groups is analyzed and discussed elsewhere (König in press). The purpose of this paper is, first, to determine the extent to which different components of lifetime reproductive success contribute to variation in breeding success among females in monogamous pairs and polygynous groups with familiar sisters or previously unfamiliar, unrelated females; and second, to compare the determinants of breeding success in these different social groups. Although the variance of individual components is not a measure of adaptation but of the opportunity for selection (see Crow 1958; Arnold and Wade 1984), such an investigation might help to determine why familiar sisters have such a high weaning success. For a recent discussion of how partitioning the variance in breeding success is helpful in understanding behaviour see Brown (1988), Clutton-Brock (1988a) and Grafen (1988).

## Methods

The experimental animals were the first filial generation of wild-trapped house mice (*Mus domesticus* Schwarz and Schwarz). All experimental animals were born in the laboratory and kept under standardized conditions ( $22 \pm 2^\circ\text{C}$ ;  $55 \pm 10\%$  relative humidity;

12:12 L:D cycle, light on at 0800 hours). Food and water were always available *ad libitum*. At the age of 6–8 weeks females were assigned at random to one of the following social groups:

1. Monogamous (MON): 1 female kept alone
2. Polygynous pairs of familiar sisters (RELATED): two full sisters that had never been separated from each other were kept together.
3. Polygynous pairs of previously unfamiliar, unrelated females (UNRELATED): two females reared apart and from parents that had been trapped at different sites 2–15 km apart (and thus assumed not to be closely related) were kept together.

One week later an unrelated adult male was introduced into each breeding group. This timing will be referred to as the time of "mating". For a more detailed description of cage sizes, procedure of introduction of the male to the female(s), and of female age and weight at the time of mating see König (1993). After mating, each breeding group was kept for at least 5 months and was checked daily for litters and any other occurrences. The day a litter was first seen is referred to as day 1 of lactation. Litters were removed from a breeding group when they were 28 days old.

Numbers and weight of offspring born and weaned and weight of the females in the three different social groups are described in König (1993). Because of missing data, not all breeding groups could be used for the analyses presented here. For the purpose of this paper, sample sizes were as follows: MON females,  $n = 20$ ; RELATED females,  $n = 20$  pairs of sisters (40 females); UNRELATED females,  $n = 22$  pairs of unrelated females (44 females).

Lifetime reproductive success of females in the three different social groups was measured as the number of offspring weaned within an experimental "lifespan" of 120 days after mating at the age of about 2 months. Weaning in house mice begins at day 17 of lactation when young shift to solid food but still get some milk from the mother, and is completed after 20–23 days (small litters are weaned earlier than large ones; König and Markl 1987). Under laboratory conditions, mortality of young is negligible after the age of 17 days. A "lifespan" of 6 months simulates the life cycle of a female that is born in the spring, survives until maturity, reproduces during the summer, and dies in autumn or during the next winter. This seems realistic for female house mice that have survived the period of high juvenile mortality under natural conditions (Berry 1971, 1981b; Pennycuik et al. 1986).

In the polygynous breeding groups females always pooled dependent litters in a communal nest. Weaned young also continued to rest and sleep in the same nest as much younger litters. Two litters were considered to be communally nursed if they spent at least 7 days in the same nest before the older one was weaned. Litters were considered to be reared solitarily if they were born either in the absence of another litter or in the presence of a litter aged 17 days or more and if the mother's female partner did not give birth to another litter within the next 16 days.

Partitioning of the variation in lifetime reproductive success of breeding females (that produced at least one litter within the experimental "lifespan") was performed following Brown (1988). This method utilizes an exact relationship between the variance of lifetime reproductive success and the variances and covariances of its components. Lifetime reproductive success was broken down into three multiplicatively combined components: (i) number of litters produced within a "lifespan" ( $L$ ), (ii) mean litter size ( $Y$ ), and (iii) survival probability of young born ( $S$ ; proportion of offspring reaching an age of 17 days within 120 days after mating of the mother). The first step is to calculate the variances of all components and their products after the individual variables have been divided by their means ( $G$ -values). To facilitate interpretation,  $G$ -values are expressed as a percentage of the overall product of the scaled components ( $LxYxS$ ), yielding the percentage of  $V(LYS)$  accounted for by the individual variables or their products.  $V(LYS)$  can be further broken down into the independent contributions of each single component and additional contributions of the products of each combination of components in excess of the sum of the respective single component contributions.

For statistical analysis, independent sample sizes are the numbers of different breeding groups (in polygynous breeding groups

the mean of both females was used). The only exceptions were numbers of successful versus unsuccessful females and the evaluation of correlations between groups of data, in which the independent sample size was the number of different females. To compare the three social groups, Mood's multisample median test was used (Zar 1984), since breeding success and its components were typically not normally distributed and were heterogenous in their dispersions. In case of a significant difference between the three social groups, data sets were tested pairwise with a Tukey-type multiple comparison test among medians (Zar 1984). For clarity, only statistically significant differences between pairs are given in the results. Differences were regarded as significant for two-tailed error probabilities of  $P \leq 0.05$ . For error probabilities  $P \leq 0.10$  (marginal significance) a trend was indicated. Means are followed by standard errors.

## Results

### *Variation in lifetime reproductive success among females*

The means and variances of the lifetime reproductive success of females in the different social groups are given in Table 1. Not all females reproduced within the experimental "lifespan": 10% of the monogamously paired females (MON) failed to produce young, 5% of the females living with a familiar sister (RELATED), and 20% of the females living with a previously unfamiliar unrelated partner (UNRELATED) were nonbreeders. All MON and RELATED females survived until the end of the experiment. In the group of UNRELATED partners, however, 14% of the females (6 females in 6 out of 22 pairs) died due to female-female aggression on average 52 days after mating (range: 40–63 days). Three of these females had produced a litter before dying but none of the young survived. The fact that some females failed to reproduce reduced the mean lifetime reproductive success of MON females by 1.25 offspring (in comparison to the mean for the breeding females), that of RELATED females by less than 1 young (0.77) and that of UNRELATED females by almost 3 young (2.73). Accordingly, the contribution to the total variance in lifetime reproductive success by nonbreeding females was approximately twice as high in UNRELATED than in RELATED or MON females (Table 1).

**Table 1.** Lifetime reproductive success (LRS; given as means and variances of the number of offspring weaned within 120 days after mating) of female house mice living monogamously (MON) or polygynously either with a familiar sister (RELATED) or with a previously unfamiliar, unrelated female (UNRELATED). LRS is given for all females within each social group (total sample) and for the females who produced at least one litter (breeders)

Social group	LRS for total sample	<i>n</i> of Non-breeders	Breeders		Contribution to total variance by:	
			<i>n</i>	LRS	Breeders	Nonbreeders <sup>a</sup>
MON	11.25	2	18	12.50	88.0%	12.0%
	117.46			114.73		
RELATED	14.57	2	38	15.34	81.6%	18.4%
	60.97			52.18		
UNRELATED	11.65	9	35	14.38	67.1%	32.9%
	96.09			79.46		

<sup>a</sup> The contribution to total variance by breeding and nonbreeding females was calculated according to Brown 1988 (p 448) as  $pV(LRS) + p(1-p)\overline{LRS}^2$  (the proportion of breeders is given by  $p = n_{\text{breeders}} / (n_{\text{breeders}} + n_{\text{nonbreeders}})$ ); the first term in the equation is the proportion due to variation among breeding females, the second term is the proportion of the overall variation due to failure to breed by some females

**Table 2.** Means and variances of the individual components and the products of the lifetime reproductive success of reproducing female house mice in 3 different social groups. The means and variances of the product of  $LxYxS$  differ slightly from the values given in Table 1 which are based on counting number of offspring weaned.  $G$ , variances of components and products after individual components have been divided by their means;  $G'$ ,  $G$  expressed as percentage of  $V(LxYxS)$  (Brown 1988);  $L$ , number of litters born within 120 days after mating;  $Y$ , mean litter size at birth;  $S$ , survival probability of young born

Social group	Component	Mean	Variance	$G$	$G'$
MON <i>n</i> = 18	L	2.78	1.01	0.130	17.0
	Y	6.67	2.80	0.063	8.2
	S	0.66	0.15	0.351	45.7
	$LxY$	19.27	97.29	0.283	37.0
	$LxS$	1.77	1.45	0.431	56.2
	$YxS$	4.36	8.41	0.433	56.5
	$LxYxS$	12.49	114.86	0.766	100.0
RELATED <i>n</i> = 38	L	3.21	0.60	0.058	25.0
	Y	7.26	2.08	0.039	16.8
	S	0.64	0.06	0.150	64.1
	$LxY$	23.46	52.75	0.097	41.4
	$LxS$	2.08	0.85	0.202	86.3
	$YxS$	4.72	4.21	0.194	83.0
	$LxYxS$	15.35	52.26	0.234	100.0
UNRELATED <i>n</i> = 35	L	3.37	1.24	0.109	24.1
	Y	6.85	2.21	0.047	10.4
	S	0.57	0.07	0.223	49.2
	$LxY$	23.68	103.30	0.194	42.8
	$LxS$	2.04	1.12	0.303	67.0
	$YxS$	3.93	4.39	0.288	63.6
	$LxYxS$	14.41	78.41	0.453	100.0

For the breeding females, lifetime reproductive success was broken down into the three components  $L$  (number of litters produced),  $Y$  (mean litter size), and  $S$  (survival probability of young born) following Brown (1988). The means and variances of the components and their products are given in Table 2. Most individual components of breeding success were not significantly interrelated (Table 3). Only for MON and UNRELATED females was there a significant positive correlation between number of litters produced and mean litter size. The full parti-

**Table 3.** Correlations between the components of breeding success in females in 3 different social groups. *L*, number of litters born within 120 days after mating; *Y*, mean litter size at birth; *S*, survival probability of young born

Social group		<i>L</i>	<i>Y</i>
MON <i>n</i> = 18	<i>Y</i>	0.4727*	
	<i>S</i>	-0.2864	-0.0482
RELATED <i>n</i> = 38	<i>Y</i>	0.0937	
	<i>S</i>	0.1366	0.1142
UNRELATED <i>n</i> = 35	<i>Y</i>	0.3338*	
	<i>S</i>	0.2302	-0.0354

\*  $P < 0.05$  (Spearman rank correlation)

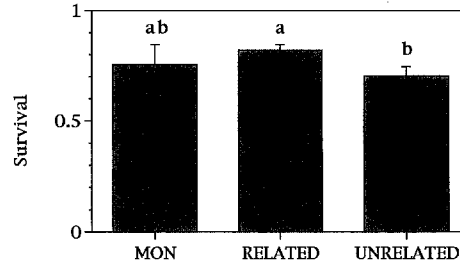
**Table 4.** Percentage contribution of the three components of lifetime reproductive success (LRS) and their interactions to variation in LRS of reproducing females in 3 different social groups. Contribution to  $V(LYS)/(LYS)^2$ : the diagonals give the single-component contributions ( $G$  in Table 2), and the off-diagonal elements give the joint-variation terms corresponding to row and column labels.  $LxYxS$ , Joint-variation term for variation between the 3 components. Data are expressed as a percentage of  $V(LxYxS)$  (see Table 2). *L*, number of litters born within 120 days after mating; *Y*, mean litter size at birth; *S*, survival probability of young born

Social group	Component	<i>L</i>	<i>Y</i>	<i>S</i>
MON <i>n</i> = 18	<i>L</i>	17.0		
	<i>Y</i>	11.8	8.2	
	<i>S</i>	-6.5	2.6	45.7
	$LxYxS$	21.2		
RELATED <i>n</i> = 38	<i>L</i>	25.0		
	<i>Y</i>	-0.4	16.8	
	<i>S</i>	-2.8	2.1	64.1
	$LxYxS$	-4.8		
UNRELATED <i>n</i> = 35	<i>L</i>	24.1		
	<i>Y</i>	8.3	10.4	
	<i>S</i>	-6.3	4.0	49.2
	$LxYxS$	10.3		

tioning of the variance in lifetime reproductive success (Table 4) shows that variation in offspring survival between breeding females made the largest contribution in all three social groups. Covariation in *L* and *Y* (significant positive correlation, Table 3) contributed 12% to the variance in MON females and 8% in UNRELATED ones. All other joint-variation terms were small and the component variables in the product varied fairly independently of each other.

#### Comparison of the components of lifetime reproductive success

For statistical analyses of the components of breeding success, each pair in the polygynous groups (RELATED or UNRELATED) is represented by the mean of both females or, in pairs where only one female reproduced, by the value of the breeding female. The resulting means in the three social groups differ only slightly from the ones



**Fig. 1.** Offspring survival probabilities (mean  $\pm$  SE) of females living monogamously (MON; *n* = 18) or polygynously with either a familiar sister (RELATED; *n* = 20 pairs) or a previously unfamiliar unrelated female partner (UNRELATED; *n* = 19 pairs). Survival was measured as the proportion of offspring weaned for all litters born within 120 days after mating of the mother. Different indices (*a*, *b*) above columns refer to significant differences between groups of data

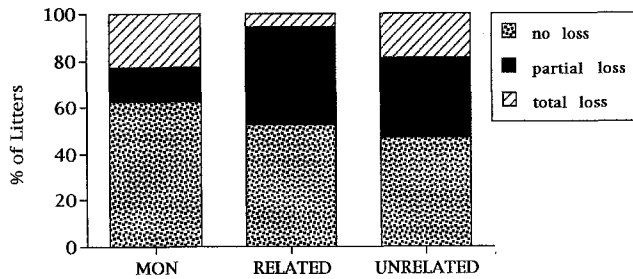
evaluated for individual breeding females given in Table 2.

Breeding females in the 3 social groups did not differ significantly in mean litter size or in the survival of young within 120 days after mating ( $Y$ :  $\chi^2_2 = 0.46$ , ns;  $S$ :  $\chi^2_2 = 2.19$ , ns). There was a trend for breeding polygynous females to produce more litters than monogamously paired females ( $\chi^2_2 = 4.88$ ,  $P < 0.10$ ). The number of females which reproduced successfully within "lifespan" differed significantly between the social groups: 95% of the RELATED females were successful in weaning young in comparison to 70% of the MON and 73% of the UNRELATED females ( $\chi^2_2 = 8.36$ ,  $P < 0.05$ ; multiple comparisons: RELATED vs. MON:  $P < 0.01$  and vs. UNRELATED:  $P < 0.01$ ).

#### Survival of young in different social groups

According to Table 4, survival of young is the single component with the highest contribution to variation in lifetime reproductive success among females. In the data presented so far offspring were only considered as "surviving" if they reached a minimum age of 17 days within 120 days after mating of the mother. Due to this criterion almost every second female "lost" her entire last litter during lifespan (MON: 28% of the females, RELATED: 50%; UNRELATED: 51%;  $\chi^2_2 = 3.07$ , ns). To test whether the social group had an influence on the survival of young irrespective of a standardized "lifespan", mean weaning data were evaluated for all litters born within the experimental period. Because all groups were kept for at least another month after the period of 120 days after mating, the actual fate of the last litter was known. Survival probabilities differed significantly between the social groups ( $\chi^2_2 = 6.79$ ,  $P < 0.05$ ; Fig. 1) with the highest weaning success reached by RELATED females and the lowest by UNRELATED ones (RELATED vs. UNRELATED:  $P < 0.05$ ).

Of the MON females, 39% did not suffer any loss of young within "lifespan". In polygynous breeding groups, however, significantly fewer females weaned all of their offspring (RELATED: 24%, UNRELATED: 9%;



**Fig. 2.** Percentage of litters born to females living monogamously (*MON*) or polygynously with either a sister (*RELATED*) or an unrelated female (*UNRELATED*) which did not suffer any loss of young until weaning (*no loss*), which were partially lost (*partial loss*), and which were entirely lost before weaning (*total loss*). Sample sizes as in Fig. 1

$\chi^2_2 = 6.64$ ,  $P < 0.05$ , no significant difference between *RELATED* and *UNRELATED*). On average, each female weaned 1.6 litters without the loss of any young (Fig. 2; no significant difference between social groups:  $\chi^2_2 = 0.42$ , ns). The number of litters in which some young died before weaning, however, was significantly lower for *MON* than for *RELATED* or *UNRELATED* females ( $\chi^2_2 = 9.15$ ,  $P < 0.05$ ; *MON* vs. *RELATED*:  $P < 0.05$  and vs. *UNRELATED*:  $P < 0.05$ ). The number of litters which were lost entirely, on the other hand, was lowest for *RELATED* females ( $\chi^2_2 = 10.03$ ,  $P < 0.01$ ; *RELATED* vs. *UNRELATED*:  $P < 0.01$ ; see Fig. 2). Offspring survival was independent of the number of young per female. In none of the three social groups was there a significant correlation between survival probability of a litter and either mean litter size (*MON*: Spearman  $r_s = -0.1137$ ,  $n = 18$ , ns; *RELATED*:  $r_s = 0.0525$ ,  $n = 38$ , ns; *UNRELATED*:  $r_s = -0.0393$ ,  $n = 34$ , ns) or total number of offspring born per female (*MON*:  $r_s = -0.1337$ ,  $n = 18$ , ns; *RELATED*:  $r_s = -0.0782$ ,  $n = 38$ , ns; *UNRELATED*:  $r_s = 0.1689$ ,  $n = 34$ , ns).

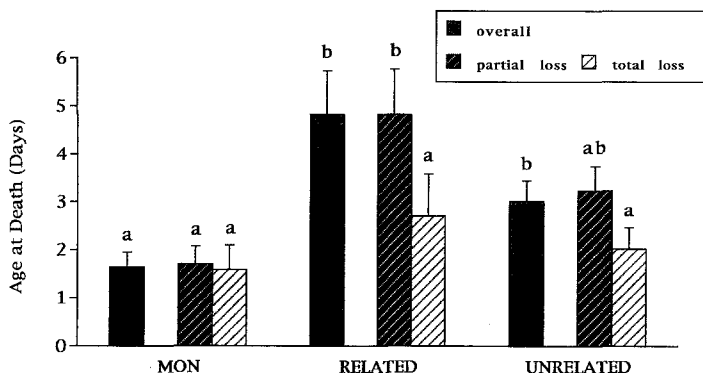
#### Age of young at death

Two types of mortality of young were observed. First, pups died directly after birth. Newborn pups or entire litters were found outside the nest, often still in the amniotic sac with the placenta attached (female house mice usually lick and clean the pups directly after birth). Such

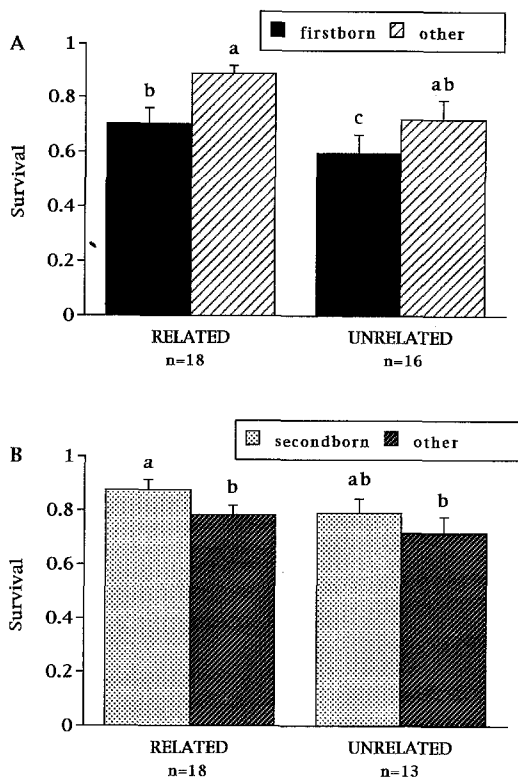
pups were not retrieved or nursed by the mother and were found dead (sometimes partially eaten) on day 1 or 2 of lactation. The second type of mortality occurred after pups had been nursed in the nest for at least 1 day. Single dead and partially eaten pups were found outside the nest, typically with wounds in the neck region and on the back. On five occasions the following behaviour was observed in different polygynous groups (*RELATED* and *UNRELATED*). A highly pregnant female (1–4 days before giving birth) picked up a pup from the top of the litter of her partner, carried it away from the nest, licked the pup vigorously on the back and finally killed it by a couple of bites in the neck region. The entire sequence lasted between 40 s and 2 min.

In litters of *MON* females 87% of all pup deaths prior to weaning were due to entire litter mortality. *RELATED* females, however, lost most of their young due to partial-litter mortality (75%) and *UNRELATED* females lost equal portions due to entire- (53%) and partial-litter mortality (47%). The age at which offspring died (defined as the day of lactation at which a corpse was found) was lower for young of *MON* females than for young of *RELATED* or *UNRELATED* females (Fig. 3, “overall”;  $\chi^2_2 = 7.34$ ,  $P < 0.05$ ; *MON* vs. *RELATED*:  $P < 0.01$  and vs. *UNRELATED*:  $P < 0.10$ ). In the same figure, age at death of young is shown separately for litters which were lost entirely and for litters which were only partially lost before weaning. Offspring died on average at an age of  $2 \pm 0.3$  days in litters which were lost entirely ( $\chi^2_2 = 2.39$ , ns). In litters with partial loss of young, however, offspring were significantly older at death in the polygynous breeding groups than in the monogamous ones ( $\chi^2_2 = 6.51$ ,  $P < 0.05$ ; *MON* vs. *RELATED*:  $P < 0.05$  and vs. *UNRELATED*:  $p = 0.10$ ). The oldest age at which an offspring was found dead was 17 days in a breeding pair of sisters and 16 days in a pair of unrelated females. For monogamously paired females, however, the oldest age at death of a pup was day 5 (only 8 out of 86 offspring were older than 2 days when found dead).

*RELATED* females reared a significantly higher proportion of litters in communal nests than *UNRELATED* females ( $\chi^2_1 = 13.24$ ,  $P < 0.01$ ). In breeding groups of sisters, 74% of the litters were reared in a communal nest and 20% in the absence of another litter (6% of the litters did not survive until weaning). Pairs of unrelated females reared 56% of their litters communally and 27% solitar-



**Fig. 3.** Age at death of young born to females living monogamously (*MON*;  $n = 18$  females) or polygynously with either a sister (*RELATED*;  $n = 20$  pairs) or an unrelated female (*UNRELATED*;  $n = 19$  pairs). Means ( $\pm$ SE) are given for all offspring lost (*overall*) and separately for litters which were lost partially (*partial loss*) or entirely (*total loss*). Different indices (*a*, *b*) above columns refer to significant differences between groups of data



**Fig. 4A, B.** Mean ( $\pm$  SE) survival probabilities of litters in polygynous social groups (either pairs of familiar sisters, *RELATED*, or pairs of previously unfamiliar, unrelated females, *UNRELATED*). **A** Survival is shown for litters which were followed within 16 days by a newborn litter of the partner female (*firstborn* litters in a communal nest) and for litters which were reared in the absence of a younger litter (*other*; such litters might be either secondborn litters in a communal nest or litters reared solitarily). **B** Survival of litters which were born in a nest with older young present (less than 17 days old at day of birth; such litters are *secondborn* litters in a communal nest) and of litters reared in the absence of older nestmates (*other*; either firstborn litters or litters reared solitarily). Different indices (*a, b, c*) above columns refer to significant differences between groups of data

ily (17% of the litters died). Litters in communal nests differed in age on average by 7.8 days (*RELATED*:  $7.5 \pm 0.9$  d, *UNRELATED*:  $8.2 \pm 1.0$  d;  $z = -0.4604$ , ns). To test whether the birth of another litter affected the survival of dependent young, mean values of survival probabilities were evaluated per female for litters which were followed within 16 days by a newborn litter of the partner female (such litters are firstborn litters in a communal nest), and for litters which did not fulfil that criterion (either secondborn litters in a communal nest or litters which were reared solitarily in a polygynous breeding group). Both in *RELATED* and *UNRELATED* females survival probabilities of such "firstborn" litters were significantly lower than for the "other" litters (each pair of females is represented by the average of their means for firstborn and other litters; Wilcoxon matched pairs signed rank test: *RELATED*:  $T = 21$ ,  $n = 18$ ,  $P < 0.01$ , *UNRELATED*:  $T = 25$ ,  $n = 16$ ,  $P < 0.05$ ; Fig. 4A). The presence of a litter less than 17 days old had no significant influence on the survival probability of a newborn litter in *UNRELATED* females (Wilcoxon:

$T = 39$ ,  $n = 13$ , ns; Fig. 4B). In *RELATED* females, however, offspring survival was significantly improved by the presence of older but still dependent young in the communal nest ( $T = 33$ ,  $n = 18$ ,  $P < 0.05$ ).

## Discussion

Under laboratory conditions, female house mice maximize lifetime reproductive success by choosing a familiar sister for communal care of their litters rather than rearing litters alone or with a previously unfamiliar, unrelated partner (König 1989, 1993). These differences in breeding success are insignificant at the level of single reproductive events but accumulate to become significant at the level of lifetime reproduction. This might explain why Manning et al. (1992), who described similar numbers of pups born to communally and singly nesting female house mice, excluded improved reproductive success as a function of communal nursing. An analysis of the components of lifetime reproductive success and their contributions to variance in weaning success should allow identification of those components which are most influential for breeding success. Females differed within and among the different social groups only insignificantly in terms of number and size of litters produced within an experimental "lifespan" (120 days after mating with a male at the age of about 2 months). A more pronounced difference, however, was revealed for survival probabilities of young until weaning which contributed with 46–64% to differences in lifetime reproductive success among females. In this respect female house mice are similar to many other mammalian and avian species in which individual differences in offspring survival are the most important component of variation in lifetime reproductive success among breeding females (see Clutton-Brock 1988b).

A comparison of reproductive behaviour in the different social groups revealed that a female's probability of reproducing and successfully weaning offspring was significantly improved in pairs of familiar sisters (*RELATED*) compared to females in the other groups. The contribution to variance in reproductive success due to non-breeding females was highest in females living with a previously unfamiliar, unrelated partner (*UNRELATED*). In this group, furthermore, 14% of the females died because of female-female aggression. Although females probably would have left a group in response to overt aggression under more natural (unrestricted) conditions, the data indicate costs of immigration for females. If no other option is available, breeding success can be drastically reduced after immigration into an unfamiliar breeding group.

Weaning probabilities of young within the experimental "lifespan" of the mother were highest for *RELATED* females but did not differ significantly between the social groups. This analysis relied on the (conservative) assumption that offspring will not survive after the death of the mother within the first 16 days of lactation. However, due to indiscriminate nursing of their own and alien young by communally nesting females (Saylor and Salmon 1971;

König 1989) offspring might still have some chance of surviving until weaning after the death of their mother in a polygynous breeding group if the other female continued to nurse both litters. In three breeding groups (one RELATED and two UNRELATED) kept for over a year, one of the females died when two dependent litters were present in the communal nest. The surviving female always continued to nurse both litters and 86% of the dead female's young survived until weaning.

The fact that almost every second female "lost" her last litter within "lifespan" due to the strict criterion used might have masked some subtle influence of the social group on weaning probabilities of young. To test that hypothesis, actual survival probabilities of the last litter were included in a further analysis, yielding a significant difference with highest survival values achieved by RELATED females and lowest by UNRELATED ones. In none of the social groups analyzed was survival of young dependent on mean litter size or on the total number of offspring produced which excludes the hypothesis that females generally tend to give birth to larger litters than they are able to rear (female house mice are known to spontaneously kill some pups in response to large litters; Gandelman and Simon 1977; Fuchs 1982). In monogamously paired females (MON), offspring survival was dependent on whether the entire litter was "accepted" and nursed directly after birth or not. In the majority of litters all young survived until weaning. In the remainder, offspring were almost exclusively lost during the first 2 days of lactation (93% of the young were found dead when they were 1 or 2 days old), and mortality of young was characterized by the loss of an entire litter. Thus, once a MON female had cared for and nursed a litter early during lactation, her offspring had a very high chance of surviving until weaning. In polygynous breeding groups, loss of an entire litter also occurred early during lactation. Here, however, more litters suffered the loss of some young and offspring died on average at an older age. Furthermore, in nests of RELATED females offspring survival directly after birth was improved and fewer litters were lost entirely than in the other social groups analyzed. Compared to MON females, UNRELATED females lost a similar percentage of entire litters directly after birth but also suffered a higher loss of individual young which was similar to that observed for RELATED females. It is not yet known how and why familiar sisters are more successful at rearing young. Future experiments have to focus on the females' behaviour towards newborn young in the different social groups. Furthermore, detailed observations of the females' behaviour towards each other in polygynous groups should analyze whether aggression, as observed in groups of UNRELATED females during the first weeks of the experiment, is responsible for higher entire-litter mortality than in RELATED females.

The loss of some young in a litter, observed in polygynous groups even when offspring were up to 17 days old, was dependent on the timing of the birth of the litter. Individual offspring had a reduced survival probability if they were firstborn young in a communal nest (another litter was born within 16 days). Pregnant females were

observed to kill one or few dependent young of her partner shortly before they gave birth themselves. Such infanticidal behaviour might result in re-distribution of milk from alien to own young. In house mice, the amount of milk produced is dependent on the sucking stimulus of young which increases with increasing litter size (Hanwell and Peaker 1977; König et al. 1988). If a female kills alien young shortly before she gives birth herself, communal and indiscriminate nursing might result in a higher proportion of the other female's milk being available for her offspring. It is not yet known whether females would refrain from cooperative nursing after the loss of an entire litter which would prevent killing of all dependent young by pregnant females. Pup-cannibalism is an integrated part of the behaviour in rodents (for a recent review see Elwood 1992). A similar behaviour of reproducing females killing each other's young has been described for prairie dogs (Hoogland 1985) and for communally nesting birds (Vehrencamp 1977; Mumme et al. 1983). Under more natural feeding conditions competition between females for the number of and investment into own versus alien young might be even more pronounced than under the luxurious feeding conditions in the laboratory, especially if females are previously unfamiliar and unrelated.

For Norway rats, Mennella et al. (1990) described a reduced survival probability of litters born in the presence of 15- to 28-day-old litters due to inter-litter competition; under such conditions newborn pups were often excluded from access to the teats of a female by the older pups and died. In house mice, such inter-litter competition was not observed. In polygynous groups, eight litters were born in the presence of 17- to 28-day-old young and reared solitarily (no other litter was born within 16 days); under such conditions young had a very high survival probability (100% in three litters of RELATED females and 91.5% in five litters of UNRELATED ones). Obviously, survival of young was mainly dependent on whether another litter was born within 16 days or not.

To conclude, females living with a familiar sister had an improved probability of reproducing and reared more litters cooperatively in communal nests than females living with a previously unfamiliar, unrelated partner. Furthermore, living with a familiar sister resulted in an improved probability of successfully rearing young, in improved survival of litters directly after birth, and in improved survival of secondborn litters in a communal nest. Familiarity with a partner during juvenile development rather than relatedness seems to be responsible for better reproduction and higher offspring survival in RELATED females compared to UNRELATED ones (König in press). Nevertheless, behavioural analyses are still lacking to determine the parameter which generates such differences in reproductive success between females living with a familiar and related or unfamiliar and unrelated partner.

A high reproductive output in house mice can be interpreted as an adaptation to a colonizing life strategy which has to cope with variable environmental conditions and high mortality (Berry 1981a; Bronson 1984; König et al. 1988). Under such conditions the number of young raised is of paramount importance for a female's

fitness, especially in a growing population after colonization of a new habitat. Communal care among familiar and related female house mice seems to be an adaptation to improve the probability of successfully weaning young. The fact that UNRELATED females also always communally nursed litters and the observation by Manning et al. (1992) that "most single-mother nests occurred when communal nesting options were not available" (legend of Table 1, page 582) support the hypothesis that under more natural conditions other factors further improve breeding success of communally nesting house mice even among unrelated females. Besides improved growth of young in communal nests (Saylor and Salmon 1969), such factors might include a higher survival probability during periods of cold temperatures in larger groups of adults than in smaller ones, or a decreased likelihood of infanticide by non-group members (Manning et al. in press, cited in Manning et al. 1992).

*Acknowledgements.* I sincerely thank Robert Elwood, Raghavendra Gadagkar, Robert Gibson, Eduard Linsenmair, Hubert Markl and two anonymous referees for helpful comments. For excellent help with animal maintenance I very much thank Brigitte Dick, Ute Diedrichsen, Armin Götzke, Gerald Kerth, Judith Korb, Stefan Meßner, and Edda Schmitt. This work was supported by the Deutsche Forschungsgemeinschaft (Ko 1170/1-1).

## References

- Anderson PK (1965) The role of breeding structure in evolutionary processes of *Mus musculus* populations. Proc Symp Mutation Proc, Prague, pp 17–21
- Arnold SJ, Wade MJ (1984) On the measurement of natural and sexual selection: Theory. Evolution 38:709–719
- Baker AEM (1981) Gene flow in house mice: behavior in a population cage. Behav Ecol Sociobiol 8:83–90
- Beauchamp GK, Gilbert AN, Yamazaki K, Boyse EA (1986) Genetic basis for individual discriminations: the major histocompatibility complex of the mouse. In: Duvall D, Müller-Schwarze D, Silverstein RM (eds) Chemical signals in vertebrates, 4 Ecology, evolution, and comparative Biology. Plenum Press, New York, pp 413–422
- Berry RJ (1971) Life and death in an island population of the house mouse. Exp Gerontol 6:187–197
- Berry RJ (1981a) Population dynamics of the house mouse. Symp Zool Soc London 47:395–425
- Berry RJ (1981b) Town mouse, country mouse: adaptation and adaptability in *Mus domesticus* (*M. musculus domesticus*). Mammal Rev 11:91–136
- Bronson FH (1983) Chemical communication in house mice and deer mice: Functional roles in reproduction of wild populations. Spec Publ Am Soc Mamm 7:198–238
- Bronson FH (1984) The adaptability of the house mouse. Sci Am 250:90–97
- Brown D (1988) Components of lifetime reproductive success. In: Clutton-Brock TH (ed) Reproductive success. Chicago University Press, Chicago, pp 439–453
- Clutton-Brock TH (1988a) Reproductive success. In: Clutton-Brock TH (ed) Reproductive success. Chicago University Press, Chicago, pp 472–485
- Clutton-Brock TH (1988b) Reproductive success. Chicago University Press, Chicago
- Creel SR, Creel NM (1991) Energetics, reproductive suppression and obligate communal breeding in carnivores. Behav Ecol Sociobiol 28:263–270
- Crow JF (1958) Some possibilities for measuring selection intensities in man. Hum Biol 30:1–13
- Crowcroft P, Rowe FP (1963) Social organization and territorial behaviour in the wild house mouse (*Mus musculus* L.). Proc Zool Soc London 140:517–531
- DeFries JC, McClearn GE (1970) Social dominance and Darwinian fitness in the laboratory mouse. Am Nat 104:408–411
- Elwood R (1992) Pup-cannibalism in rodents: causes and consequences. In: Elgar MA, Crespi BJ (eds) Cannibalism. Ecology and evolution among diverse taxa. Oxford University Press, Oxford, pp 299–322
- Fuchs S (1981) Consequences of premature weaning on the reproduction of mothers and offspring in laboratory mice. Z Tierpsychol 55:19–32
- Fuchs S (1982) Optimality of parental investment: the influence of nursing on the reproductive success of mother and female young house mice. Behav Ecol Sociobiol 10:39–51
- Gandelman R, Paschke RE, Zarrow M, Denenberg VH (1970) Care of young under communal conditions in the mouse (*Mus musculus*). Dev Psychobiol 3:245–250
- Gandelman R, Simon NG (1977) Spontaneous pup-killing by mice in response to large litters. Dev Psychobiol 11:235–241
- Grafen A (1988) On the uses of data on lifetime reproductive success. In: Clutton-Brock TH (ed) Reproductive success. Chicago University Press, Chicago, pp 454–471
- Hamilton WD (1964) The genetical evolution of social behaviour (I and II). J Theor Biol 7:1–52
- Hanwell A, Peaker M (1977) Physiological effects of lactation on the mother. Symp Zool Soc London 41:297–312
- Hoogland JL (1985) Infanticide in prairie dogs: lactating females kill offspring of close kin. Science 230:1037–1040
- König B (1989) Behavioural ecology of kin recognition in house mice. Ethol Ecol Evol 1:99–110
- König B (1993) Maternal investment of communally nursing female house mice (*Mus musculus domesticus*). Behav Proc 30:61–74
- König B (in press) Fitness effects of communal rearing in house mice: The role of relatedness versus familiarity. Anim Behav
- König B, Markl H (1987) Maternal care in house mice. I. The weaning strategy as a means for parental manipulation of offspring quality. Behav Ecol Sociobiol 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. J Zool London 216:195–210
- Lidicker WZJ (1976) Social behaviour and density regulation in house mice living in large enclosures. J Anim Ecol 45:677–697
- Mackintosh JH (1981) Behaviour of the house mouse. Symp Zool Soc London 47:337–365
- Manning CJ, Wakeland EK, Potts WK (1992) Communal nesting patterns in mice implicate MHC genes in kin recognition. Nature 360:581–583
- Mennella JA, Blumberg MS, McClintock MK, Moltz H (1990) Inter-litter competition and communal nursing among Norway rats: advantages of birth synchrony. Behav Ecol Sociobiol 27:183–190
- Møller AP (1987) Advantages and disadvantages of coloniality in the swallow, *Hirundo rustica*. Anim Behav 35:819–832
- Mumme RL, Koenig WD, Pitelka FA (1983) Reproductive competition in the communal acorn woodpecker: sisters destroy each other's eggs. Nature 306:583–584
- Mumme RL, Koenig WD, Pitelka FA (1988) Costs and benefits of joint nesting in the acorn woodpecker. Am Nat 131:654–677
- Packer C, Scheel D, Pusey AE (1990) Why lions form groups: food is not enough. Am Nat 136:1–19
- Pennycuik PR, Johnston P, Westwood N, Reisner A (1986) Variation in numbers in a house mouse population housed in a large outdoor enclosure: seasonal fluctuations. J Anim Ecol 55:371–391
- Petras ML (1967) Studies of natural populations of *Mus*. I. Biochemical polymorphisms and their bearing on breeding structure. Evolution 21:259–274



- Reimer J, Petras ML (1967) Breeding structure of the house mouse in a population cage. *J Mammal* 48:88–99
- 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. *Behaviour* 40:60–85
- Selander RK (1970) Behavior and genetic variation in natural populations. *Am Zool* 10:53–66
- Singleton GR, Hay DA (1983) The effect of social organization on reproductive success and gene flow in colonies of wild house mice, *Mus musculus*. *Behav Ecol Sociobiol* 12:49–56
- Southwick CH (1955) Regulatory mechanisms of house mouse populations: social behavior affecting litter survival. *Ecology* 36:627–634
- Vehrencamp SL (1977) Relative fecundity and parental effort in communally nesting anis, *Crotophaga sulcirostris*. *Science* 197:403–405
- Werboff J, Steg M, Barnes L (1970) Communal nursing in mice: strain-specific effects of multiple mothers on growth and behavior. *Psychonomic Sci* 19:269–271
- Wilkinson GS (1992) Communal nursing in the evening bat, *Nycticeius humeralis*. *Behav Ecol Sociobiol* 31:225–235
- Wilkinson GS, Baker AEM (1988) Communal nesting among genetically similar house mice. *Ethology* 77:103–114
- Zar JH (1984) *Biostatistical analysis*, 2nd edn. Prentice-Hall International, Englewood Cliffs

Communicated by R. Gibson