

Inter-litter competition and communal nursing among Norway rats: advantages of birth synchrony

Julie A. Mennella*, Mark S. Blumberg**, Martha K. McClintock, and Howard Moltz

Department of Psychology, The University of Chicago, 5730 Woodlawn Avenue, Chicago, IL 60637, USA

Received November 9, 1989 / Accepted March 23, 1990

Summary. The effect of inter-litter competition on pup survival was investigated in pairs of female rats (*Rattus norvegicus*) living and breeding in the same environment. If a female gave birth when a 0- to 14-day-old litter was already present in the environment, her pups had a very high chance of surviving, similar to the situation in which no other litter was present. Moreover, the mother was likely to nurse communally with the mother of the 0- to 14-day-old litter. This communal nursing benefitted the newborn pups as evidenced by their being heavier at weaning than litters that were not nursed communally. In contrast, if a female gave birth when a 15- to 28-day-old litter was already present in the environment, her newborn pups were likely to die within 3 days postpartum, owing to the fact that they were often prevented from suckling at their mother's teats, resulting in milk deprivation, and were often beneath the older pups, resulting in physical trauma. These findings suggest that inter-litter competition is an important source of pup mortality when litters are born 15–28 days apart. The data are discussed in terms of the advantages of birth synchrony.

Introduction

In many species of mammals, lactating females build a nest jointly and nurse communally (Crowcroft and Rowe 1963; Dieterlen 1962; Emlen 1984; Gurski and Scott 1980; MacDonald et al. 1987; McShea and Madison 1984; Southwick 1969; Spencer-Booth 1970; Zimmerman 1974). The likelihood, however, of two females nursing communally is often dependent upon their being pregnant at the same time and subsequently giving birth at approximately the same time, customarily referred to as birth synchrony (Gurski and Scott 1980; Packer

and Pusey 1983a; Rood 1980; Sayler and Salmon 1971). Females and their young should benefit from birth synchrony and the subsequent communal nesting because the mothers can share the energetic burdens of protecting and nursing young (Baldwin 1970; Boinski 1987; Gurski and Scott 1980; McClintock 1981; Sayler and Salmon 1969, 1971). Furthermore, it has been demonstrated, although as yet only in mice, that growth rate is enhanced when young are nursed in a communal nest, even when the ratio of young to lactating females remains the same (Sayler and Salmon 1969, 1971).

In the lion (*Panthera leo*), another advantage of birth synchrony is evident: cub litters of similar age (inter-birth interval < 2 months) have a lower mortality rate than cub litters of dissimilar age, owing in part to the fact that older cubs can prevent younger cubs from gaining access to teats (Bertram 1975; Packer and Pusey 1983b; Rudnai 1973; Schaller 1972). Thus birth synchrony minimizes inter-litter competition.

The mechanisms that affect the timing of breeding among female rats have been well documented (Aron 1973; Gudermuth et al. 1984; McClintock 1978, 1983a–c, 1984). The consequences of synchronous or asynchronous breeding, however, are less well understood (McClintock 1981, 1983a–c). In this study, we followed the reproductive histories of pairs of adult female rats while each pair was living with a male in the same environment. Specifically, we monitored the timing of mating and births, the incidence of communal nursing, and the incidence of pup mortality over a period of some 4 months. From literature on other species, we expected communal nursing to occur when females gave birth synchronously and expected pup mortality to be high when they gave birth asynchronously.

Methods

Animals. Wistar rats were born in the authors' laboratory and reared in mixed-sex litters. Following weaning at 30 days of age, they were housed with animals of the same sex and age in groups of 6–8. A lighting schedule of 12L:12D was in effect throughout the study. The ambient temperature was $22^{\circ} \pm 2^{\circ}$ C, with a relative humidity of 60%–90%.

* Present address: Monell Chemical Senses Center, 3500 Market Street, Philadelphia, PA 19104, USA

** Present address: Department of Psychology, Indiana University, Bloomington, IN 47405, USA

Offprint requests to: M.K. McClintock

At approximately 90 days of age (range: 77–109 days old), 18 virgin females were chosen as experimental subjects. From this pool, nine pairs of females were constituted, each pair consisting of females of comparable age. One female of each pair was marked with methyl violet dye so that the two females could be distinguished throughout the study.

Environment. Each pair of females was placed in an environment constructed of 2.54 cm plywood joined to enclose an area $120 \times 120 \times 90$ cm and covered with 0.64 cm hardware cloth (see Guder-muth et al. 1984). A partition having two open doorways divided the area in half. One side was an open area containing food and water as well as a platform of wire mesh, a cylindrical tunnel of wire mesh, and a large brick. The other side contained two adjacent nest boxes constructed of red Plexiglas. The floor of each environment was covered with pine chips for sanitation and shredded newspaper for nesting material.

Procedure. Four to six days after a given pair of females was placed in the environment, a sexually-experienced male was introduced. Observations of each triad were then made at least once daily for the duration of the study; each observation period lasted approximately 5 min. During the first week of the study, we looked for sperm in the vaginal smear of each female to determine the date of first fertilization. Subsequent fertilizations were determined by the presence of sperm in the vaginal smear within 1 day following the birth of each litter during which time the female rat usually experiences a postpartum estrus. In six cases, postpartum fertilization was not successful, making it difficult to determine the precise day of fertilization. Because of this, and because the next successful fertilization necessarily occurred during a cycling estrus, we inferred date of fertilization for these litters by counting back 22 days from the day of parturition (the length of a typical pregnancy conceived at a cycling estrus; Mantalenakis and Ketchel 1966; Smart and Dobbing 1971).

Prior to parturition, we noted when each female first appeared pregnant and built a nest, and we recorded the location of the nest. At parturition, we recorded the date of birth and the size of each litter. Daily observations were made to determine the number of pups alive on each postpartum day, the number of pups nursed by each female, and the location of the nest. In the event that a litter was born within 1 week of another litter, the pups in one litter were toe-clipped for identification. If pups survived to weaning, i.e., to approximately 30 days of age (Calhoun 1962; Stoloff and Blass 1983), they were weighed. In order to maintain the initial population density of the environment, these pups were not returned to the environment. Thirty days of age also corresponds to the age at which pups start leaving the nest chamber in the wild (Calhoun 1962).

Each triad of 2 females and 1 male remained in its assigned environment for a period potentially sufficient to allow each female to give birth to and wean 3 litters. Thus, a maximum of 54 litters could have been born to and weaned by the 18 females in the study.

Statistical analyses. Because rats give birth to more than one pup per litter and because the characteristics of litter mates are likely to be inter-correlated, problems of independence arise when each pup is treated as an individual case (see Martin and Bateson 1986). Therefore, when appropriate, statistical tests treated the litter as the unit of analysis.

Temporal data were analyzed by constructing log survivor plots, and statistical comparisons of the curves were made using the generalized Savage (Mantel-Cox; Mantel 1966). It should be noted that in a log survivor analysis, individuals are analyzed, not groups. Therefore, in this case alone, we used the pup rather than the litter as the unit of analysis. Similar results were obtained when the litter was treated as the unit of analysis and "litter death" was defined as the death of the majority of pups in the litter. Log survivor analyses, analyses of variance, and post-hoc compar-

isons were carried out using BMDP (Dixon 1985). Percentages were transformed with the arcsine-root transformation to meet the assumptions of normative statistics. Summary statistics are expressed as mean (\pm SE).

Results

Every female gave birth to at least 2 litters (2.4 ± 0.1) with approximately 14 pups in each litter (13.5 ± 0.5 pups). In the course of this study, 44 litters were born and each litter, if it survived, was followed to weaning. Fifty-five percent of these litters were conceived during a cycling estrus, and the remainder were conceived during a postpartum estrus, similar to the distribution found among wild rats (Davis and Hall 1951). Furthermore, 59% were born when another litter was already present in the nesting environment, with birth intervals ranging from 0 to 28 days.

Inter-litter competition

Pup survival was significantly lower when a litter, hereafter referred as the "focal litter," was born in the presence of another litter than when no other litter was present ($52.6 \pm 8.8\%$ of the pups in the focal litters survived in the presence of another litter as compared with $75.6 \pm 8.0\%$ in the absence of another litter; $t = 2.672$; $df = 25$; $P < 0.02$). The distribution of survival rates, however, was bimodal; that is, almost two-thirds of the litters had survival rates greater than 70%; the remainder had survival rates less than 20% (Fig. 1). This suggests that the mere presence of another litter is insufficient to explain lower pup survival. Therefore, we examined the effect of the age of the other litter on pup survival. To do so, we distinguished litters that were 0–14 days old (mean = 5.9 ± 1.5 days) from those that were 15–28 days old (mean = 22.4 ± 1.1 days). We chose 15 days of age as the dividing point because it is the age when pronounced developmental changes begin to occur in the

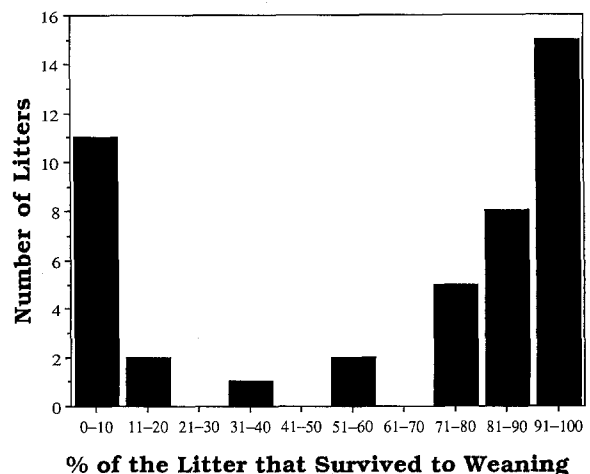


Fig. 1. Bimodal frequency distribution of the litter's survival rate (percentage of the litter surviving to weaning; total number of litters = 44)

Table 1. Summary table of reproductive parameters associated with the presence and age of another litter in the environment

	No other litter present	Age of other litter	
		0-14 days	15-28 days
Number of litters	18	12	14
Mean (modal) percentage of litter surviving to weaning	75.6 ± 8.0 (100)	80.9 ± 8.0 (100)	28.4 ± 11.5 (0)
Age of pups in other litter	-	5.9 ± 1.5	22.4 ± 1.1
Number of pups born per litter	12.4 ± 1.0	14.0 ± 0.8	14.5 ± 0.8
Number of pups in other litter	-	10.2 ± 1.3	10.4 ± 0.9

Values are expressed as mean ± SE. All comparisons between groups are non-significant except percentage of litter surviving to weaning: $F(2,41)=9.69$; $P<0.0005$, and age of pups in other litter: $t=-9.17$; $P<0.0001$. See text for further discussion

pups' physiology and behavior (Alberts and Gubernick 1983). It is also the median age of pre-weanling rats.

Survival was low when focal litters were born in the presence of 15- to 28-day-old litters; in contrast, when focal litters were born in the presence of 0- to 14-day-old litters, survival was comparable to the situation in which no other litter was present (Table 1; one-way analysis of variance: $F(2,41)=9.69$; $P\leq 0.0005$). Furthermore, most focal litters in which no pups survived to weaning were born in the presence of 15- to 28-day-old litters (82%, $N=11$; $P\leq 0.001$; Binomial Test). Thus, when two litters of rats were born in the same nesting environment, pup survival in the younger litter was reduced when the interval between births was large (15-28 days) and was unaffected when the interval was small (0-14 days).

When a litter was born in the presence of a 15- to 28-day-old litter, 50% of the focal pups died by the time they were 2 days of age. An additional 19% died over the next 4 days, after which there was no further mortality (Fig. 2). At the time of death of the focal litter, the older litter was at least 17 days of age. Pups born in the absence of another litter and pups born in the presence of a 0- to 14-day-old litter, on the other hand, exhibited a low mortality rate that extended over the first 14 days postpartum, with no further mortality thereafter (80% survival). The survival distribution for pups born in the presence of 15- to 28-day-old litters is significantly different from the survival distributions of the other two groups ($P\leq 0.0001$ for each comparison, generalized Savage), whereas the survival distributions of these other two groups are not significantly different from each other.

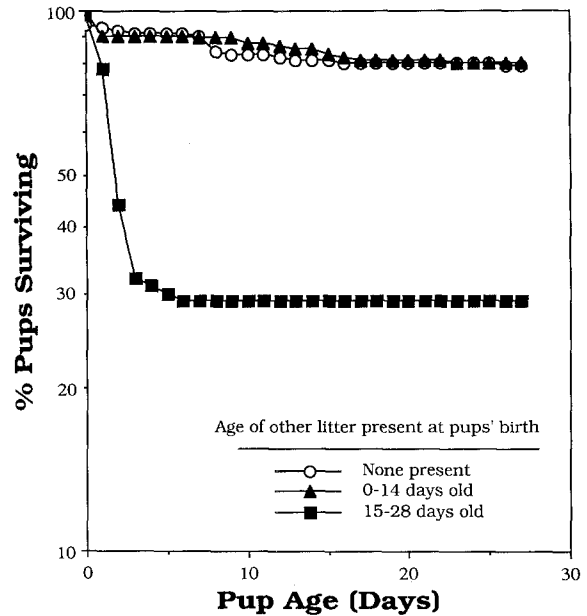


Fig. 2. Log survivor plot of mean percent of pups alive in each litter on the day of birth (day 0) through day 28 postpartum for (1) litters that had no other litter present on day of birth, (2) litters that had a 0- to 14-day-old litter present on day of birth, and (3) litters that had a 15- to 28-day-old litter present on day of birth

It appears that 15- to 28-day-old pups caused the death of the focal litter; two-thirds of the litters born in the presence of 15- to 28-day-old litters had no survivors. Our daily observations revealed that the nests of 78% of these destroyed litters had been invaded by 15- to 28-day-old pups. Such nest invasions occurred soon after the focal litter was born (mean = 1.0 ± 0.7 days) at which time the 15- to 28-day-old pups were found suckling at the teats of the focal mother. This often prevented the focal mother's own pups from suckling and may have damaged her nipples as described by Sachs and Rosenblatt (1974), thus depriving them of milk as evidenced by the absence of "milk bands" (i.e., the milk visible through the skin as a white band around the abdomen). In addition, focal pups were often found beneath the 15- to 28-day-old pups while the latter were suckling. Whether milk deprivation or physical trauma was the primary cause of death among focal pups born in the presence of 15- to 28-day-old pups is unknown. On one occasion we observed the 15- to 28-day-old pups cannibalizing pups in the focal litter.

Given the relative brevity of our observation periods, we should mention that 78% is probably an underestimate of the incidence of nest invasion. For example, in one of the two cases in which none of the focal pups survived to weaning, we did not directly observe 15- to 28-day-old pups in the nest of the focal mother; however, we did note the absence of milk bands in the focal pups, suggesting that their death was the result of milk deprivation. Hereafter, we use the phrase "inter-litter competition" to refer to the fact of nest invasion and the subsequent interaction between the two litters.

Although the evidence for competition between 15-

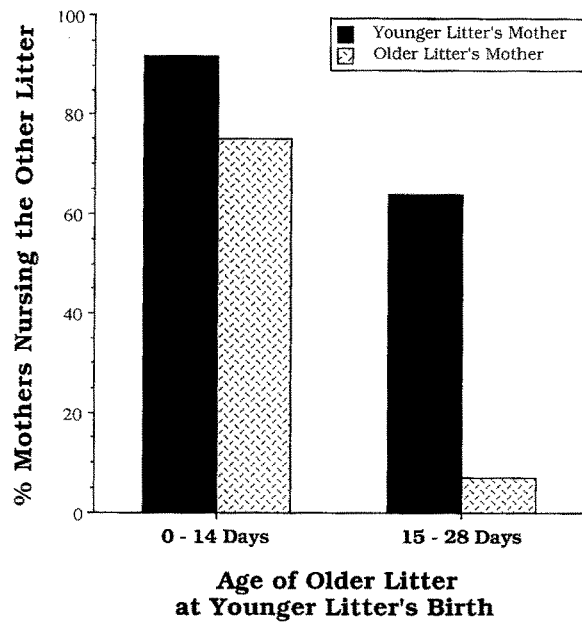
Table 2. Summary table of reproductive parameters that were not associated with the percentage of the litter surviving to weaning

	Mean % surviving to weaning	Significance
Estrous condition at conception		$t=0.50$, NS
Cycling estrus	64.0 ± 8.4	
Postpartum estrus	58.6 ± 9.4	
Nest location		$t=0.56$, NS
Together	58.3 ± 12.2	
Apart	67.4 ± 7.0	
	Correlation with % surviving to weaning	Significance
Age of mother	$r=0.20$	$F=1.81$, NS
Weight of mother	$r=0.15$	$F=0.93$, NS
Gestation length	$r=0.02$	$F=0.01$, NS
Number of older pups present	$r=0.07$	$F=0.10$, NS

to 28-day-old litters and focal litters is strong, it is possible that factors other than inter-litter competition played a role in the mortality of the focal pups. We were, however, able to rule out several non-competitive factors. First, there was no difference in the number of pups in focal litters born either in the absence of another litter or in the presence of 0- to 14-day-old or 15- to 28-day-old litters, nor were the number of pups in the 0- to 14-day-old and 15- to 28-day-old litters different (see Table 1).

Second, we found no evidence that sires contributed to the death of focal pups. Nor should we expect them to, given that male infanticide is significantly reduced by sexual experience and cohabitation with a pregnant female (Mennella and Moltz 1988; Mennella 1988). Seven of nine males sired litters that were born under each of our three conditions: no other litter, a 0- to 14-day-old litter, and a 15- to 28-day-old litter present. Each of these males sired litters with survival rates ranging from 0% to greater than 85% (mean = $56.2 \pm 5.4\%$). Furthermore, the remaining two males that had not sired litters born in the presence of 15- to 28-day-old pups had litters with survival rates significantly higher than the survival rate of the other males' litters ($86.5 \pm 8.0\%$; $P \leq 0.05$, Mann-Whitney U Test).

Third, litter survival was not associated with the individual identity of the mother. Eight of the 18 females gave birth to a litter with a very low survival rate (< 20%). These litters were likely to be born in the presence of a 15- to 28-day-old litter (88%, $P \leq 0.005$, Fisher's Exact Test). Furthermore, 7 of these 8 females successfully raised another litter to weaning (mean survival rate = $79.8 \pm 11.2\%$). Females that had just successfully weaned a litter ($t=0.85$, NS), and those that were carrying a viable litter postpartum ($t=1.05$, NS), were no different at successfully rearing pups to weaning than

**Fig. 3.** Pattern of communal nursing presented in terms of the percentage of mothers that nursed the other mother's litter

females without recent litters. Clearly, low litter survival rates were not a function of an individual female's capacity to rear young successfully.

And finally, the survival of newborn pups was not affected by such standard parameters of reproductive history as estrous condition, age of mother, weight of mother, and gestation length, or by nest location and number of older pups present (Table 2). We suggest, therefore, that when our focal young failed to survive, the primary cause was the social circumstances of their birth, specifically the presence of 15- to 28-day-old pups.

Communal nursing

When a female gave birth in the presence of a 0- to 14-day-old litter, the nursing pattern was reciprocal. Specifically, both the mothers of the newborn litters (92%) and the mothers of the 0- to 14-day-old litters (75%) were observed nursing the other mother's pups (Fig. 3). Moreover, the two mothers began nursing each other's litter at approximately the same time: the mother of the newborn litter when her pups were 4.3 ± 1.5 days old and the mother of the 0- to 14-day-old litter when the newborn pups were 4.2 ± 1.6 days old. Reciprocal nursing then continued for 13.4 ± 1.8 days. Half of the time, mothers built a single nest, either in the nest box (67%) or outside it (33%), and their pups formed a single huddle. In the remaining cases, the mother of the newborn litter nested outside and the newborn litter was brought inside where they also formed a single huddle. At the time of the daily observation, $40\% \pm 6\%$ of the pups being nursed by the mother of the newborn litter belonged to the other mother. Likewise, $43\% \pm 7\%$ of pups being nursed by the mother of the older litter were newborns. Thus, when the age difference between a giv-

en pair of resident litters was only 0–14 days, the mothers shared the burden of lactation.

In contrast, when a female gave birth in the presence of 15- to 28-day-old young, the nursing pattern was asymmetric: the mother of the 15- to 28-day-old litter rarely (7%) nursed newborn pups whereas the mother of the newborn litter often (64%) nursed both the newborn and the 15- to 28-day-old litter. This nursing pattern is significantly different from the reciprocal pattern observed when the age disparity between the litters was 0–14 days ($X^2=9.87$; $P\leq 0.002$). In fact, most of the pups being nursed by the mother of the newborn litter belonged to the other mother ($79\%\pm 9\%$ of nursing pups). Just how she came to nurse both sets of young is readily explained by nest invasion. As already mentioned, these older young literally intruded into the nest of the focal mother. And once in the nest, they promptly began to suckle, which often resulted in the death of the younger litter. They continued to nurse for only 2.9 ± 0.7 days although they had the opportunity to nurse longer, given that they were weaned on average 7 days later.

Although we did not measure growth rate, we did record individual pup weights at weaning. From these weights two findings emerged that are worthy of mention. First, from the perspective of the focal litter, those that were born and survived in the presence of 15- to 28-day-old litters tended to be heavier at weaning than those born in the presence of 0- to 14-day-old litters (86.7 ± 5.9 g vs 73.2 ± 3.8 g). There were no differences in the size of surviving litters at weaning to confound this comparison ($t=0.02$, NS). There were, however, sex differences in weaning weights. Thus, males and females were analyzed separately to control for the sex difference (analysis of variance: age of older pups, $F=4.12$, $P\leq 0.06$; sex of pups, $F=23.01$, $P\leq 0.0002$; interaction, $F=0.75$, NS). Presumably, a 15- to 28-day-old litter suckling at the teats of the focal mother provided a stronger suckling stimulus than a 0- to 14-day-old litter, thereby increasing the milk supply of the focal mother. And second, from the perspective of the older litter, those pups that were 0–14 days old when the focal litter was born tended to weigh more at weaning than those that were 15–28 days old because, as stated above, the former were more likely to be nursed reciprocally and reciprocal nursing enhances milk supply. In contrast, 15- to 28-day-old pups were rarely nursed reciprocally because their mothers rarely nursed newborn young (see Fig. 3). As expected, the weaning weights of male pups were higher in those litters that were 0–14 days older than the focal litter than those that were 15–28 days older (90 ± 5 vs 80 ± 4 g); the same was true for the female pups at weaning (84 ± 4 vs 73 ± 4 g; analysis of variance: age of older litter, $F=4.5$, $P\leq 0.05$; sex of pups, $F=44.0$, $P\leq 0.0001$; interaction, $F=0.89$, NS).

Birth cycle synchrony

We have distinguished three conditions in which focal litters were born: in the absence of another litter, in

the presence of 0- to 14-day-old litters, or in the presence of 15- to 28-day-old litters. We now need to determine the relationship between these three conditions and the degree of synchrony between their mothers' birth cycles in order to interpret our results on inter-litter competition and communal nursing in terms of birth cycle synchrony.

A birth cycle is the interval between successive births, including the intervening lactation, conception and pregnancy (birth cycle length = 35.3 ± 1.8 days). Thus, the birth of a given litter represents the end of one birth cycle and the beginning of the next. We quantified birth cycle synchrony in terms of the proportion of the other female's birth cycle that had elapsed on the day that a given litter was born. When females gave birth in the presence of 0- to 14-day-old litters, only $21\%\pm 7\%$ of the other female's birth cycle had elapsed (Fig. 4). Thus, these birth cycles were synchronized, with the birth cycle of the focal litter's mother phase delayed (i.e., the newborn litter was born slightly later than the other litter). When females delivered without another litter present in the environment, only $19\%\pm 6\%$ of the other females' birth cycle remained before her next birth (Fig. 4). These birth cycles were also synchronized, but the birth cycle of the focal litter's mother was phase advanced (i.e., the focal litter was born slightly before the other mother's litter and after she had weaned her previous litter). Therefore, the seemingly disparate conditions of giving birth in the presence of 0- to 14-day-old litters or in the absence of another litter are in fact the same situation, but seen from the different perspectives of the two mothers (Fig. 4).

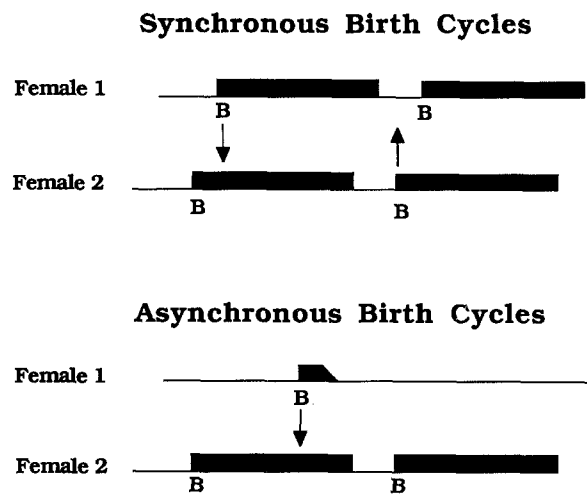


Fig. 4. Relationship between birth cycle synchrony and the age of pups present in the environment when the focal litter was born. Each female has a birth cycle time line indicating the birth of her litter (B) and the subsequent nursing period (horizontal bar). Synchronous birth cycles: female 1's birth cycle is phase delayed and she gives birth when female 2's pups are young, 0–14 days of age (indicated by the first arrow). Female 2's birth cycle is phase advanced and she gives birth after the other female's litter has been weaned, when there is no other litter in the environment (indicated by the second arrow). Asynchronous birth cycles: female 1 gives birth when female 2's litter is older (15–28 days of age, indicated by the third arrow), and she is likely to lose her newborn litter through inter-litter competition

In contrast, when females gave birth in the presence of 15- to 28-day-old litters, the other female was midway through her birth cycle (Fig. 4). Birth cycles were significantly more asynchronous when 15- to 28-day-old litters were present than when 0- to 14-day-old litters were present ($t=2.18$, $P\leq 0.04$) and tended to be more asynchronous than when no other litter was present ($t=1.8$, $P\leq 0.10$).

As expected, pup survival was high when cycles were synchronized (either phase advanced or phase delayed relative to the other females birth cycle) and low when the birth cycles were asynchronous (a second order curvilinear relationship between pup survival and degree of synchrony: $r=0.52$, $P\leq 0.05$).

When a female gave birth in the presence of a 15- to 28-day-old litter and lost her entire litter, she soon returned to estrus and became pregnant. This reduced the age difference between her next litter and the next litter of the other female (reduction in birth interval = 12.3 ± 4.8 days). In those few cases in which a newborn litter survived in the presence of a 15- to 28-day-old litter, the age difference between the subsequent litter of the focal female and that of the other female did not change (reduction in birth interval = 0.0 ± 1.0 days, $P < 0.05$, Mann-Whitney U Test). Thus, inter-litter competition "resynchronized" asynchronous birth cycles.

Discussion

When females occupying the same environment gave birth asynchronously, that is, 15–28 days apart, the younger pups were likely to die owing to nest invasion by the older pups. Rat young, when they reach 15 days of age, have open eyes and are sufficiently mobile to explore their environment (Alberts and Gubernick 1983; Smart and Dobbing 1971). At the same time, the milk supply of their mother begins to diminish (Babicky et al. 1970; Keen et al. 1981), and their mother begins to avoid suckling (Rosenblatt 1965). Thus when the opportunity is present, young between 15 and 28 days will often enter the nest of another female and attempt to suckle. If that mother has recently given birth, her newborn young are almost always displaced from the nipple, and either because of milk deprivation, physical trauma, or both, they eventually die.

Prewanling litter loss in rodents is known to be an important factor in population dynamics and life history (Hoffmann 1958). Whole-litter loss may result from the death of the mother or from predation (Hoffmann 1958), whereas partial-litter loss may reflect the manipulation of litter size by the mother (McClure 1981) or loss due to an "inherent weakness or disease in some of the young" (Hoffmann 1958). The present study is the first to demonstrate death from inter-litter competition in rodents and suggests that such competition may be an important factor influencing pup survival.

There are several strategies that could reduce the incidence of inter-litter competition. First, a given female could build her nest far from females nursing 15- to

28-day-old pups (see also Brown 1986; Calhoun 1962). Second, she could physically defend her young from invasion by older pups. Surprisingly, neither of these strategies was observed in the present experiment, although the opportunity existed. And finally, two or more females could give birth synchronously and thus reduce risk of inter-litter competition. The results of the present study suggest that when birth cycles are synchronized, inter-litter competition is indeed reduced.

When females give birth synchronously, that is within 0–14 days of each other, there is a high rate of litter survival. It is also noteworthy that litters born synchronously are usually collected in a common nest and nursed reciprocally. Such mutualism among females may have several advantages for their young. First, when young are living with more than one adult female, they are likely to have an adult female nearby to provide defense against predators (Bertram 1975; Boinski 1987; MacDonald et al. 1987; Saylor and Salmon 1971). Second, communal nursing may increase the probability of a given litter surviving in the event its mother dies (Hoffmann 1958; Saylor and Salmon 1971; Zimmerman 1974). Third, communal nursing may increase the efficiency of food-gathering and time utilization of their mothers, freeing energy for milk production (Bertram 1975; Rudnai 1973; Schaller 1972). Fourth, communal nursing may increase, and indeed did increase, the growth rate of preweanling young, presumably by increasing the milk supply of each reciprocally nursing mother (Saylor and Salmon 1969, 1971). And finally, communal nursing may also affect the thermoregulatory efficiency of the huddle (Alberts and Gubernick 1983). This is the first detailed study of communal nursing in the Norway rat, although it has been suggested by earlier reports (Calhoun 1962; Leslie et al. 1951) and reported also for other rodents (Gurski and Scott 1980; Saylor and Salmon 1971).

To our knowledge, the only papers in the literature that describe the effect of birth synchrony and inter-litter competition on litter survival are on the lion (Bertram 1975; Rudnai 1973; Schaller 1972). The social factors influencing reproduction in this species are similar to those reported herein for the rat. Specifically, pre-weanling lion cubs are more likely to die when born in the presence of 7- to 12-month-old cubs, owing presumably to unequal competition at the teat (Rudnai 1973). In addition, the survival rates of litters born synchronously is higher than for litters born asynchronously (Bertram 1975).

In discussing possible mechanisms underlying birth synchrony within a pride, Bertram (1975) noted that although lionesses show estrous synchrony, estrous synchrony alone cannot account for birth synchrony (see also Packer and Pusey 1983a, b). Nor indeed does it appear to be the sole determinant of birth synchrony in other mammals and birds (Bronson 1985; Darling 1938; McClintock 1981, 1983b). For example, birth synchrony may occur when females in a group respond concurrently to such changes in the environment as day length (Hoffman 1973; van Horn 1975), temperature (Heroux et al. 1959), rainfall (Jones 1980), and food

availability (Jones 1980; Lack 1968; Lancaster and Lee 1965). Mechanisms contributing to birth synchrony may also include social or pheromonal cues produced either by breeding females or by males living within the group (Boinski 1987; Gudermuth et al. 1984; Kummer 1968; McClintock 1981, 1983a–c; Wallis 1985, 1989; Wallis et al. 1986). In addition, behavioral interactions within the group may result in birth synchrony as when, in the present study, loss of a newborn litter from inter-litter competition helps resynchronize birth cycles. Although there are undoubtedly diverse mechanisms generating birth synchrony, the present study suggests that the disadvantages of inter-litter competition and the advantages of communal nursing have been selective forces in the evolution of birth synchrony.

Acknowledgements. This work was supported by NIMH Grant 1RO1 MH41788 and Biomedical Research Support Grant PHS 2 S07 RR-07029-23 to M.K.M. as well as NIH grant HD06872 to H.M.

References

- Alberts JR, Gubernick DJ (1983) Reciprocity and resource exchange: a symbiotic model of parent-offspring relations. In: Rosenblum LA, Moltz H (eds) *Symbiosis in parent-offspring interactions*. Plenum Press, New York, pp 7–44
- Aron C (1973) Phéromones et régulation de la durée du cycles oestral chez la ratte. *Arch Anat Embriol Norm Exp* 56:209–216
- Babicky A, Ostadalova J, Parizek J, Kolar J, Bibr B (1970) Use of radioisotope techniques for determining the weaning period in experimental animals. *Physiol Bohemoslov* 19:457–467
- Baldwin JD (1970) Reproductive synchronization in squirrel monkeys (*Saimiri*). *Primates* 11:317–326
- Bertram BCR (1975) Social factors influencing reproduction in wild lions. *J Zool (London)* 177:463–482
- Boinski S (1987) Birth synchrony in squirrel monkeys (*Saimiri oestedi*): a strategy to reduce neonatal predation. *Behav Ecol Sociobiol* 21:393–400
- Bronson FH (1985) Mammalian reproduction: an ecological perspective. *Biol Reprod* 32:1–26
- Brown RE (1986) Social and hormonal factors influencing infanticide and its suppression in adult male Long-Evans rats (*Rattus norvegicus*). *J Comp Psychol* 100:155–161
- Calhoun JB (1962) The ecology and sociology of the Norway rat. (USPHS Publication No. 1008). Washington, DC, US Government Printing Office
- Crowcroft P, Rowe FP (1963) Social organization and territorial behavior in the wild house mice (*Mus musculus* L.). *Proc Zool Soc London* 140:517–531
- Darling FF (1938) *Bird flock and the breeding cycle*. Cambridge University Press, Cambridge
- Davis DE, Hall O (1951) The seasonal reproductive conditions of female Norway (Brown) rats in Baltimore, MD. *Physiol Zool* 24:9–20
- Dieterlen F (1962) Geburt und Geburtshilfe bei der Stachelmaus, *Acomys cahirinus*. *Z Tierpsychol* 19:191–222
- Dixon WJ (1985) *BMDP Statistical software*. University of California Press, Berkeley
- Emlen ST (1984) Cooperative breeding in birds and mammals. In: Krebs JR, Davies NB (eds) *Behavioral ecology: an evolutionary approach*. Sinauer, Sunderland, MA, pp 305–339
- Gudermuth DF, McClintock MK, Moltz H (1984) Suppression of postpartum fertility in pairs of female rats sharing the same nesting environment. *Physiol Behav* 33:257–260
- Gurski JC, Scott JP (1980) Individual vs. multiple mothering in mammals. In: Bell RW, Smotherman WP (eds) *Maternal influences and early behavior*. Spectrum Publications, New York, pp 403–438
- Heroux O, Depocas F, Hart JS (1959) Comparison between seasonal and thermal acclimation in white rats. *Can J Biochem Physiol* 39:473–478
- Hoffman JC (1973) The influence of photoperiods on reproductive functions in female mammals. *Handbook of physiology, endocrinology II, part I*, p 57
- Hoffmann RS (1958) The role of reproduction and mortality in population fluctuations of voles (*Microtus*). *Ecol Monogr* 28:79–109
- Horn RN van (1975) Primate breeding season: photoperiodic regulation in captive *Lemur catta*. *Folia Primatol* 24:203–230
- Jones CB (1980) Seasonal parturition mortality and dispersal in the mantled howler monkey, *Alouatta palliata* Gray. *Brenesia* 17:1–10
- Keen CL, Lonnerdal B, Clegg M, Hurley LS (1981) Developmental changes in composition of rat milk: trace elements, minerals, protein, carbohydrate and fat. *J Nutr* 111:226–230
- Kummer H (1968) *Social organization of hamadryas baboons*. University of Chicago Press, Chicago
- Lack D (1968) *Ecological adaptations for breeding in birds*. Methuen, London
- Lancaster J, Lee T (1965) The annual reproductive cycle in monkeys and apes. In: De Vore I (ed) *Primate behavior*. Holt, Rinehart and Winston, New York
- Leslie PH, Venables UM, Venables LSV (1951) The fertility and population structure of the brown rat (*Rattus norvegicus*) in corn-ricks and some other habitats. Bureau of Animal Population, Department of Zoological Field Studies, Oxford University, Oxford
- MacDonald DW, Apps PJ, Carr GM, Kerby G (1987) Social dynamics, nursing coalitions and infanticide among farm cats *Felis catus*. *Advances in ethology*, no. 28. Paul Parey, Berlin
- Mantalenakis SJ, Ketchel M (1966) Frequency and extent of delayed implantation in lactating rats and mice. *J Reprod Fertil* 12:391–392
- Mantel N (1966) Evaluation of survival data and two new rank order statistics arising from its consideration. *Cancer Chemother Rep* 40:163–170
- Martin P, Bateson P (1986) *Measuring behaviour: an introductory guide*. Cambridge University Press, Cambridge
- McClintock MK (1978) Estrous synchrony in the rat and its mediation by airborne chemical communication (*Rattus norvegicus*). *Horm Behav* 10:264–276
- McClintock MK (1981) Social control of the ovarian cycle and the function of estrus synchrony. *Am Zool* 21:243–256
- McClintock MK (1983a) Modulation of the estrous cycle by pheromones from pregnant and lactating rats. *Biol Reprod* 28:823–829
- McClintock MK (1983b) Pheromonal regulation of the ovarian cycle: enhancement, suppression and synchrony. In: Vandenberg JG (ed) *Pheromones and reproduction in mammals*. Academic Press, New York, pp 113–149
- McClintock MK (1983c) Synchronizing ovarian and birth cycles by female pheromones. In: Muller-Schwarze D, Silverstein RM (eds) *Chemical signals in vertebrates*. Plenum Press, New York, pp 159–178
- McClintock MK (1984) Estrous synchrony: modulation of ovarian cycle length by female pheromones. *Physiol Behav* 32:701–705
- McClure PA (1981) Sex-biased litter reduction in food-restricted wood rats (*Neotoma floridana*). *Science* 211:1058–1060
- McShea WJ, Madison DM (1984) Communal nesting between reproductively active females in a spring population of *Microtus pennsylvanicus*. *Can J Zool* 62:344–346
- Mennella JA (1988) *Social control of infanticidal behavior in rats*. Doctoral dissertation, University of Chicago
- Mennella JA, Moltz H (1988) Infanticide in rats: male strategy and female counter-strategy. *Physiol Behav* 42:19–28
- Packer C, Pusey AE (1983a) Male takeovers and female reproduc-

- tive parameters: a simulation of oestrous synchrony in lions (*Panthera leo*). *Anim Behav* 31:334-340
- Packer C, Pusey AE (1983 b) Adaptations of female lions to infanticide by incoming males. *Am Nat* 121:716-728
- Rood JP (1980) Mating relationships and breeding suppression in the dwarf mongoose. *Anim Behav* 28:143-150
- Rosenblatt JS (1965) The basis of synchrony in the behavioral interaction between the mother and her offspring in the laboratory rat. In: Foss BM (ed) *Determinants of infant behavior*, vol 3. J. Wiley, New York, pp 3-41
- Rudnai JA (1973) The social life of the lion: a study of the behaviour of wild lions (*Panthera leo massaica* [Newmann]) in the Nairobi National Park, Kenya. MTP Press, Lancaster
- Sachs BJ, Rosenblatt JS (1974) Prepartum suckling reduces survival of newborn in the rat. *Dev Psychobiol* 7:399-406
- Sayler A, Salmon M (1969) Communal nursing in mice: influence of multiple mothers on the growth of the young. *Science* 164:1309-1310
- Sayler A, Salmon M (1971) An ethological analysis of communal nursing by the house mouse (*Mus musculus*). *Behaviour* 40:60-85
- Schaller GB (1972) *The Serengeti lion: a study of predator-prey relations*. University of Chicago Press, Chicago
- Smart JL, Dobbing J (1971) Vulnerability of developing brain. II. Effects of early nutritional deprivation on reflex ontogeny and development of behaviour in the rat. *Brain Res* 28:85-95
- Southwick CH (1969) Population dynamics and social behavior of domestic rodents. In: Sladden BK, Bang FB (eds) *Biology of populations*. American Elsevier, New York, pp 284-298
- Spencer-Booth Y (1970) The relationships between mammalian young and conspecifics other than mother and peers: a review. *Adv Study Behav* 3:119-194
- Stoloff ML, Blass EM (1983) Changes in appetitive behavior in weanling-age rats: transitions from suckling to feeding behavior. *Dev Psychobiol* 16:439-453
- Wallis J (1985) Synchrony of estrous swelling in captive group-living chimpanzees (*Pan troglodytes*). *J Primatol* 6(4):335-350
- Wallis J (1989) Synchrony of menstrual cycles in captive group-living baboons (*Papio cyanocephalus* and *P. anubis*). *Am J Primatol* 18:167-168
- Wallis J, King BJ, Roth-Meyer C (1986) The effect of female proximity and social interaction on the menstrual cycle of crab-eating monkeys (*Macaca fascicularis*). *Primates* 27:83-94
- Zimmerman GD (1974) Cooperative nursing behavior observed in *Spermophilus tridecemlineatus* (Mitchill). *J Mammal* 55:680-681