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Paternal care in the mound building mouse reduces inter-litter intervals.

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Running head: Paternal care in *M. spicilegus*

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Abstract:

In many rodent species males display paternal behavior. The primary reported effect of this paternal care is to increase pup survival. In mammal females, pregnancy and lactation are energetically demanding, especially when they are concurrent in post-partum reproduction. To face this energy requirement, females generally lengthen the duration of their post-partum pregnancy. In the present study we tested whether paternal care could affect this duration in the monogamous mound building mouse *Mus spicilegus*. In this species, females have a short reproductive life that does not exceed four months. Reduction of inter-delivery latencies would then be an efficient way to increase reproductive success. In a male removal experiment, we showed that inter-delivery latency was indeed shortened by male presence. Moreover, behavioral estimations of paternal involvement were correlated with inter-delivery latency. The longer the male spent inside the nest the shorter the inter-delivery latency. In the mound building mouse, the female might be able to monopolize the parental care of a single male, which could be important for the evolution of monogamy. The characteristics of first reproduction as compared to post-partum reproduction suggest that it may contribute to the formation of a strong and exclusive social bond between the reproductive partners.

Introduction

Because of the important energetic cost of gestation and lactation (Trivers 1972; Eisenberg 1981), small mammal females have developed strategies to ensure the help of conspecifics in achieving successful reproduction. According to social context, this help may come from nearby females that share care for litters (König 1994), from juveniles and adults of both sexes (Schradin and Pillay 2004) and in particular from fathers.

Extensive paternal care can be observed in several rodent species in captivity (Dewsbury 1985) although only little evidence for paternal care in nature exists (Schradin and Pillay 2003). Males may provide direct parental care (thermoregulation, huddling, licking, retrieving) or indirect parental behavior (nest building, foraging, protection) (Kleiman and Malcolm 1981; Elwood 1983). Even though benefits of biparental care are not exclusive to monogamous species (Schradin and Pillay 2005), paternal care has been abundantly documented in monogamous mammals (Wittenberger and Tilson 1980; Kleiman and Malcolm 1981; Clutton-Brock 1989). In some of these species the presence of the father can increase pup survival (Wynne-Edwards 1987; Gubernick and Teferi 2000). Other benefits may however be expected.

Many rodents have postpartum estrus the day after delivery (Bateman 1957; Asdell 1964). Conception during this post-partum estrus decreases the inter-delivery duration which may improve reproductive success. Concurrent pregnancy and lactation are, however, energetically demanding for females. To deal with this concurrent demand of energy, females may delay embryonic implantation for a few days which will lengthen the inter-delivery duration (Johnson *et al.* 2001). Male cooperation during this period could help females to cope better with these energetic costs by reducing their costs of parental care. The benefits of paternal care would then allow females to optimize the inter-delivery duration. By reducing this duration, paternal behavior would consequently increase

female and male reproductive success in particular in monogamous species. The aim of the present study was to test this hypothesis in the mound building mouse *Mus spicilegus*. This exclusive outdoor species lives in agricultural fields in the steppe zone of central and eastern Europe (Orsini *et al.* 1983; Sokolov *et al.* 1998). According to field data, the complete reproductive period of a given female does not exceed four months (Milishnikov *et al.* 1998). To deal with this temporal constraint, one may expect mound-building females to have developed physiological and behavioral characteristics allowing a sustained rhythm of reproduction. This species is known to have a monogamous mating system (Patris and Baudoin 1998; Baudoin *et al.* 2005; Gouat and Féron, 2005), and males display intense paternal care (Patris and Baudoin 2000). Because of the absence of concurrent lactation, we hypothesized that first pregnancy was shorter than subsequent ones. In order to test our hypothesis, and because data concerning the temporal characteristics of reproduction of this species are very scarce, we first recorded the duration of first and following pregnancies. The duration of pregnancy was defined as the latency between fecund mating and next delivery. Our second hypothesis, the effect of paternal care on interdelivery duration, was evaluated in two ways: in male removal experiments, we assessed the effects of male presence on interdelivery delay. In couples where males were present, behavioral estimates of male collaboration to parental care were used to study the direct effect of paternal care on interdelivery duration.

Methods

The experiments complied with the current laws of France (authorisation 93-0033 for CF; authorisation 93-006 for PG, Laboratory approval from the Prefecture of Seine Saint Denis, prefectorial decree 02-2651), and adhered to the Association for the Study of

Animal Behaviour/Animal Behaviour Society Guidelines for the Use of Animals in Research.

Animals and general breeding conditions

In natural conditions, *Mus spicilegus* juveniles build, in autumn, voluminous mounds composed of vegetal materials (mostly seeds and stalks) covered with earth. Beneath these mounds they dig tunnels and nest chambers where they overwinter (Garza *et al.* 1997). Adults disappear soon after the construction of mounds. No reproduction occurs during this winter period (Gouat *et al.* 2003a). Mice leave the mounds in spring, disperse and then begin reproduction (Gouat *et al.* 2003b). Overwintered females cease to reproduce in June and current year-born females begin reproduction in July (Milishnikov *et al.* 1998).

In this study, experimental animals were derived from a stock of 80 wild mound-building mice caught in Hungary in October 1999 and bred to the F₂ generation under laboratory conditions (20 ± 1°C) with a 14:10 light dark cycle. Food (mice pellets type M20, Special Diet Services, Witham, Essex, GB), water and bedding material (saw-dust, cotton) were provided. Mice were weaned at 28 d of age and housed in same-sex sibling groups from 35 d of age.

Adult males and adult females were isolated one week before pairing to promote sexual activation (Féron and Gheusi 2003). They were then caged (at the end of the light phase) with an unrelated and unfamiliar sexual partner. A total of 27 reproductive pairs differing in their parental origins were used in this study (age at pairing, mean ± SE; males: 127.9 ± 6.7 days; females: 126.3 ± 7.5 days).

Start of first and post-partum pregnancy

First mating was observed in 9 pairs which were videotaped continuously for the 7 first days of cohabitation. Post-partum mating was surveyed in 7 other pairs which were continuously videotaped from the date of unquestionable detection of first pregnancy to the 7th day post-partum. Recordings were made with an infrared night vision camera. They started at the beginning of the dark phase. Videotapes were analyzed to define the moment and the characteristics of sexual activities. Three behavioral items were considered: 1 – mount without lordosis: the male attempts to mount but the female does not present a vertebral dorsiflexion (lordosis) permitting penile intromission and, therefore, fertilization; 2- mount with lordosis; 3 - ejaculation: the male stops his pelvic movements, stays for few seconds in an immobile tonic position, then lies on his side (Ivantcheva and Cassaing 1996). A lordosis quotient (LQ) was determined by dividing the number of mounts with lordosis by the total number of mounts (with and without lordosis) and multiplying this value by 100.

Mice often achieve several ejaculations before sexual exhaustion. A mount bout is defined as a sequence of sexual behavior that begins with the first mount attempt and ends with sexual exhaustion. Sexual exhaustion is established with the last sexual item of this sequence, no further sexual behavior being displayed for at least the next 24 hours.

Survey of gestation and delivery

Pairs were checked daily for reproduction. A non intrusive inspection was held during the light period, and birth was detected by looking inside the nest through the bottom of the cage. Every week nests were opened to detect gestation. The increase in body mass and the change of body shape are conspicuous in the last week of pregnancy. As a result, we assume that all gestations reaching the last week were detected and no abortion or

cannibalism of newborns could have been missed (Gouat and Féron 2005). Date of birth and number of pups were recorded.

Male influence on inter-delivery durations

Male removal:

We studied the role of the male on interval duration between the second and third delivery. Two groups were set up from eighteen reproductive pairs. In the “male-removal group” (eight reproductive units), males were removed one day after the second delivery had been detected, whereas in the “control group” (ten reproductive units), males and females remained together after the second delivery. All females had a third litter. Pregnancy and delivery of females in both groups were checked daily using the previously described procedure.

Male behavior:

The time spent inside the nest by males (TiN) was used as an index of male potential help to the female (Patris and Baudoin 2000). This value may be measured precisely because *Mus spicilegus* build well-made nests allowing thereby an easy definition of each entry and exit. TiN was recorded in the seven pairs used previously to describe post-partum sexual behavior. In order to avoid confusion with behaviors related to post-partum sexual activities, quantification of TiN began at least 24 hours after delivery. The end of delivery was identified when the female came out of the nest with an obvious thinner belly. Observations began on the next dark phase and the recording ended 6 days later. To distinguish males from females on videotapes, one or two fur-stripped cuts were made on male sides with surgical scissors.

Statistical analysis

Because of the small number of animals in each group ($N \leq 10$), we used non-parametric statistics. We used permutation tests for paired samples when comparing data from the same cage or for independent samples in other cases. Correlation between TiN and inter-delivery duration was tested using a Spearman correlation test. All tests were two-tailed and were performed on StatXact-7 (Cytel Software Corporation) using exact procedures. Data are given as mean \pm SE.

Results

Duration of first and next pregnancy

The time of first mating differed in the 9 pairs. Five pairs mated on the 3rd day of cohabitation, 2 on the 5th day and the remaining 2 others mated on the 7th day. Three of the 5 pairs that mated on the 3rd day had a new bout of sexual activities 4 days later (on day 7). Pregnancy lasted 19-20 days for 7 of the 9 pairs when sole or last observed mount bout was used to define the beginning of the pregnancy. The two other pairs mated for the first time on day 7. Delivery was observed 24 days later which suggests that these mount bouts had been infertile, and that fecundation occurred during a second mount bout on day 11, out of the observation period. Consequently, the mean duration of the first pregnancy was 19.56 ± 0.18 days.

With regards to post-partum matings, all pairs began their sexual behaviors in the hours following the end of the delivery ($7h17 \pm 1h05$). No second mount bout was observed in the 6 following days. Lasting 27.43 ± 1.09 days ($N=7$), the post-partum pregnancies were much more enduring than the first pregnancies ($p=0.0002$).

During the first mating, the mount bouts were characterized by an important number of mounts and ejaculations. Post-partum mating encompassed significantly less mounts and

ejaculations (tab 1). During the first mating and whatever the mount bout, females responded more positively to the male sexual solicitations, displaying lordosis more frequently than during post-partum mating (tab 1).

Male influence on inter-delivery durations

Male removal:

All reproductive units (control and male-removal) had a third litter in the 40 days following their second delivery. The removal of the male significantly increased the inter-delivery duration (N=8; p=0.047) (figure 1). No such difference between the second and the third pregnancy durations was observed in the control group (N=10; p=0.922). Prior to male removal, inter-delivery duration was equal between the two experimental groups (male-removal group: 28.00 ± 0.80 days, N=8; control group: 28.00 ± 0.84 days; N=10; p<0.0001). During the third pregnancy, inter-delivery duration was longer in the male-removed group than in the control group (N₁=8, N₂=10; p=0.032).

The number of pups per litter did not differ between male-removal and control groups (respectively: 8.25 ± 0.53 and 8.1 ± 0.35 ; p=0.952) and no significant correlation was established between litter size and inter-delivery duration (Rs = 0.11; N=18; p=0.66). No case of mortality was recorded in pups before weaning.

Male behavior:

A significant negative correlation was found between TiN and the inter-delivery duration (Rs = -0.85; N=7; p=0.025). The longer males spent in the nest, the shorter the inter-delivery durations (figure 2).

Discussion

In *M. spicilegus*, post-partum pregnancies lasted about eight days more than first pregnancies. This delay was approximately twice the mean delay as described by Johnson *et al.* (2001) in post-partum pregnancies of *M. musculus* mice. This important delay of the second delivery in *M. spicilegus* females suggested concurrency between pregnancy and lactation to be very costly. Females consequently spread out their energy expenditure by delaying delivery to an unusual extent. Breeding data, furthermore, showed that when a female did not have to feed her litter because of early mortality, post-partum pregnancy was shortened (20-22 days instead of 28 days; Féron and Gouat, unpublished data). The extended post-partum pregnancies were presumably caused by delayed implantation (Bateman 1957; Bindon 1969). The benefits of post-partum reproduction were somehow annihilated by this delayed implantation. *M. spicilegus* females were able, however, to moderate this cost if the male partner cooperated. Inter-delivery duration was indeed shortened when the male was present. Although male withdrawal might stress the female and gave rise to lengthened inter-delivery duration, the intense paternal behavior observed in this species strongly suggested the lack of the direct support of the male to be the essential factor. In comparison with *M. musculus domesticus*, *M. spicilegus* males spend more time covering pups and perform more efficient pups retrieving (Patris and Baudoin 2000). Mechanisms by which males achieved the shortening inter-litter interval remain to be clarified.

However, we observed important individual differences, with some males spending much more time inside the nest than others. This estimate of paternal investment was correlated with the duration of post-partum pregnancy. The longer the male spent inside the nest, the shorter the inter-delivery latency. Male cooperation, therefore, has true fitness consequences for the reproductive couple, at least under laboratory conditions. By

relieving the female of part of the cost of parenting, highly paternal males helped to reduce the delay between consecutive litters which leads to the production of a more numerous offspring. In field conditions, the cumulative days saved at each pregnancy by male cooperation might allow the female to have an additional litter. Males with a highly paternal behavioral profile should then be particularly advantageous for females. Their ability to discriminate this kind of male at pairing should be tested. Paternal care was therefore an efficient way for *M. spicilegus* females to bear the cost of reproduction and to sustain a high reproductive rate during a short reproductive life.

Characteristic of first matings are also peculiar in our model species. The study of mating behaviors indicated that first impregnation of *M. spicilegus* females was often delayed. Although first matings occurred from the third day to the seventh day of cohabitation, more than half of them proved to be infecund. A second mount bout, 4 days later, was then necessary to impregnate the female. *M. spicilegus* females seem to have difficulties starting their reproductive life. Social intolerance of *M. spicilegus* females against unfamiliar partner (Patris *et al.* 2002) and their infrequent sexual receptivity (Féron and Gheusi 2003) may delay their first sexual behaviors. Moreover, females have to cope with infecund matings before impregnation.

No such infecund matings occurred in post-partum reproduction. All couples mated in the 24h after delivery and no second mount bout was observed in the next days. Furthermore, all the females from whom the male had been separated one day after delivery had a new litter. This proves that females were impregnated at this unique and fecund post-partum mating. The reason for low fecundity of the first mating remains unknown. According to the temporal constraints of the reproductive period, this delay in reproduction is extremely surprising. These infecund matings may reflect low fertility of male ejaculates. However, such a transient lack of fertility in males - particularly associated with intense sexual

activity - has never been described to the best of our knowledge. We favor, therefore, the hypothesis of a female origin of this infertility, since social modulation of fecundity in females has been widely documented in rodents (Brown 1985; Marchlewska-Koj 1997) as well as in *Mus spicilegus* (Féron and Gheusi 2003; Gouat *et al.* 2003; Gouat and Féron 2005). Female sexual receptivity was, nevertheless, indisputable in both the mount bouts. Neither was therefore similar to the sterile matings reported in laboratory mice which occur when males mate with sexually unreceptive females (Whittingham and Wood 1983). Because behavioral sexual receptivity in mice occurs only around the time of ovulation, we assume that *M. spicilegus* females were at a similar physiological state during the two mount bouts. In this monogamous species, the imposed period of familiarization before successful mating promotes the formation of a social bond between the two partners, as demonstrated by Patris and Baudoin (1998). The role of familiarization in the formation of a social bond has been described in another monogamous rodent species, *Microtus ochrogaster* (Carter *et al.* 1995; Williams *et al.* 1992). In this species, the formation of a strong and exclusive social bond between males and females is also increased by sexual intercourse and particularly by prolonged mating (Insel *et al.* 1995; Winslows *et al.* 1993). Assuming that the mechanisms of pair bonding in mound-building mice are similar to those described in prairie voles (Williams *et al.* 1992; Wang and Aragona 2004), the important sexual activity displayed by *M. spicilegus* during first matings may be seen as a way to promote the social bond between partners. The role of copulation in the establishment of the exclusive pair bond in *M. spicilegus* remains, nevertheless, to be tested. This bond would then prompt the male to stay with the female, and help her in parental care, which as a result would shorten inter-litter intervals.

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Figure legends:

Figure 1: Durations in days (mean \pm SE) between the first and the second delivery and between the second and the third delivery in case of male presence (control) or male removal after the second delivery (male-removal).

Figure 2: Correlation between the amounts of time males spent inside the nest for 6 post-partum consecutive days and inter-delivery durations.

Table 1: Characteristics of mount bouts at first and post-partum mating.

	First mating		Post-partum mating
	1 st mount bout (mean ± SE; N=9)	2 nd mount bout (mean ± SE; N=3)	sole mount bout (mean ± SE; N=7)
Duration (min)	286 ± 48	331 ± 51	374 ± 113
number of mounts without lordosis	19.11 ± 14.74	3.33 ± 2.33 ***	18.71 ± 6.32
number of mounts with lordosis	23.56 ± 7.27 *	22.67 ± 10.09 **	4.57 ± 0.72
number of ejaculations	7.44 ± 1.12 *	10.67 ± 3.28 **	1.43 ± 0.20
LQ	77.82 ± 8.68 *	80.80 ± 15.43 **	23.24 ± 4.14

Significant differences versus post-partum mating: * : p<0.002; ** : p=0.017; *** : p=0.033

LQ: lordosis quotient

Figure 1

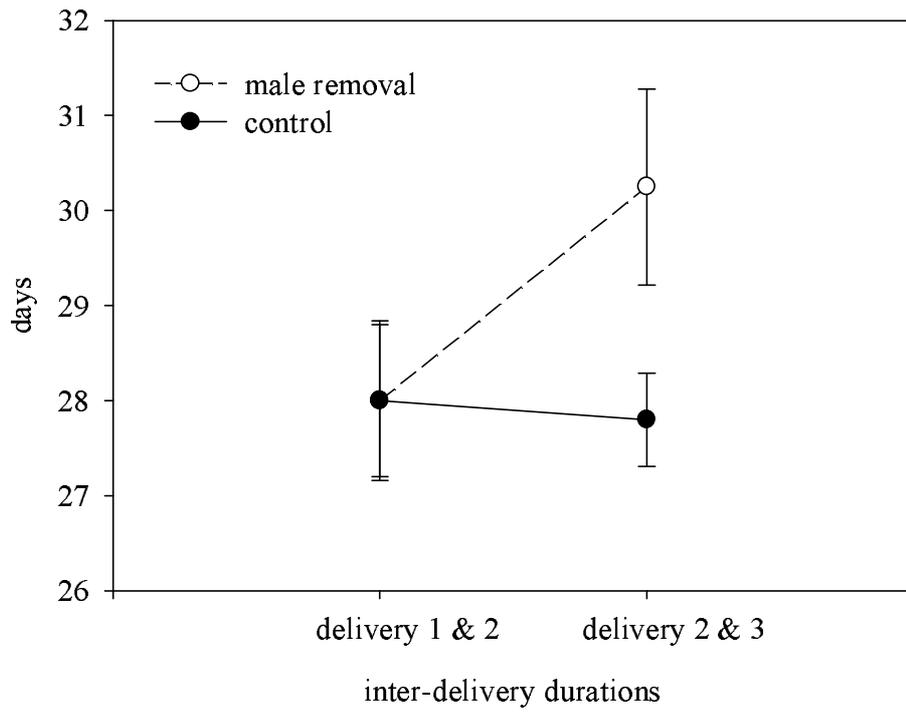


Figure 2

