Copulatory behaviour and coagulum formation in the female reproductive tract of the Australian hopping mouse, *Notomys alexis*

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Summary. Hopping mice were examined to study two interrelated questions: (1) when groups of adults of both sexes are kept together in one cage in the laboratory is there evidence that the females copulate with only one male, and (2) is a copulatory plug formed in the female tract after ejaculation? The findings indicate that a female will sometimes lock with more than one male in the group during an oestrous period induced by administration of exogenous gonadotrophins, and that a small 'plug' of soft material forms *post coitum* in the more caudal parts of the female tract. Individuals of this species, therefore, do not appear to be strictly monogamous, at least in this artificial laboratory situation. Although a coagulum is formed, this is quite different from the typical hard copulatory plug that occurs in common laboratory murids; it may possibly reduce sperm backflow from the lower region of the female reproductive tract.

Keywords: hopping mouse; copulation; plug

Introduction

The Australian hopping mouse, *Notomys alexis*, has a most unusual reproductive anatomy in which males have extremely small testes and epididymides with relatively low stores of highly pleiomorphic spermatozoa (Breed & Sarafis, 1979, 1983; Breed, 1981, 1982, 1986; Suttle *et al.*, 1988; Peirce & Breed, 1989). If one can extrapolate across mammalian orders such features might suggest low levels of inter-male sperm competition, perhaps due to a monogamous mating system or the occurrence of single male breeding units, and/or low copulatory frequency (Short, 1980; Harcourt *et al.*, 1981; Harvey & Harcourt, 1984; Kenagy & Trombulak, 1986; Møller, 1988; Baker & Bellis, 1989).

The arrangement of the accessory sex glands is also highly divergent in these animals with all glands, apart from the ventral prostate, being minute (Breed, 1981, 1982, 1986). Studies on New World muroids with a simple baculum have shown an association between reduced accessory sex glands, absence of a copulatory plug, and locking during copulation (Dewsbury, 1975; Estep & Dewsbury, 1976; Hartung & Dewsbury, 1978; Voss, 1979; Baumgardner *et al.*, 1982). Voss (1979) has also suggested that locking during copulation might tend to evolve in monogamous species and assume a role in assistance of sperm transport through the cervix that, in the ancestral condition, is aided by the presence of the copulatory plug (Blandau, 1945; Matthews & Adler, 1977, 1978). It might be anticipated from these data, therefore, that the hopping mouse also locks during copulation and does not form a copulatory plug. These features have in fact recently been found to occur in this species by Dewsbury & Hodges (1987), although previously a small amount of material was found after histology was performed on the cranial part of the vagina which was thought to be a minute vaginal plug (Breed, 1985).

Groups of adult, laboratory bred, hopping mice of both sexes living in the same cage exhibit much huddling behaviour, although when strangers are placed together the female is usually the more aggressive sex (Happold, 1976). Thus, in order to explain a possible relaxation of intermale sperm competition in this species of murid rodent in which adult males are remarkably unaggressive and huddle together in groups with the females, it was suggested that once a female had mated with one of the males, she may then prevent others from copulating with her (Breed, 1986). The following study was therefore carried out to determine (a) whether an adult female existing with a group of adult males within the confines of a cage will, in fact, only mate with one male and thus tend to exhibit monogamy, and (b) whether any evidence of a copulatory plug occurs in this species.

Materials and Methods

Two to five adult, laboratory bred, male hopping mice, most of which were sexually experienced, were placed in a cage, 56 × 35 × 17 cm, on one side of a central wire partition and 1–7 adult, laboratory bred, usually virgin, females were placed on the other side. Each animal had a small, but different, region of hair removed so that all animals could be individually recognized. After allowing the animals to acclimatize to the environment for several days, the females were given an intraperitoneal injection of 20–30 i.u. pregnant mares' serum gonadotrophin (PMSG) and, 48, or more frequently, 72 h later 20–30 i.u. human chorionic gonadotrophin (hCG) were administered similarly. These doses, and the 72-h interval, have previously been found to maximize the chances of inducing ovulation in this species which generally occurs about 10 h after the hCG injection (W. G. Breed, L. McGregor & S. P. Flaherty, unpublished observations). The doses were so timed that the hCG was given 6–10 h before the animal room lights went out. The lighting regimen of the animal room was 12 h of light and 12 h of dark and, soon after the dark period started, the barrier partition was removed and a transparent plastic lid placed on top of the cage which was placed beneath a red light and a low light intensity television camera. The behaviour of the animals was then monitored for up to the next 9 h using a Spectar Javelin television monitor and recorded on video cassettes. At irregular intervals, from about 3 h after the start of the observation period, the females were removed, lavages were taken from the vagina of all individuals, and the resultant cell population was observed under phase-contrast optics. If spermatozoa were found, the female was killed with an overdose of pentobarbitone (Nembutal: Abbott Labs, Hornsby, NSW, Australia) at the end of the experiment, 9 h 30 min–17 h 2 min after the hCG injection.

In most animals 10% buffered formalin was injected intraperitoneally shortly after death and the reproductive tract removed 10 min to 1 h later. In other animals the whole reproductive tract was removed, taking care not to grip the tissue except at the distal end, and then immersed in 10% formalin for at least 10 h. Subsequently the uterus, cervix and vagina were cleaned of adherent fat, and cut with a razor blade into 5–8 mm segments. These, together with the ovaries and oviducts, were subsequently dehydrated, embedded in paraffin wax, and 7–10 µm serial sections were cut for histology on a rotary microtome. They were mounted on glass slides and stained with haematoxylin and eosin or periodic acid–Schiff (PAS). The sections of the lower parts of the tract were scanned for presence of coagulum in the lumen of the reproductive tract and for the presence and distribution of spermatozoa. The ovarian sections were inspected for recently formed corpora lutea and the oviducts for recently ovulated oocytes. Eight control females, given 30 i.u. PMSG followed by 30 i.u. hCG 72 h later, were killed between 13 and 17 h after the hCG injection. Histological sections of the upper vagina, cervix and lower uterus were prepared similarly to those of the mated animals and scanned for any intraluminal material.

Results

Sixteen separate tests were performed on groups of males and females that were available for study. Generally, after the removal of the partition, much chasing between the animals initially took place. However wounds were not inflicted and, after a variable period of time, all the animals settled down and usually huddled together in one of the corners of the cage. There was no indication that group size or sex composition in any way influenced the behaviour of the animals. Periodically, at various times after huddling had started, bouts of chasing and mounting by most of the males and females took place. Sometimes, when a period of chasing and mounting occurred, a male would switch from one animal to another and mount 2 or more females as well as other males more or less indiscriminately. Occasionally during such chasing and mounting bouts the male would penetrate the vagina of a female with his penis; this resulted in an obvious lock or tie between the two individuals.

There were between 1 and 5 locks for variable lengths of time which took place between 8 h 0 min and 15 h 26 min after the hCG injections in 13 of the 16 experiments. A few of the locks occurred

Table 1. Numbers of locks between male and female hopping mice primed with gonadotrophins when tested over a 9–11 h period

Exp.	No. of animals in group		No. of locks	Time from start of Exp. to first lock (min)	Length of lock (sec)*	No. of females locking twice within the test period†	No. of males locking with 2 females‡	No. of females with spermatozoa in vaginal lavage
	Females	Males						
1	4	2	0	—	—	—	—	—
2	3	2	3	257	<i>140, 12, 15</i>	1 (10)	1 (18)	1
3	4	2	2	23	<i>29, 226</i>	0	0	—
4	4	3	0	—	—	—	—	—
5	5	3	3	165	<i>15, 51, 20</i>	1‡ (254)	1 (25)	1
6	5	3	0	—	—	—	—	—
7	7	5	4	217	<i>315, 14, 19, 77</i>	1‡ (79)	1 (73)	2
8	5	5	3	27	<i>553, 17, 60</i>	1 (101)	0	2
9	4	4	3	239	<i>37, 25, 37</i>	1‡ (230)	1 (117)	0
10	1	3	1	135	203	—	0	1
11	2	3	1	5	111	—	—	0
12	4	4	2	320	<i>39§, 26</i>	0	1 (113)	0
13	4	3	2	309	<i>86, 22</i>	0	0	1
14	6	4	3	1	<i>428, 181, 18</i>	1 (144)	0	2
15	2	2	2	53	<i>21, 21§</i>	0	0	2
16	4	3	5	1	<i>98, 50, 178, 66, 404</i>	2‡ (336, 88)	1¶ (146, 72)	2

*The time for the locks is given in the order in which they occurred; when the same female mated twice the two values are italic. In Exp. 16 one female that mated twice locked for 98 and 404 sec; the second female that mated twice locked for 50 and 66 sec.

†Interval (in min) between the two locks or matings given in parentheses.

‡In these cases 2 separate males locked with the 1 female, whereas in Exp. 14 the same male mated twice; in the other experiments the results were ambiguous. In one of the females in Exp. 16 spermatozoa were found in vaginal lavage shortly after the first lock occurred.

§These two individuals were found to be pregnant with small implantations on dissection, even though a lock with the male had taken place and in Exp. 15 ejaculation had occurred.

¶Male locked with 3 separate females.

shortly after the experiment started whereas others took place considerably later (Table 1). Over half the locks (19 out of 34) lasted from 12 to 51 sec but there were a few much longer locks with 3 lasting from 404 to 553 sec (Table 1); the average length of all locks was 106 sec. During the period of the lock the pair fell on their sides, the female often struggled violently, even occasionally biting the male whilst the 2 were locked together. No thrusting was seen and it was not possible to ascertain if, or when, ejaculation occurred. From the time the pair fell on their sides the male would clasp the female with his front limbs and the female sometimes dragged the male around the cage. At times the pair turned back to back; this usually took place for up to several seconds towards the end of the lock period, but on two occasions they remained back to back for much of the lock duration with the female dragging the male around the cage. During the lock one or more of the other cohabiting animals would investigate the pair and, in particular, the anogenital region of the locked individuals. Occasionally another male would attempt to mount the mating pair but showed no overt aggression. When the locked pair finally disengaged a period of anogenital washing took place in both sexes; this sometimes triggered off similar behaviour in some of the other animals. No agonistic or aggressive behaviour was subsequently evident between either of the pair or any of the other animals after the completion of the lock. The pair subsequently huddled amicably with the rest of the individuals and reacted to each other in a way similar to that which took place before the locking episode.

In 11 of the tests, 2 or more locks between the individuals took place and on 5 occasions the same female exhibited a lock with 2 of the males within the group, whereas in one case the same

Figs 1 & 2. Histological sections of coagulum in the lower cervix of a female killed 15 min after mating (Fig. 1), and in the lumen of the uterus of female killed about 6 h after mating (Fig. 2). $\times 130$.

Figs 3 & 4. Histological sections, both from the female killed 15 min after mating, showing that most spermatozoa occur between the coagulum and the epithelial lining of the cervix (Fig. 3); a tangled mass of spermatozoa in the lower uterus is also evident (Fig. 4). $\times 520$.

male locked twice with the same female. In the other cases it was not clear whether it was the same or a different male that locked twice with the female. In 5 of the tests 1 of the males locked with 2 of the females, and in one test (Exp. 16) a male locked with 3 separate females. In 4 cases 1, and on 5 occasions 2, of the females had spermatozoa in the vaginal lavage (Table 1). One female in Exp. 16 was found to have vaginal spermatozoa shortly after the first lock of 98 sec and subsequently

locked again for 404 sec with a second male 336 min later. None of the females that failed to lock were found to have spermatozoa in the vaginal lavage and clearly not all locks resulted in ejaculation (Table 1).

Neither of the 2 females that mated and were killed between 9 h 30 min and 11 h 10 min after hCG had ovulated, whereas 7 out of 10 of those killed between 12 h 55 min and 17 h 2 min after hCG had recently ovulated oocytes in the oviducts.

In a female killed 20 min after the first lock extensive eosinophilic, and PAS-positive, material was present in the lumen of the upper vagina and throughout much of the cervical canal (Figs 1, 3). A few spermatozoa were present within this material, but they were more abundant just cranial to the coagulum where a tangled mass of spermatozoa occurred (Fig. 4), together with some weakly stained eosinophilic material. In the lower region of the uterus groups of spermatozoa were congregated at the base of some of the uterine glands, whereas other spermatozoa were found scattered throughout the uterine lumen. Some groups of spermatozoa were also present in the cranial part of the vaginal lumen, and between the edge of the coagulum and the epithelial lining of the cervix (Fig. 3).

In another 7 animals killed between 34 min and 8 h 10 min *post coitum* eosinophilic coagulum, usually surrounded by spermatozoa, was found in the lower region of the female tract (e.g. Fig. 2). In none of the control animals, however, was any such eosinophilic material found in any region of the tract.

Discussion

Previous conclusions from behavioural observations (Kleiman, 1977), male reproductive anatomy (Breed, 1981, 1986; Kenagy & Trombulak, 1986) and copulatory behaviour (Dewsbury & Hodges, 1987) have all suggested that the hopping mouse may exhibit a monogamous mating system. This is, however, difficult to reconcile with what is known about the animals' social behaviour, at least within the laboratory, where all individuals within any one group, including adult males and females, huddle together in the cage for much of the time and show virtually no aggressive behaviour towards each other. However, Happold (1976) showed that when strangers were introduced to each other in a neutral cage considerable agonistic interactions took place for a short period, with the levels of aggression usually being significantly greater between adult females than between adult males for which fighting in contact was rare and bites seldom inflicted. These observations therefore indicate that the female is generally the more aggressive sex in this species, with male hopping mice showing remarkably low levels of aggression both towards each other and towards females regardless of their endocrine state. As a consequence, in an attempt to resolve the apparent paradox that small testis size and low sperm numbers occur in adult hopping mice that appear to exhibit group living of both sexes, it was suggested that once a female had been mated by one of the males she might then prevent others from mating with her (Breed, 1986). This could thus lead to depressed levels of intermale sperm competition and hence the evolution of small testis size and low sperm numbers in this species.

However, the present findings indicate that, when groups of laboratory bred adults of both sexes are kept together in one cage, an oestrous female will sometimes lock with more than one of the males within the group. Insemination occurs intravaginally and the pattern of copulatory behaviour, including locking, was similar to that previously recorded by Dewsbury & Hodges (1987) for mating during natural oestrus and after priming with steroids. The maximum length of the lock observed by these workers was 163 sec, whereas in this study the average length was 106 sec with the longest lock lasting for 553 sec. On 5 occasions a female clearly locked with 2 males and on at least one occasion sperm transfer took place during the first locking episode. Although it was not possible to verify insemination on the second occasion this may have taken place, thus raising the possibility of the occurrence of intermale sperm competition. From observations on the subsequent

behaviour of the animals after the first mating there was no suggestion of the male showing any behaviour that could be interpreted as protecting or guarding his investment, nor did the female show any difference in behaviour towards the other males including the second male before, or when, he subsequently locked with her.

Other instances were observed when a male exhibited a lock with 2 of the females and on one occasion with 3 separate females within the observation period of a few hours. However, more than one insemination was not proven and, as locks do not always result in ejaculation, and this cannot be determined from behavioural observations, it has yet to be shown that a male can successfully inseminate 2 or more females within a short period of time. It is therefore not yet known whether a male is compromised in his fertility after one ejaculation due to his low sperm numbers. It has however previously been found that a male hopping mouse can successfully sire litters of 3 separate females within a period of 7 days (Breed, 1981). These observations on laboratory bred and maintained hopping mice thus do not support the proposition that the behaviour of the female after mating prevents another male from mating with her, at least within the confines of a laboratory cage, nor do they indicate that a male locks with only one female when several females come into oestrus at about the same time. Whether these findings reflect the situation in the natural environment remains to be determined but the very limited data suggest that 2 or 3 reproductively active pairs can occur in the same nest in the one burrow system (Stanley, 1971; Happold, 1976). Thus the occurrence of multimale, multifemale breeding groups during at least some stages of the population cycle is suggested for this species and the possibility of a female mating with more than one male cannot be excluded. Other reasons for the evolution of the small testis size in males may therefore have to be sought. Perhaps they are, in some way, related to the remarkably unaggressive nature of the males (Happold, 1976; Breed, 1982), although testosterone concentrations (Breed, 1983) are only slightly lower than in some other species of murid rodents with much larger testes.

The second finding of the present study is the indication that, after ejaculation, the lower portion of the female reproductive tract has a small amount of coagulum or 'plug' of soft material. This is, however, very different in position and composition from the much larger, hard, intravaginal plug that occurs in most other murids (see Hartung & Dewsbury, 1978; Voss, 1979). Much of the material of the coagulum of the hopping mouse is highly eosinophilic, and PAS-positive, and it occurred in the lumen of the cervix and even lower uterus as well as in that of the cranial region of the vagina. In the common laboratory murids the vaginal plug is largely produced from secretions of the seminal vesicles and coagulating glands (Blandau, 1945; Gotterer *et al.*, 1955; Price & Williams-Ashman, 1961; Pang *et al.*, 1979; Queen *et al.*, 1981) and it is probably necessary for sperm transport through the cervix (Blandau, 1945; Matthews & Adler, 1977, 1978; Dewsbury, 1988). It may also assist in protecting the male's investment (Voss, 1979), although the results obtained by Dewsbury (1984, 1988) cast doubt on this. In the hopping mouse it would seem unlikely that this coagulum originates only from the seminal vesicles and coagulating glands as these glands are minute. The secretion may, in part, also come from the ventral prostate perhaps interacting with secretions of the female reproductive tract: it appears similar to the viscous gel-like material found in the uterus of recently mated rats (Joshi *et al.*, 1972). The previous association found in New World muroids between reduced accessory sex glands and absence of a large copulatory plug may be generally applicable, but the present study suggests that a small plug of soft material occurs *post coitum* in at least this species of Australian murid in which reduced accessory sex glands exist in the male. The function of this coagulum is probably quite different from that of the vaginal plug of laboratory rats and mice; it may reduce leakage and/or backflow of the spermatozoa that are destined to pass to the higher reaches of the female tract. Clearly, however, many spermatozoa also become trapped around this 'plug' but whether they, together with the coagulum, reduce the chances of spermatozoa from a second possible mating passing up to the site of fertilization as recently suggested by Baker & Bellis (1988) is conjectural. Clearly further studies are needed to investigate these, and related phenomena, in this species of murid rodent that has such an anomalous reproductive anatomy.

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