Copulatory behaviour of the vlei rat *Otomys irroratus*

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Laboratory experiments were undertaken to describe and quantify the copulatory behaviour in 10 pairs of the vlei rat *Otomys irroratus*. Mean mount latency from the beginning of testing was 39.9 s (*SE* = ± 10.2), and males achieved first intromission at a mean time of 181.1 s (± 30.3). Mean duration of tests was 64.8 min (± 2.4), and males ejaculated a mean of 6.8 (± 0.4) times during tests. The copulatory pattern was characterized by no lock, intra-vaginal thrusting, multiple intromissions and multiple ejaculations. All females had sperm in the vaginal tract at the end of testing, and some developed a copulatory plug. Analysis of the pre-copulatory behaviour indicated that females were significantly more aggressive than males, and were less inclined to participate in sexual activity. In contrast to females, males displayed more amicable behaviour towards females, and readily participated in tactile and olfactory investigations of their mates. The copulatory behaviour of *O. irroratus* appears to be related to the ecological circumstances and the social organization of the taxon.

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Rodents show considerable diversity in copulatory behaviour, although species-specific patterns have been identified (Dewsbury 1975). Patterns of copulatory behaviour are highly stereotypic in a species (Dewsbury 1974), and are usually related to differences in the reproductive physiology and anatomy, and habitat of a species (Dewsbury 1975), as well as differences in social organization (Oglesby, Lanier & Dewsbury 1981). For example, males of rodent species which have a locking pattern (a tie that holds the penis firmly in the vagina) during copulation have elaborate penile spines and reduced reproductive accessory glands, and the females do not develop a copulatory plug after copulation (Hartung & Dewsbury 1978). Also, mating occurs in protected nest sites, where the locked pair is less vulnerable to predation (Dewsbury 1975).

Several aspects of the reproductive biology of the vlei rat *Otomys irroratus* have been studied, including breeding (Pillay 1993; Pillay, Willan & Meester 1995b), postnatal development (Davis & Meester 1981; Pillay *et al.* 1995b) and pre-copulatory behaviour (Davis 1972; Willan 1982; Brown 1988; Pillay, Willan & Cooke 1995a). Aside from anecdotal accounts (Pillay 1990), however, nothing is known about copulation in this taxon. Thus, the aim of the present study was to describe and quantify the copulatory behaviour of *O. irroratus*. In order to understand the adaptive significance of the results obtained here, another aim of the study was to relate the copulatory behaviour of *O. irroratus* to the general biology of the species. Considerable use was made of the methods pioneered by Dewsbury (1975). This was done to facilitate comparison with other muroid rodent studies, so that *O. irroratus* copulation could be viewed in the broader context of copulation in other members of the order Rodentia.

Animals were captive-born (F1) individuals whose parents were live-trapped at Hans-Merensky Holdings in the Kwa-Zulu-Natal Midlands (29°17'S, 30°11'E). They were housed under partially controlled environmental conditions of 20–25°C and 60–80% r.H. *Otomys irroratus* breeds optimally under conditions of long day (Pillay, Willan & Meester 1992), and thus all experiments were conducted under a light regime of 15L:9D (lights on at 05h00).

Copulation was studied in 10 pairs, each of which was housed in a glass tank 90 × 30 × 40 cm. All animals used in the study were adult, with a mean mass of 211.6 g (*SE* = ± 3.2) and 198.5 g (*SE* = ± 2.2) recorded for males and females respectively.

Prior to observations, a tank was divided into two parts with a wire mesh partition. A female in pro-oestrus, ascertained by means of vaginal smears, and a male were placed on either side of the partition at 18h00. Each animal had access to a nest-box (15 × 15 × 15 cm) and was fed coarse grass, cabbage, carrot and commercial rabbit pellets. Wood shavings were provided as litter, and animals used uneaten plant material for nesting. At approximately 10h00 the next day, when females displayed oestrus, the wire mesh partition and the nest-boxes were removed, and interactions of the pair video-recorded. Recordings were made under fluorescent white light, using a Chinon C8-C80E video camera attached to a Hitachi VTL-30ED time-lapse video cassette recorder. Tests were terminated when pairs attained a satiety criterion of 30 min with no copulations (after Dewsbury 1979).

The copulatory behaviour of males was divided into 'series', each of which terminated with an ejaculation, and comprised all copulatory behaviour patterns leading to ejaculation (after Gray & Dewsbury 1975). Ten temporal and frequency characteristics (*inter alia* Dewsbury 1975) were measured in respect of each pair: (i) mount latency — time from beginning of testing until first mount; (ii) intromission latency — time from beginning of testing to first intromission; (iii) ejaculation latency — time from first intromission in a series until ejaculation; (iv) mount frequency — number of mounts in a series; (v) intromission frequency — number of intromissions in a series; (vi) mean inter-intromission interval — mean interval separating intromissions of a series; (vii) post-ejaculatory interval — period between ejaculation and next intromission; (viii) ejaculation frequency — number of ejaculations prior to attainment of the satiety level; (ix) mean ejaculation duration — mean duration of intromissions with ejaculation; and (x) satiety latency — time from start of test to satiety.

Pre-copulatory behavioural patterns that occurred during the first series (i.e. period from the beginning of testing until first ejaculation) were recorded. Mean percentages were calculated for each sex.

The copulatory behaviour of *O. irroratus* was similar to that described for other muroid rodents (see Dewsbury 1973, 1974, 1975). Female *O. irroratus* indicated their readiness to mate by sidling up to the male, extending the fore-limbs anteriorly and lifting the perineal region and tail slightly away from the substrate; lordosis was not evident. The male mounted the female from the rear, grasping her flanks with his fore-limbs. The male often restrained the female by seiz-

Table 1 Mean time and frequency characteristics of motor patterns measured in the first three and last three series of the copulatory behaviour of *Otomys irroratus*. All times are in seconds. *SE* given in brackets. Stats = Kruskal-Wallis values, except for post-ejaculatory interval for which Mann-Whitney *U* values are given (after Zar 1984). N = last series

Motor patterns	First three series				Last three series			
	1	2	3	Stats	N-2	N-1	N	Stats
Intromission	2.3	3.0	2.8	1.94 ns	3.1	3.7	1.9	9.53**
frequency	(0.3)	(0.4)	(0.2)		(0.4)	(0.4)	(0.3)	
Ejaculation	118.5	261.65	256.5	4.80 ns	280.2	372.5	97.8	11.66**
latency	(35.5)	(63.0)	(44.4)		(50.9)	(53.4)	(35.5)	
Mount	6.4	3.9	2.1	13.95***	2.4	1.7	1.6	0.70 ns
frequency	(0.8)	(0.7)	(0.5)		(0.6)	(0.3)	(0.3)	
Mean inter-	65.9	115.1	135.6	7.66*	130.1	137.8	61.6	9.14*
intromission interval	(13.7)	(17.9)	(15.2)		(11.4)	(12.5)	(18.8)	
Post-	183.9	416.7	–	96***	564.1	734.2	–	82.5*
ejaculatory interval	(23.4)	(18.8)			(40.8)	(48.5)		

* $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$; ns = non-significant.

ing her by the nape of the neck with his mouth. Intromissions were of short duration (< 2 s), with several intra-vaginal pelvic thrusts. Ejaculation occurred at the termination of some intromissions, and was characterized by deeper, longer thrusts, spasmodic muscle contractions of the legs and pelvis, and a longer duration of intromission (range: 2.2–4.2 s).

Vaginal smears taken at the end of all tests indicated that all females had sperm in the vaginal tract, and some ($n = 4$) had a copulatory plug.

Mean mount latency from beginning of testing was 39.9 s ($SE = \pm$ 10.2). Males achieved intromission at, or shortly after, the first mount, and a mean latency to the first intromission of 181.1 s ($SE = \pm$ 30.3) was recorded. Pairs reached satiety in a mean of 64.8 min ($SE = \pm$ 2.4), during which time males achieved a mean of 6.8 ($SE = \pm$ 0.4) ejaculations or series.

Quantitative measures of motor patterns recorded during the first and last three series of all pairs are presented in Table 1. Mount frequency measures decreased significantly over the first three series. In contrast, mean inter-intromission interval and post-ejaculatory interval values increased significantly. Interestingly, intromission frequency and ejaculation latency values were higher during the second series than during the first and third series.

The values of all parameters except that of mount frequency showed significant changes across the last three series (Table 1). Patterns of change (i.e. increase or decrease) of motor pattern values in the first three series were identical to those in the last three series preceding attainment of satiety. Mean inter-intromission interval was unusual, however, in that values increased from the third last to the second last series and then decreased in the last series (Table 1).

Mean percentages in respect of male and female pre-copulatory behavioural acts recorded during the first series are given in Table 2. Females displayed significantly more inactive behaviour and upright sparring than males. Males explored their surroundings significantly more frequently than females, although both sexes showed comparatively high levels of exploratory behaviour. Males also made signifi-

Table 2 Mean percentages of female and male behaviour patterns preceding first ejaculation. *SE* given in brackets. *T* value = Wilcoxon paired-sample values (Zar 1984)

Behaviour patterns[1]	Female	Male	*T* value
Inactive	29.0 (2.5)	15.5 (2.5)	55 **
Explore	22.5 (2.1)	29.6 (2.8)	55 **
General groom	5.8 (1.4)	3.0 (0.9)	44 ns
Allogroom	2.1 (0.5)	8.2 (0.8)	55 **
Genital groom	3.5 (0.4)	4.2 (0.7)	27 ns
Sniff partner	4.4 (0.6)	8.7 (1.5)	50 *
Naso-nasal contact	4.7 (0.7)	5.9 (0.7)	48 *
Upright spar	6.4 (1.2)	4.9 (0.8)	49 *
Follow[2]	–	29.6 (3.5)	
Dart[2]	8.9 (0.9)	–	
Present[2]	2.6 (0.5)	..	

[1] — detailed descriptions of the behaviour patterns are available in Swanson (1974) and Gray & Dewsbury (1975).

[2] — sex-specific behaviour pattern.

* $p < 0.05$, ** $p < 0.001$; two-tailed Wilcoxon paired-sample test

cantly more tactile and olfactory investigations of their mates than did females. Females appeared to resist attempts at copulation by males, as evidenced by comparatively low levels of presenting and high levels of darting behaviour (Table 2). In contrast, high levels of mounting in the first series (Table 1) and follow behaviour (Table 2) suggested that males favoured behaviour patterns directly related to copulation.

Dewsbury (1975) recognized that the copulatory behaviour of muroid rodents could be classified in terms of 16 patterns, based upon four major features: the presence or absence of a lock and intra-vaginal thrusting; whether or not multiple intromissions precede ejaculation; and the occurrence of single or multiple ejaculations. *Otomys irroratus* had no lock, and displayed intra-vaginal thrusting and multiple ejaculations. While multiple intromissions were not always a

pre-requisite for ejaculation during the first series, they became important in the subsequent series. Therefore, *O. irroratus'* copulatory pattern corresponds with Dewsbury's (1975) pattern number 9, which is found also in *Mus musculus*, two species of *Microtus* and *Peromyscus eremicus*.

As in most other muroid rodents (Dewsbury 1974), initiation of copulation in *O. irroratus* was comparatively rapid (i.e. short mount and intromission latency values). Long intromission latency values are characteristic of species that have pair-bonding (Dewsbury & Jansen 1972). *Otomys irroratus* has a dispersed (solitary) social system, incorporating elements of hierarchical ranking, territorial defence of a core area of the home range, and temporal territoriality (Davis 1972; Willan 1982; Brown 1988; Pillay 1993). Therefore, rapid initiation of copulation is consistent with the lack of pair-formation in *O. irroratus*.

In attempting to relate copulatory behaviour of rodents to their reproductive morphology, Dewsbury (1975) showed that males of species which do not lock during copulation have well developed reproductive accessory glands, and possess comparatively thin glans penes, which have fewer and/or shorter spines. In these species, the female normally develops a copulatory plug after copulation (Hartung & Dewsbury 1978). Likewise, *O. irroratus* had no lock during copulation, and some females formed a copulatory plug at the end of testing. Examination of the reproductive anatomy of *O. irroratus* males (pers. obs.) revealed that, except for a lack of an anterior prostate gland, males had all other reproductive glands described by Dewsbury (1974). Pillay (1990) has shown that the glans penes of male *O. irroratus* have short simple spines, and that the relative size of the glans (glans width : glans length) was 3.4, which is typical of species which have intra-vaginal thrusting and absence of locking (Dewsbury 1974, 1975).

Locking during copulation (Dewsbury 1975) and a greater number of ejaculations/series (Dewsbury 1979) are apparently favoured by those species nesting in protected nest sites (e.g. burrows), where a locked pair is not very vulnerable to predation. In contrast, ejaculation on a single brief insertion, as well as the absence of a lock, is common in species that inhabit exposed habitats (Dewsbury 1975).

Otomys irroratus nests on the surface, either on platform nests (De Graaff 1981; Skinner & Smithers 1990) or in enclosed cup nests (Pillay & Willan, unpublished), and the lack of locking and the comparatively few ejaculations (6.8) in this taxon is consistent with Dewsbury's (1975) findings.

Despite nesting on the surface, *O. irroratus* does not achieve ejaculation on a single insertion. This apparent contradiction may be explained by the fact that the vlei rat preferably inhabits areas with dense vegetation that provides good cover (Willan & Meester 1989; Pillay 1993), and which would presumably reduce the risk of predation, allowing for prolonged copulation.

The pre-copulatory behaviour of pairs in the present study was similar to that observed in other studies involving *O. irroratus* (see Pillay *et al.* 1995b). Like other solitary rodent species (Dewsbury 1974), the pre-copulatory behaviour of females in the present study was characterized by high levels of aggression and low levels of sexual activity, while males readily participated in sexual and amicable behaviour. Such

asymmetry between the sexes appears to be an important component of the courtship behaviour of individuals of taxa which are solitary (Spieth 1958; Parker 1974; Pillay 1990), like *O. irroratus*.

In conclusion, the copulatory behaviour of *O. irroratus* appears to reflect the ecological circumstances and the social structure of the taxon.

Acknowledgements

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