

New evidence of pseudosexual behaviour and female aggression in mice: neutral cage interactions in *Mus spicilegus* and *Mus spretus* (Rodentia: Muridae)

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Abstract. Intrasexual dyadic interactions performed in a neutral cage were studied in two species of aboriginal house mice. Encounters in the mound-building mouse, *Mus spicilegus*, were highly agonistic. Females spent equally important proportion of time in agonistic behaviour as did males. In addition, males of this species regularly exhibited pseudosexual behaviour, involving excessive sniffing and even mounting of their opponents. The above mentioned peculiar features of the behavioural profile of *Mus spicilegus* are discussed. In contrast to *Mus spicilegus*, both sexes of the Algerian mouse, *Mus spretus*, were fairly peaceful. However, as in most species of murids, male-male interactions were more agonistic than those female-female ones.

Key words: agonistic behaviour, behavioural ecology, wild mouse, homosexual behaviour

Introduction

The mound-building mouse, *Mus spicilegus* Petényi, 1882, and the Algerian mouse, *Mus spretus* Lataste, 1883, are strictly outdoor species. They have colonized Europe and/or North Africa in the ancient times, long before the appearance of neolithic man (Thaler 1986, Auffray et al. 1990). Behaviour of these species has been repeatedly studied in recent years. Pioneering studies in behavioural ecology of *M. spretus* (Cassaing 1984, Cassaing & Croset 1985) were followed by extensive studies of some interesting facets of behaviour of this species (Cassaing 1990, Hurst et al. 1994, 1996). Some features, e.g., manipulating of its own fresh faeces (Hurst & Smith 1995), are rather peculiar when compared to other species of house mice. Similarly, studies dealing with *M. spicilegus* behaviour (e.g., Simeonovska et al. 1995, see Sokolov et al. 1990 for a review of earlier literature) have shown considerable differences between this species and commensal mice. *M. spicilegus* is known to build winter shelter constructions called hillocks or mounds (Festetics 1961). Mounds serve as winter storerooms and contain up to 10 kg of food reserve (Mikěš 1971). Earlier suggestions about multiple parentage of individuals in a mound (Muntyanu 1990) were confirmed by genetic analysis with microsatellites (Garza et al. 1997).

Understanding the behaviour of *M. spretus* and *M. spicilegus* may play a key role in interpretation of house mice behaviour. Both are the closest relatives of the *M. musculus* sensu lato lineage that includes laboratory mice as well as the commensal *M. domesticus*, i.e., the forms to which most experimental effort has been devoted. Moreover, both these species are non-commensal and, therefore, they share some parameters of their ecological niche.

However, the above mentioned evidence of considerable behavioural differences among European mice species is still scattered and new data collected following a comparative design are needed.

The aim of this study was to describe social behaviour performed in a simple standard situation, and to evaluate both interspecific and intersexual differences. For these purposes we selected dyadic interactions in a neutral cage.

Although there exist some literary data on neutral cage interactions in both *M. spicilegus* and *M. spretus* (Cassaign 1990), they are not fully comparable with our results in comparative studies of aggressive behaviour in Palearctic murids (Frynta et al. 1995, Čiháková & Frynta 1996, Frynta & Čiháková 1996). Therefore, we performed dyadic encounters in these two species following a standard procedure, that enabled quantification of the behavioural elements. However, owing to the peculiar behaviour of these mice in our experiments, we elaborated neutral cage behaviour of the two species separately and paid attention to pseudosexual behaviour and female aggression.

Material and Methods

In each species, the studied animals were descendants of 2 males and 3 females obtained from the Université Montpellier II (France) in September 1993. These were the 11th generation of the ZYP strain of *M. spicilegus* derived from Pancevo (Vojvodina, Serbia) and the 20th of the SFM strain of *M. spretus* from the territory of Montpellier (France).

The animals were housed in heterosexual pairs in standard plastic cages 27 x 15 x 15 cm. Cages were placed in a light-controlled room (14L : 10D at the time of testing). Water and food (mouse and rat breeder diet, wheat etc.) were provided ad libitum. Each cage contained sawdust bedding and a shelter.

Encounters between mice were carried out in a 50 x 30 x 35 cm glass cage. The cage was divided by a thick card partition into two equal parts. During testing, the cage was illuminated by a single 40 W red light bulb. Mice were tested during the dark phase of their light-dark cycle. At the beginning of each experimental session, two mice were placed in the pen, on the opposite sides of the partition, and left for five minutes. The central partition was then removed and video recording with a single VHS-camera started. The video camera was stopped at the end of the session, i.e., ten minutes after the moment when one or both animals started to pay attention to the other for the first time. The cage was thoroughly cleaned using 96% ethanol after each session.

We used 8 males and 8 females of *M. spicilegus*, and 10 males and 10 females of *M. spretus*. All the individuals included in experiments were sexually mature, yet females were neither pregnant nor lactating at the time of testing. Each animal was tested with different opponents 3-4 times. Repeated tests of the same individual occurred no earlier than 24 hours after the preceding test. No effect of multiple tests was evinced (Two-way ANOVA on log-transformed scores of main functional blocks did not show any significant results for the effect of testing order or its interaction with species or sex).

In total, 82 dyadic encounters were performed. Sixteen male-male and 16 female-female interactions in *M. spicilegus* were carried out in September 1994, whereas 19 male-male and 19 female-female interactions in *M. spretus* were performed in April/May 1995. In addition, we performed 12 interactions between other 8 *M. spicilegus* males that had been housed individually for at least three months before testing in April 1995.

We distinguished 35 elements with minor changes adopted from G u r n e l l (1977) and M o n t g o m e r y (1978), (see Č i h á k o v á & F r y n t a 1996 for description), which were summarized into 20 categories (Roman numerals) and 6 functional blocks (capital letters):

- (A) Agonistic: (I) Threat-attack, (II) Chase, (III) Roll-over fight, (IV) Box, (V) Neutral upright, (VI) Ambivalent (To-from and/or Tail-rattle), (VII) Defensive (Upright or Threat), (VIII) Avoid-retreat, (IX) Flee-freeze (including Jump-avoid), (X) Submissive.
- (B) Introductory: (I) Attend, (II) Approach, (III) Nose.
- (C) Amicable: (I) Mutual groom, (II) Body contact (i.e., Lie on, Crawl under/over, Block).
- (D) Individual: (I) Self groom, (II) Crouch-sit.
- (E) Exploratory: (I) Loco-explore, (II) Rear-jump.
- (F) Sexual: (I) Mount.

Video records of encounters were subsequently observed and quantified using the computer program package ACTIVITIES (V r b a & D o n á t 1993). Data on total duration (in seconds) of each of these elements for a particular session in each animal were used as the input for further analysis. Data for both interacting animals were pooled, and further treated with non-parametric statistics (Mann-Whitney U-test).

Results

Both male-male ($U = 49$, $p = 0.0006$) and female-female ($U = 14$, $p < 0.0001$) interactions were much more agonistic in *M. spicilegus* than in *M. spretus*. Moreover, significant differences prevailed when the individual categories of this behaviour were compared separately (Table 1). *M. spicilegus* also spent more time by non-olfactory elements of social investigation (Attend, Approach) as well as by the Rear-jump. On the other hand, female *M. spretus* were more amicable ($U = 75$, $p = 0.003$).

No significant differences were found between male *M. spicilegus* kept in pairs and those housed individually. The only difference among 25 comparisons between these groups was found in the Self-groom ($U = 51$, $p = 0.038$) (Table 1), but it can be explained by multiple-trait testing (G i l l 1985). Differences between sexes in the representation of main functional blocks of behaviour were only slight. It is worth noticing that female-female interactions were comparably agonistic as were those male-male. Nevertheless, when individual categories were considered, the amount of time spent by Threat-attack was significantly higher in males ($U = 65$, $p = 0.015$). Another difference, the higher representation of Nose (sniffing of the opponent) in males was in part associated with following peculiar behavioural sequence. This sequence usually started with extensive sniffing of the anal region and body of the opponent. The active animal then attempted to groom or climb on the other one, which was continually retreating and/or performing defensive postures, in some cases even resulting in an attack. While the previous part of the sequence was composed of common behavioural elements, the final stage was accompanied with attempted or even realized mounting postures of the active animal. The sequence described above will be further referred as pseudosexual behaviour. The occurrence of this behaviour was fairly regular in *M. spicilegus*. It was found in a considerable proportion of the studied dyads (Table 2).

Male-male encounters in *M. spretus* were significantly more agonistic than female-female ones (Table 1). It was obvious not only in the total time spent by agonistic behaviour ($U = 103.5$, $p = 0.024$), but also in comparisons concerning three individual categories of this behaviour:

Table 1. Mean duration (in seconds) of different behavioural categories and comparison between species by non-parametric statistics (Mann-Whitney test). Means are calculated per encounter. Explanations: n = number of dyads, M = males, F = females, IM = isolated males, + p < 0.05, * p < 0.01, ** p < 0.001, *** p < 0.0001.

species	<i>Mus spicilegus</i>			<i>Mus spretus</i>		Mann-Whitney	
	F	M	IM	F	M	F	M
n =	16	16	12	19	19		
threat-attack	2.3	15.9	17.6	0.2	4.5	*	NS
chase	21.7	20.2	4.4	0.0	0.8	*	*
roll-over fight	4.3	7.5	3.9	5.7	20.9	NS	NS
neutral upright	0.0	1.7	0.0	1.4	5.8	+	*
box	0.0	0.0	1.0	0.3	3.4	NS	NS
ambivalent	51.0	23.7	32.5	0.3	4.0	***	*
avoid-retreat	26.6	41.2	62.8	1.1	1.2	***	***
defensive	66.5	69.0	99.1	1.9	20.8	***	*
flee-jump-freeze	34.1	18.6	15.1	0.2	1.2	***	***
submissive	0.0	0.1	0.0	0.0	0.1	NS	NS
AGONISTIC	206.5	198.1	236.3	11.0	62.8	***	**
(S.E.)	40.5	34.6	36.7	6.3	20.9		
attend	17.1	10.7	7.8	1.6	1.5	***	**
approach	16.6	12.8	12.4	1.2	1.4	***	***
nose	55.0	126.3	164.6	96.4	144.3	+	NS
INTRODUCTORY	88.6	149.8	184.8	99.2	147.2	NS	NS
(S.E.)	11.2	24.2	32.9	14.2	15.4		
mutual groom	0.3	4.7	1.8	1.0	0.4	NS	NS
body contact	0.0	1.1	0.0	19.0	4.1	**	+
AMICABLE	0.3	5.8	1.8	20.0	4.5	*	NS
(S.E.)	0.2	3.7	1.3	8.1	1.5		
self groom	152.1	136.2	92.6	220.9	181.2	NS	+
crouch-sit	89.1	75.3	109.3	361.4	366.9	***	***
INDIVIDUAL	241.2	211.6	201.9	582.4	548.1	***	***
(S.E.)	30.3	24.7	27.4	41.6	30.4		
loco-explore	527.0	518.9	481.1	454.6	415.8	NS	NS
rear-jump	136.3	112.6	91.5	32.8	21.6	***	***
EXPLORATORY	663.4	631.5	572.5	487.4	437.5	+	+
(S.E.)	56.3	52.2	52.3	40.1	37.8		
SEXUAL	0.0	3.4	2.7	0.0	0.0		+
(S.E.)	0.0	1.7	2.2	0.0	0.0		

Table 2. Numbers of male-male dyads in *Mus spicilegus* with different expression of homosexual behaviour.

	kept in pairs	housed individually
absent	6	5
prolonged sniffing	4	2
attempted mount	3	4
mounting present	3	1

the Threat-attack ($U = 111$, $p = 0.006$), Roll-over fight ($U = 117$, $p = 0.021$), and Defensive ($U = 110.5$, $p = 0.011$). Also the Introductory behaviour ($U = 91$, $p = 0.009$), represented mostly by Nose ($U = 91$, $p = 0.009$), was more common in males than in females.

Discussion

Although female aggression has been repeatedly described in house mice, it has been restricted either to the pup defence and/or to the cohabitation with a territorial male (e.g. Hood 1988, Brain & Parmigiani 1990, Parmigiani & Palanza 1994, Palanza et al. 1996). Female commensal mice (including laboratory strains) usually showed only low levels of agonistic behaviour in neutral cage conditions (Van Zegeren 1980). While female *M. spretus* behaved in the same manner (1% of time spent by agonistic behaviour) as commensal species in our experiments, female *M. spicilegus* did not. They were without doubt highly agonistic (17%). It should be emphasized that female *M. spicilegus* were agonistic toward closely related but unfamiliar females, suggesting that relatedness itself does not prevent female aggression. The phenomenon of highly agonistic interactions between females (27% of time spent by agonistic behaviour) has also been described in *M. macedonicus* (Frynta & Čiháková 1996), which is the closest relative to *M. spicilegus* (Bonhomme 1986, She et al. 1990, Prager et al. 1996). Moreover, our results with *M. spicilegus* challenged the common view that female-female encounters should be inevitably less agonistic than those between males. Nevertheless, even in *M. spicilegus* aggressive threats and attacks were more expressed in males.

In males we found a considerable contrast in levels of agonistic behaviour between the two species. Whereas male-male interactions were fairly 'peaceful' in *M. spretus* (5%), they were agonistic in *M. spicilegus* (17%). The proportion of agonistic behaviour in the latter species was comparable to *M. domesticus* (16-19%, our unpubl. results), but lower than in *M. macedonicus* (41%, Frynta & Čiháková 1996). Taking into account differences between species and/or populations of commensal mice (Thuesen 1977, Van Zegeren & Van Oortmersen 1981, Cassaing 1990), substantial differences in the representation of agonistic behaviour between the studied species of aboriginal mice was not surprising. However, as opposed to our results with the SFM strain of *M. spretus*, Cassaing (1990) reported highly agonistic interactions between wild males of this species. Evaluating this contradiction, the effect of inbreeding known to lower aggression in commensal mice (Eklund 1996) cannot be simply excluded. On the other hand, the short total time spent by agonistic behaviour and the low relative representation of the chasing-fleeing behaviour in SMF mice are in a full accordance with other studies on captive *M. spretus* of wild origin. Hurst et al. (1996) reported that dyads of *M. spretus* "quickly established dominance relationship through brief attacks and chases, and static defensive posture, rather than persistent pursuit and flight". Similarly Gray & Hurst (1997) found that in neutral enclosures *M. spretus* dyads were less aggressive than *M. domesticus* dyads.

Although pseudosexual behaviour has been repeatedly reported in various mammal species, especially primates (Hall & DeVore 1965, Jolly 1972) and ungulates (Hall 1983, Klemm et al. 1983), it has only exceptionally been reported in rodents such as in rats (Calhoun 1962 a, b, Madlafousek, pers. comm.). However, pseudosexual behaviour has not previously been found in studies of neutral cage encounters between male mice of the genus *Mus* (e.g. Cassaing 1990, Simeonovska 1994, Frynta & Čiháková 1996) and *Apodemus* (e.g. Gurnell 1977, Montgomery 1978, Frynta et al. 1995, Čiháková & Frynta 1996). In our experiments, pseudosexual behaviour occurred in the context in which agonistic contest usually takes place, being present both in isolated males and those housed in pairs. Therefore, we hypothesize that

pseudosexual behaviour in *M. spicilegus*, as probably in some other mammals (e.g. Hall 1983), is a manifestation of social dominance, rather than social pathology.

Our observations were restricted to a single strain in each species and were performed solely in artificial neutral-cage conditions. Nevertheless, behavioural patterns performed in a standard test are worth noticing when evaluating social organization in a given species. As discussed above, peculiarities of *M. spicilegus* behaviour have never been observed in *M. spretus* or any species of commensal house mice. It supports the view that social behaviour of *M. spicilegus* differs considerably from that of other species of commensal house mice (cf. Sokolov et al. 1990). We can speculate that agonistic encounters among females of *M. spicilegus* can be associated with excessive food hoarding into mounds and cache defence.

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