

Inter-male Mating-like Behavior in the Domesticated House Musk Shrew, *Suncus murinus*

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ABSTRACT—In the present study, inter-male interaction of the domesticated house musk shrew was observed in detail under laboratory conditions. In most cases, during inter-male interaction, male house musk shrews exhibited a sequence of behavior items including tail-wagging, following, mounting and thrusting. In the minority of cases, males did not progress beyond following. Offensive behavior was not sufficiently violent to cause injury. It appeared that role assignment was decided by contact manner and vocalization. One of fundamental characters of this animal made a start of following, in which one shrew followed another, who touched and then separated. Role assignment (i.e., which male led and which followed) was decided in status battle. Roles were often reversed during following. Following behavior was maintained by ‘polite’ mutual contact, and the interaction progressed to thrusting in the majority cases. After role assignment, the variation in contact manner decreased. The ratio of time spent in front-and-behind contact to that spent in multi-lateral contact increased when both males commenced following behavior simultaneously. This ratio was maintained until the following male snapped after he finished thrusting. Even if the following male did not reach thrusting, he mounted the preceding male. The pairs who did not reach thrusting repeated following behavior or mounting. In those cases, while one male concentrated on touching the other to maintain following, the other attempted to divert attention from the following behavior. Male shrews were able to reach thrusting irrespective of sex.

Key words: house musk shrew, *Suncus murinus*, inter-male interaction, mating-like behavior, following formation

INTRODUCTION

The house musk shrew, *Suncus murinus*, belongs to the Order Insectivora. This animal can breed all the year round. The females are coitus-induced ovulators (Furumura *et al.*, 1985); i.e., they do not have estrus or an ovulatory cycle, and are induced to ovulate by the physical stimulation associated with intromission. This shrew is found from east Africa (western extent) to Guam (eastern extent), and as far north as Japan. In Japan, this shrew lives in Okinawa, Kagoshima and Nagasaki (Oda, 1985). This shrew was domesticated as a laboratory animal in the United States by Dryden (1968), and in Japan by Kondo and Oda (1977). It is easy to observe the behavior of these domesticated shrews under controlled laboratory conditions. There have been few studies of male-male interaction in other species of the Order Insectivora.

In this species, Tsuji and Naruse (1985) stated that car-

avan formation between mother and offspring in the nursing period not only facilitates care for the offspring, but also provides the young with early experiences in exploring and extending their environment. Matsuzaki (2002) speculated that following formation between adult males and females may be derived from caravan formation in the nursing period. Inter-male interaction was reported by Tsuji (personal communication) and Kawano (1992) as “mating-like behavior”. The behavior observed in heterosexual interaction probably serves to build relationships between shrews, irrespective of sex.

In the present study, inter-male interaction was recorded, and the behaviors were translated into analytical data. A specific aim of this study was to demonstrate the existence of mating-like behavior between males, and to show that it involves almost the same sequence of conspicuous behaviors observed in heterosexual interaction.

MATERIALS AND METHODS

The musk shrews used in this study were from the Jic:Sun line (Matsuzaki *et al.*, 1984), which is derived from shrews domesticated

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by Kondo and Oda (1977). The Jic:Sun line colony at the University of Tsukuba was established from animals provided by Mr. Matsuzaki (Central Institute for Experimental Animals) and animals purchased from CLEA JAPAN INC. The animal room was maintained at $25\pm 1^\circ\text{C}$, 55 to 65% humidity and 12L:12D (lights on at 07:00). Food (Nippai 5P for trout) and spring water were available ad libitum. Offspring were weaned at 30 days of age, and were housed individually in plastic mouse cages (30W×20D×13H cm). Twenty males, aged 4 to 6 months, were used for the experiment. Inter-male interaction was observed in a glass tank (60W×30D×45H cm) illuminated with four fluorescent 60W lamps, between 15:00 and 18:00. On the day prior to a trial, the glass tank was washed with hot water, ethyl alcohol was sprayed inside the tank to remove odors, and the tank was placed bottom upward to dry.

The experiment proceeded as follows. Two males were placed in the tank, separated by a cardboard septum, to acclimate to the novel environment. After they had explored the tank for 4 to 5 min, they calmed down and/or began to wash their snouts. At that time, the septum was removed. The tank was covered with a sheet of unwoven fabric to prevent air flowing directly into the tank during the observation. The sequence of behaviors was recorded with a video camera. After the observation, each frame was analyzed, paying attention to the type of contact between the individuals and the duration of each interaction. Drawings were prepared by tracing the outlines of the photographed shrews.

RESULTS AND DISCUSSION

Conspicuous behavior items between males and females include encounter, female tail-wagging, following formation, intromission, ejaculation and male continuous vocalization (Matsuzaki, 2002). The conspicuous behavior items we observed in the inter-male interaction were very similar to that observed between males and females. The behavior items we observed in inter-male interaction are itemized below (a to i), and are shown in Tables 1 and 2.

- (a) Exploration of novel environment
- (b) Approach, encounter and investigation
- (c) Tail-wagging, turning contact and squatting
- (d) Status battle with turning contact against vocalization
- (e) Following formation, mounting, genital licking and vocalization
- (f) Thrusting with or without intromission
- (g) Post-thrusting offensiveness with continuous vocalization
- (h) Scent marking
- (i) Strolling and resting

All pairs observed achieved following formation after encounter, and 7 out of the 10 pairs reached thrusting. Thrusting did not always include intromission. The time course of the interaction varied. An important difference from heterosexual interaction was that following formation was easily reversed. In the 7 pairs that reached thrusting, the mean (\pm SEM) time from initial encounter after removal of the septum to finishing continuous snap after thrusting was 3080 ± 900 s (range=1230–6775 s; Table 1). The other 3 pairs repeated following formation and reversal following formation. After interaction, the animals huddled and slept. The observation was terminated when the animals went to

sleep or at commencement of strolling (range=2640–4550 s; Table 2).

(1) Type of contact during periods between conspicuous behavior items

The contact involved with the following formation was classified into 2 types: multi-lateral contact (MLC) and front-and-behind contact (FBC). MLC involved one male touching or moving across the other's flank, back, abdomen or head, including the snout. Touching occurred all over the body. FBC involved one male moving behind the other and touching it from behind. During FBC, one male maintained contact with the other's tail, lumbar region, hind limb or urogenital orifice and its vicinity (UO). FBC occurred just before and during the following formation, and was easily reversed at status battle. In status battle, the 2 males faced each other with teeth shown, with the mouth simply open or with vocalization that was threatening and/or ordering. One male turned or passed to the other side with tail wagging. The other male followed, with its snout at the lumbar region or tail. The status battle tended to induce following formation, and was one of the main sources of following formation.

Tables 1 and 2 show the mean time (s) until occurrence of each conspicuous behavior, and the mean percentage of time spent in MLC, FBC and non-contact (NC) during each behavior period. Figs. 1 and 2 were constructed based on data in Tables 1 and 2, and show probabilities for ratio of the time spent in MLC, FBC and NC during each period.

When the ratio of time spent in MLC, FBC and NC is compared for each period with the adjacent behavior (Figs. 1 and 2), it is apparent that the proportion of time spent in FBC increased after following formation and reversal following formation. After reversal mounting, the ratio of MLC time and FBC time changed temporally, but the ratio of NC time was smaller than those of the periods ahead. The reduced ratio of NC time indicates increased intimacy of the relationship, even when the behavior appears offensive.

Status battles occurred frequently in each period. When a status battle lasted for a long duration and was accompanied by vocalization (threatening and/or ordering), the status reversed and the following male became the preceding male. The new preceding male wagged its tail alternatively. Status battle appears to be offensive, and it is important for deciding the order of following, because a characteristic of this species is that individuals will follow an animal that touches them and then moves away (Tsuji and Naruse, 1984; Matsuzaki, 2002).

In the remainder of the Results and Discussion section, we describe and discuss details of the inter-male behavior sequences.

(2) Encounter to mutual investigation

The male shrews placed in the tank sniffed all areas of the tank. One listened to the sound made by the other and oriented to it (Fig. 3). One approached the other snout to snout. They sniffed each other's snout (Fig. 4), ear, neck

Table 1. The time course of conspicuous behaviors and their type of contact in 7 pairs reaching thrusting or intromission. The mean (\pm SEM) time (s) of MLC, FBC and NC between each pair of conspicuous behaviors are shown. MLC, multi-lateral contact; FBC, front-and-behind contact; NC, non-contact; FF, following formation.

conspicuous behavior items	mean \pm SEM (sec)	contact manner	mean \pm SEM (%)
encounter (7/7)	4 \pm 1		
		MLC	57 \pm 11
		FBC	15 \pm 6
		NC	28 \pm 8
one male tail-wagging (7/7)	82 \pm 40		
		MLC	36 \pm 11
		FBC	15 \pm 4
		NC	50 \pm 11
another tail-wagging (7/7)	295 \pm 67		
		MLC	38 \pm 14
		FBC	19 \pm 9
		NC	43 \pm 12
following formation (FF) (7/7)	390 \pm 99		
		MLC	15 \pm 10
		FBC	67 \pm 15
		NC	17 \pm 8
reversal following formation (1/7)	211 \pm 0		
		MLC	0 \pm 0
		FBC	79 \pm 0
		NC	21 \pm 0
first mounting (7/7)	703 \pm 257		
		MLC	19 \pm 4
		FBC	47 \pm 6
		NC	34 \pm 4
reversal FF or reversal mounting (2/7)	6666 \pm 379		
		MLC	33 \pm 26
		FBC	60 \pm 29
		NC	7 \pm 3
final thrusting (7/7)	3799 \pm 1122		
		MLC	17 \pm 4
		FBC	42 \pm 9
		NC	41 \pm 10
finishing post-thrusting offensiveness (7/7)	3080 \pm 900		

and flank (Figs. 5 and 6), and then passed each other (Fig. 7).

Hearing is important for approach, and sniffing is important for initial conspecific recognition. Darkness did not appear to disturb behavior. Further study is needed to determine the role of vision.

(3) Tail-wagging, turning contact and squatting

After several encounters, status battle (Fig. 8) occurred and one animal turned or passed the side. When one animal turned in front of the other's snout, the turning animal's flank and tail brushed the other's snout, throat and forelimb. The

non-turning animal stayed in place and oriented its snout to the turning and leaving animal's lumbar region and tail. Turning contact (Fig. 9) occurred in this manner. If one animal turned and moved away, the other did not follow soon after. The animal whose tail or lumbar region was touched by the other's snout or forelimb tended to move forward after some turning contacts. Accumulation of contacts (MLC and FBC) and decrease of NC (Figs. 1 and 2) are necessary to start following formation (Fig. 10). In following formation, the following male touches the preceding male's tail, UO, inguinal region or lumbar region, and walks behind the preceding male.

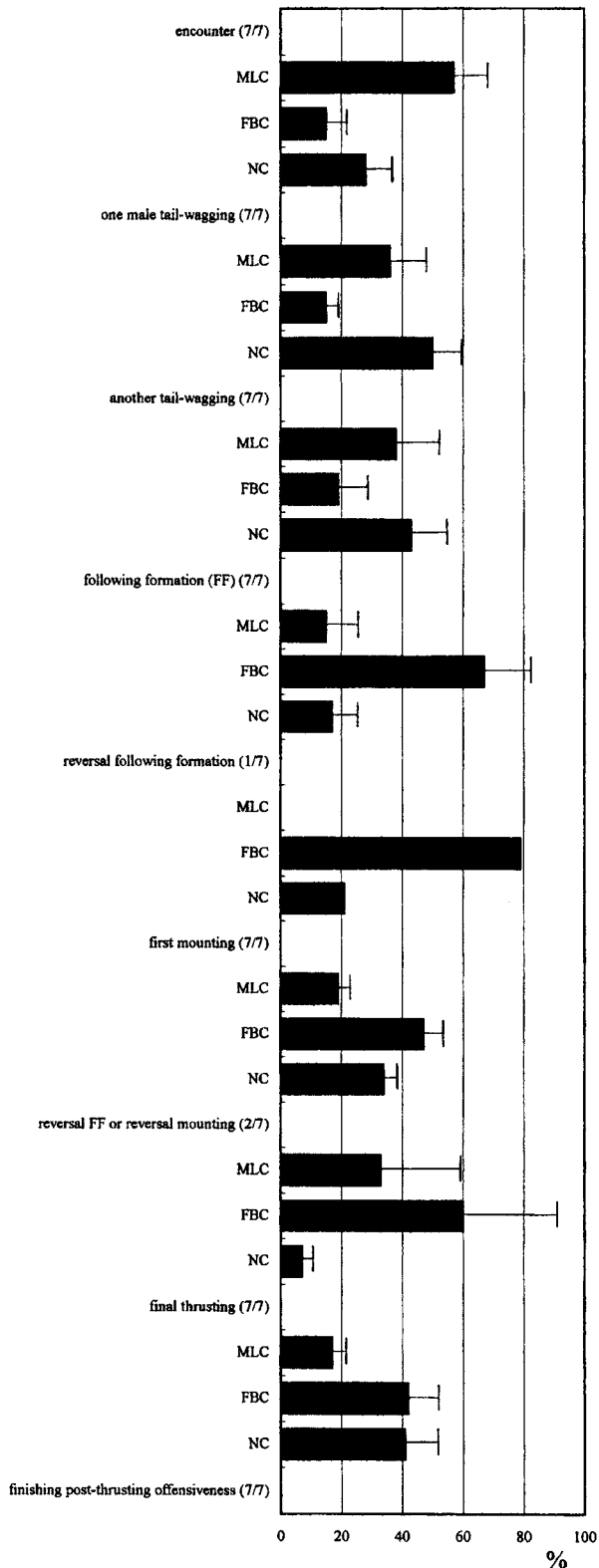


Fig. 1. Graph of Table 1. The vertical axis is a series of conspicuous behaviors and contact manners. The horizontal axis is percentage. The horizontal bars are the mean percentage of time spent for each type of contact ($n=7$ pairs), and the error bars are SEMs. Abbreviations are as for Table 1. After following formation, the ratio of time spent in FBC increased and the ratio of time spent in NC decreased. The ratio of time spent in NC increased after thrusting.

After the males encountered each other, sniffed and investigated, they appeared to avoid snout-to-snout contact. Each animal kept its head far from the other's snout. Turning was one of the behaviors that occurred when they encountered each other. Another was passing the side or passing to the other's abdominal side (Fig. 11). These actions are common elements of heterosexual interaction (Matsuzaki, 2002).

One animal oriented its snout to the moving animal's lumbar and tail. One's action leaving the tension giving rise to snout-to-snout contact appeared to call the other's attention and let his snout orient to one's lumbar and tail. When one turned back and the lumbar was put in front of the other's snout, the tail was wagged. This type of tail-wagging was by turns repeated in all cases. When one's tail was put on the other's back or flank, the tail appeared to peg the other there to prevent the other's snout from approaching one's head (Fig. 12).

There were 2 types of tail-wagging. When one's tail is wagged upward powerfully and pushes the other's neck or beats its snout, it can prevent the approach of the other's snout to one's head; Tsuji *et al.* (1999) described this behavior. On the other hand, when the tail is wagged right and left flexibly under the other's head, it appears to cause and facilitate following formation (Fig. 13).

The preceding male stopped and waited for the other to touch its tail or the lumbar region with the tail wagging flexibly (i.e., squatting), and the preceding male also moved the paw tip of the hind limb up and down. When one touched the squatting male's tail or lumbar region, the squatting male moved ahead, and the touching one followed, resulting in following formation (Fig. 10).

(4) Status battle (Fig. 8)

Status battle began after several encounters. The male who uttered the threatening call first followed the other, who turned. After several status battles, they reversed the order of following formation. One, who had repeated turning until this opportunity, uttered an ordering call, and the other turned. At that time, the order of following formation reversed. In mating behavior, the female utters a sharp threatening call, and the male utters an ordering call that sounds like chirping (Matsuzaki, 2002). In the present study, one male's threatening call appeared to prompt the other to turn and move away temporarily. At that time, one followed the other, who turned. When the preceding male looked back or turned back, another status battle occurred. As long as one uttered a threatening call one-sidedly, the other repeated turning. The order of following formation remained unchanged. Some status battles were repeated with one-sidedly uttered threatening calls. The male who had performed repeated turns eventually began to stand firm against the threatening call (Fig. 14). Alternatively, he then uttered his own ordering call. The other male, who had uttered the initial threatening call, then turned. In all cases, reversal of the order of following formation occurred at this

Table 2. The time course of conspicuous behaviors and their type of contact in 3 pairs that did not progress beyond following formation or mounting. The mean (\pm SEM) time (s) of MLC, FBC and NC between each pair of conspicuous behaviors are shown. MLC, multi-lateral contact; FBC, front-and-behind contact; NC, non-contact.

conspicuous behavior items	mean \pm SEM (sec)	contact manner	mean \pm SEM (%)
encounter (3/3)	40 \pm 38	MLC	44 \pm 19
		FBC	6 \pm 6
		NC	50 \pm 16
one male tail-wagging (3/3)	93 \pm 49	MLC	50 \pm 19
		FBC	2 \pm 2
		NC	48 \pm 20
another tail-wagging (3/3)	154 \pm 97	MLC	42 \pm 13
		FBC	21 \pm 6
		NC	37 \pm 20
following formation (3/3)	394 \pm 192	MLC	18 \pm 2
		FBC	31 \pm 11
		NC	51 \pm 9
reversal following formation (3/3)	667 \pm 247	MLC	29 \pm 11
		FBC	31 \pm 9
		NC	40 \pm 10
following or mounting (3/3)	798 \pm 264	MLC	26 \pm 13
		FBC	45 \pm 12
		NC	29 \pm 2
reversal following formation (3/3)	1258 \pm 558	MLC	18 \pm 6
		FBC	52 \pm 20
		NC	34 \pm 11
reversal mounting (3/3)	1337 \pm 540	MLC	21 \pm 3
		FBC	32 \pm 17
		NC	47 \pm 16
reserval following formation (2/3)	1863 \pm 1290	MLC	41 \pm 13
		FBC	11 \pm 5
		NC	49 \pm 17
following formation (1/3)	604 \pm 0		

time. Continuous reversal of following formation is not observed in heterosexual interaction (Matsuzaki, 2002).

(5) Following formation, mounting, genital licking and vocalization

We classified vocalization into 2 types: threatening call and ordering call. In mating behavior (Matsuzaki, 2002), the female utters a threatening call and moves ahead, and the

male utters an ordering call and follows. In the inter-male interaction, the preceding male uttered a threatening call and the following male uttered an ordering call.

In status battle, the ordering call uttered by one caused the other to turn. Then, FBC increased, following formation occurred (Fig. 10), and the order of following formation was maintained. Following formation in the inter-male interaction was often interrupted by sudden stops and sniffing around

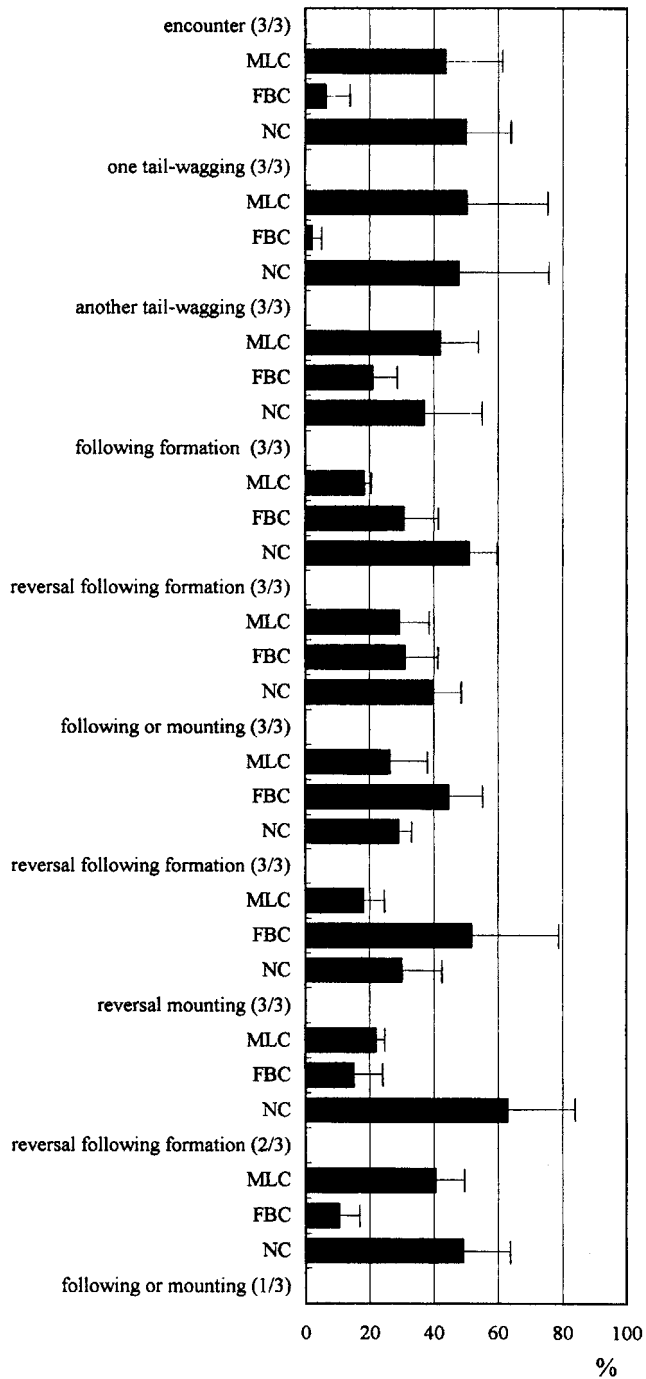


Fig. 2. Graph of Table 2. The vertical axis is a series of conspicuous behaviors and contact manners. The horizontal axis is percentage. The horizontal bars are the mean percentage of the time spent for each type of contact (n=3 pairs), and the error bars are SEMs. Abbreviations are as for Table 1. The ratio of time spent in NC because of reversal of order of following formation or interruption of following formation is shown. Prolonged observation showed that both males slept after repetition of following formation and reversal following formation.

(Fig. 15). In addition, the preceding male turned back frequently, and even uttered a threatening call. The following male showed its teeth and stood firm against the shown



Fig. 3. Listening to each other's sound, and approach.

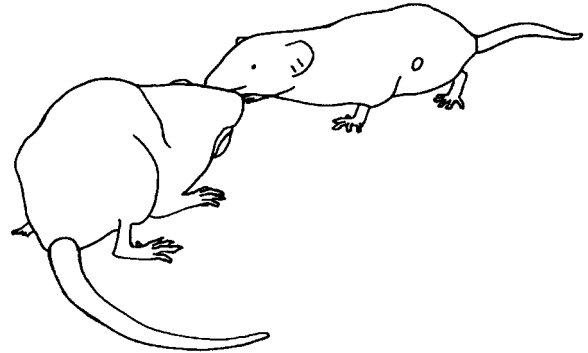


Fig. 4. Sniffing each other's snout at first encounter.

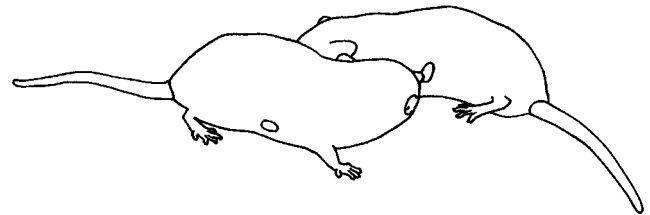


Fig. 5. Sniffing each other's flank gland at first encounter.

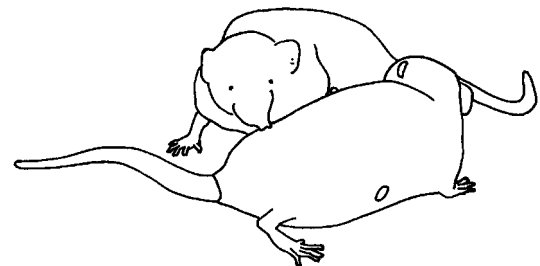


Fig. 6. Sniffing each other's lumbar region at first encounter.

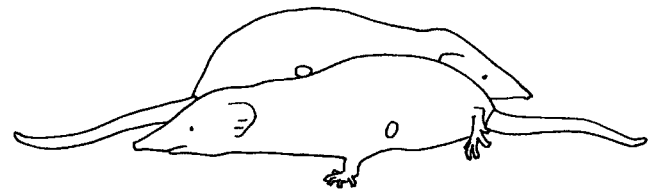


Fig. 7. Passing to the side of each other after investigation by sniffing at first encounter.

teeth or threatening call of the preceding male (Fig. 14). Then, the following male began uttering ordering calls. In many cases, the following order was maintained. When the

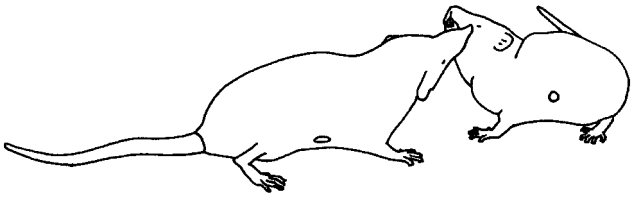


Fig. 8. Status battle with teeth shown, mouth open, or vocalization.

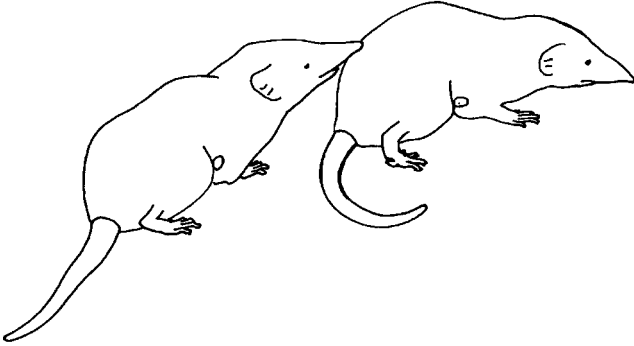


Fig. 9. Turning contact with brushing of the other animal's snout.

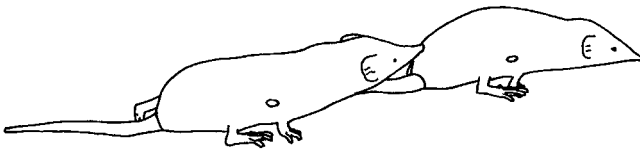


Fig. 10. Following formation



Fig. 11. Trying to pass the side or pass through.

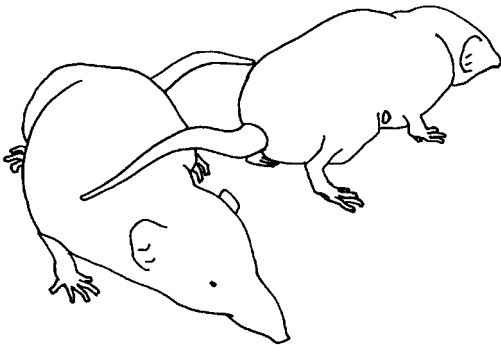


Fig. 12. Pegging by the tail being put on the back.

order reversed, it was restored after the next status battle.

After stable following formation, the following male mounted the preceding male (Fig. 16) with an ordering call. Then, the following male licked the penis. The preceding

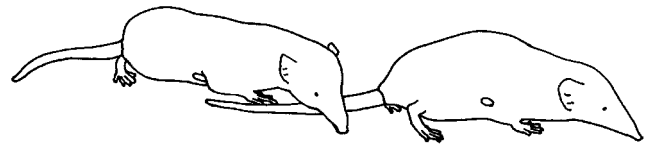


Fig. 13. Facilitation by the tail being wagged flexibly under the head.



Fig. 14. Standing firm against threatening call.

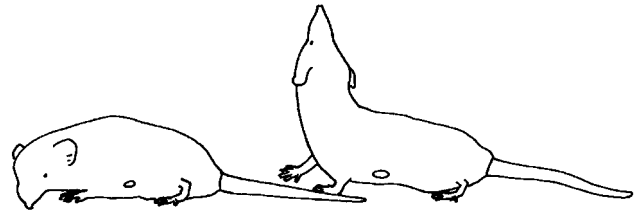


Fig. 15. Interruption by sudden stop of following formation and sniffing around.

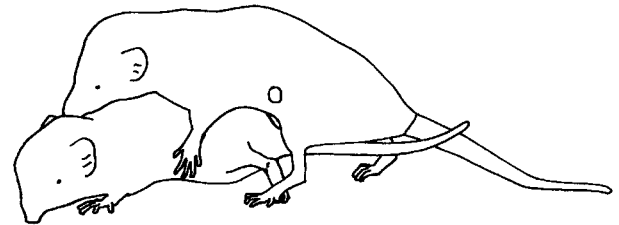


Fig. 16. Mounting

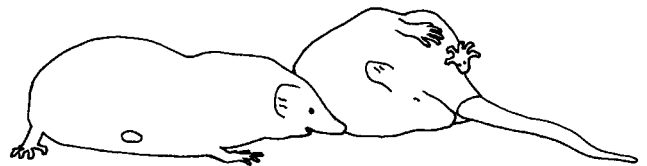


Fig. 17. Following male licking its own penis after mounting and preceding male coming to touch him.

male came back to the following male, who was licking its own penis, and touched the following male (Fig. 17). The following male oriented its snout to the snout of the preceding male, who was touching the following male's UO. The following male then recovered, and status battle occurred.

The ratio of time spent in NC was small in each period between following formation and thrusting (Figs. 1 and 2). In the 7 cases in which thrusting was reached, one male performed reversal mounting, and, in the following period, the other male reached thrusting. Stable following formation and/or status battles can change behavior of the males and lead to mounting and thrusting (Fig. 18).

In the 3 cases in which thrusting was not reached, fol-

lowing formation and reversal following formation were repeated. The pairs did not concentrate on following formation. Either a threatening call or ordering call overwhelmed one of the males and caused it to turn or pass at status battle. In addition, the males stopped suddenly and sniffed around. One's action did not always appear to correspond to the other's reaction. NC was the predominant form of behavior (Figs. 1 and 2). Following formation was unstable, and the pairs did not progress beyond mounting.

(6) Thrusting with or without intromission (Fig. 18)

After stable following formation and one-sided mountings, the following male thrust at the lumbar region while mounting. The following male held the preceding male's hind limbs by the forelimbs, and bit the preceding male's back fur. The preceding male struggled to get free and look back, but his hind limbs and back fur were held too firmly to escape. Intromission (holding period, 3–6 sec) occurred in 5 cases out of 10, and thrusting (holding period, 1–3 sec) was observed in 2 cases out of 10.

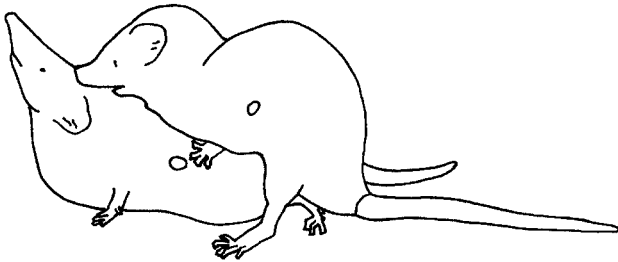


Fig. 18. Thrusting or intromission

(7) Post-thrusting offensiveness with continuous ordering call (Fig.19)

The following male licked its own penis after thrusting or intromission. The preceding male licked its UO. In the cases in which the following male performed thrusting without intromission, only the following male licked its own penis. When the preceding male approached the UO of the following male, who was licking his own penis, the following male recovered and started uttering a continuous ordering call. The following male bit the preceding male's tail and lumbar fur while uttering a continuous ordering call. This offensive behavior was directed toward any male placed near the following male. When the preceding male was replaced with an alternative male, the replacement was subjected to the same offensive behavior by the following male. This offensive behavior included snapping at the preceding

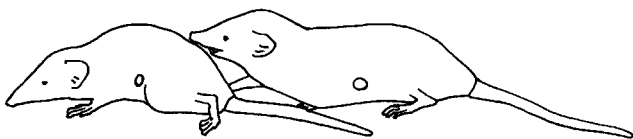


Fig. 19. Post-thrusting offensiveness by biting and scratching lumbar back fur.

male in a fit of anger.

The preceding male moved ahead with tail wagging upward powerfully, and turned back to utter a threatening call. The continuous ordering call of the following male always caused the preceding male to turn, even if the preceding male turned back and uttered a threatening call. Then, the following male turned and finished the snap with the continuous ordering call (76.7 ± 13.2 sec after final thrusting), at which point the preceding male turned and uttered an intense threatening call.

(8) Scent marking, side-scratching and snout-washing

In mating behavior, scent marking occurs after post-ejaculatory offensive behavior (Matsuzaki, 2002). In the inter-male interaction, scent marking, side scratching and snout-washing started to occur during following formation, and males showed these behaviors at all times during following formation, with the exception of the period just before thrusting. It is difficult for males to concentrate on maintaining following formation in the inter-male interaction.

After stable following formation or several mountings, the preceding male stopped suddenly and licked the penis. The preceding male also made scent markings with its flank gland, and performed side scratching and snout-washing. In mating behavior (Matsuzaki, 2002), scent marking, side scratching and snout-washing of the following male has been observed after intromission. The female performs those actions after the male performs them. Scent marking is under control of the genital gland in males and especially of the adrenal gland in females (Dryden and Conaway, 1967; Balakrishnan and Alexander, 1976; Balakrishnan *et al.*, 1984; Tennant *et al.*, 1986; Rissman and Bronson, 1987). The behaviors observed in early stages involve methods of conspecific recognition and possibly sex recognition.

Exhaustion was observed in all cases, especially after status battle and post-thrusting offensive behavior. Urine was sniffed or tasted until it dried. Feces were sniffed by both males, and were tasted by the one that did not produce it. Exhaustion can function in conspecific recognition, in addition to the large scent glands (flank gland and anal gland) (Kitoh and Ohta, 1985).

(9) Strolling and Resting

The following male started to stroll independently and sniff upward after finishing its post-thrusting offensive behavior. The preceding male approached and touched the strolling male, turned with turning contact in front of the strolling male, and then squatted with its tail wagging. The strolling male probed with its snout, but did not continue following formation.

During the 2-hr observation period, reversal following formation and reversal mounting occurred in 4 cases out of the 7 in which thrusting or intromission was reached. The males that performed thrusting or intromission started strolling and sniffing upward, and then tended to rest and close

their eyes. The thrusting male appeared to be exhausted after post-thrusting offensive behavior. The behavior did not develop beyond reversal mounting. Physical condition may be one of the factors deciding behavior after post-thrusting offensiveness.

CONCLUSIONS

Inter-male interaction of adult shrews developed clumsily, but followed a course of development similar to that of mating behavior. One male reached thrusting or intromission, and the other male received this behavior. The males of this species also show homosexual mating as widespread among mammals as a part of their behavioral repertoire. Further studies are expected to know the significance of the homosexual mating in this species.

Following formation appears to be based on the characteristic behavior of this species in which an individual follows something that touches it and leaves (Tsuji, *et al.*, 1984), and the tendency of these shrews to move ahead when something touches the tail, lumbar region, UO or inguinal region (Matsuzaki, 2002). Relationship-building behavior apparently depends mainly on touching. Following formation, which occurs after several contacts, is apparently caused by the drive to maintain and develop relationships between individuals.

Step-by-step development of a series of conspicuous behavior items gives rise to 2 types of contact, each of which include sniffing, turning contact, tail-wagging and vocalization. These 2 types of contact are also commonly observed in heterosexual interaction. Heterosexual interaction and inter-male interaction apparently share common relationship-building mechanisms. These may derive from mechanism involved in caravan formation between mother and litter or between offspring.

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