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The Force Driving Mating Behavior in the House Musk Shrew (*Suncus murinus*)

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ABSTRACT—The mating behavior of the domesticated house musk shrew was observed in detail under laboratory conditions. The observations revealed that the house musk shrew has a series of behaviors before copulation. Tactile, auditory and chemical senses appear to function as flags for the recognition of conspecifics and to promote the development of an interaction between the sexes. The tactile senses and the use of the snout were particularly important in the mating sequence, and mutual contact appeared to give rise to driving the sequence to completion. The two sexes contacted each other 'politely', came to mounting by continuous following, and the male finished with a series of post-ejaculatory offensive behaviors and scent markings. The variation in the contact reduced once the female commenced tail-wagging. The ratio of the time spent in front-and-behind contact to that spent in multi-lateral contact increased when both sexes commenced following formation. This ratio was maintained until the male's post-ejaculatory offensive behavior finished. The series of mating behavior was completed by the continuous touching of both sexes and by changes in the manner of contact.

Key words: house musk shrew, *Suncus murinus*, insectivora, mating behavior, following

INTRODUCTION

The house musk shrew, *Suncus murinus*, belongs to the Order Insectivora. This animal can breed all year around**.** The female is the coitus induced ovulator (Furumura *et al*., 1985); i.e. female musk shrews do not have estrus and ovulatory cycles and are induced to ovulate following the physical stimulation associated with intromission. The shrew inhabits east Africa to the east, Guam to the west and Japan to the north. In Japan, the shrew lives in Okinawa, Kagoshima, and Nagasaki (Oda, 1985). The shrew was domesticated as a laboratory animal in the United States by Dryden (1968) and in Japan by Kondo and Oda (1977). Therefore it has become easy to observe the behavior under the controlled condition in a laboratory. There are few studies about the mating behavior of the other species in the Order Insectivora.

The mating behavior of this shrew has been studied by researchers of endocrinology and psychology in Japan (Morita, 1968; Tsuji 1989), the United States (Rissman *et al*., 1987) and India (Balakrishnan *et al*., 1976). In particular, caravan formation and aggressiveness between adults have been investigated by researchers of psychology in Japan. Tsuji and Ishikawa (1984) stated that the visual perception of motion probably acted as a basic cue in caravan formation at the age of eye-opening. Morita (1968) reported that an aggressive female received a male in the evening. The author of the present study also observed that mating at night was performed in the same way during the day (unpublished data), indicating that vision did not have an essential role in mating behavior.

In the present study, a series of mating behaviors were recorded and the behaviors were translated into analytical data. A specific aim of this study was to elucidate the roles of the tactile, auditory and chemical senses on mating behavior in the house musk shrew, with a particular emphasis on understanding the role of touch. This paper discusses the 'force' that connects the sequence of conspicuous behaviors before and after mating.

MATERIALS AND METHODS

The ancestors of the musk shrews used in this study were from a Jic:Sun line (Matsuzaki *et al*. 1984), following domestication by Kondo and Oda (1977). The colony of the Jic:Sun line at the University of Tsukuba was established either from animals provided by Mr. Matsuzaki, in the Central Institute for Experimental Animals, or purchased from CLEA JAPAN INC. The animal room was maintained at 25±1°C, 55–65% humidity and 12L:12D (lights went on at 07:00). Food (Nippai 5P for trout) and spring water were available *ad libitum*. Offspring were weaned at 30-days old and then housed individually in plastic mice cages (20×30×13 cm). Males and females were separated into two compartments to prevent the odor

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of the sexes mixing. Eight males and eight females, aged four to six months old, were used for the experiment. Mating behavior was observed in a glass tank (60W×30D×45H cm), illuminated with two fluorescent 60W lamps, between 15:00-18:00. 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. A female was placed in the tank to acclimate to the novel environment. After a female had explored the tank for 4–5 min, she moved to a corner and began to wash her snout. A male was then placed in the corner of the tank that was furthermost from the female. 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.

Statistics

Duration and frequency data were analyzed by Wilcoxon signed rank tests. Data are summarized as the mean (±SEM) and the range.

RESULTS

The mean (±SEM) time taken from the initial placement to ejaculation was 1316±131 s (range=900–1920 s; Table 1). After mating, the female began snout-washing or side-scratching in an average of 1907±210 s (range=1440–3240 s) after initial placement in the tank (Table 1).

The conspicuous behaviors observed in a mating sequence were as follows.

(i) Exploration of novel environment (ii) Approach and Encounter (iii) Vocalization of female and/or male (iv) Investigation (v) Tail-wagging and Squat

(vi) Following, Mounting and Genital licking (vii) Intromission and Ejaculation

(viii) Post-ejaculatory offensiveness (ix) Scent marking (x) Strolling or Resting

Table 1. The time course of conspicuous behaviors and their type of contact.

conspicuous behavior items	time course (sec) mean±SEM	contact manner	mean % of contact time mean±SEM
♀ + ♂	0		
encounter	6.3 ± 1.5		
		MLC	64.8 ± 11.2
		FBC	9.9 ± 7.2
		NC	25.4 ± 8.8
♀ tail-wagging (TW)	51.8 ± 30.8		
		MLC	39.9 ± 7.4
		FBC	35.3 ± 7.5
		NC	24.9 ± 4.0
following formation (FF)	510.0 ± 397.7		
		MLC	13.6 ± 2.5
		FBC	71.9 ± 5.2
		NC	14.5 ± 3.9
first intromission (1st intro)	988.0 ± 496.5		
		MLC	8.3 ± 1.8
		FBC	69.6 ± 3.3
		NC	22.9 ± 3.1
ejaculation	1316.8 ± 130.7		
		MLC	7.5 ± 2.3
		FBC	69.9 ± 5.7
		NC	18.9 ± 6.0
♂ continuous vocalization	1430.0 ± 133.8		
		MLC	14.6 ± 1.9
		FBC	19.8 ± 4.4
		NC	65.6 ± 4.3
♀ snout-washing/side-scratching	1906.8 ± 210.1		

The mean (±SEM) time (s) of MLC, FBC and NC between each two conspicuous behaviors are shown.
MCL: multi-lateral contact, FBC: front-and-behind contact, NC: non-contact.

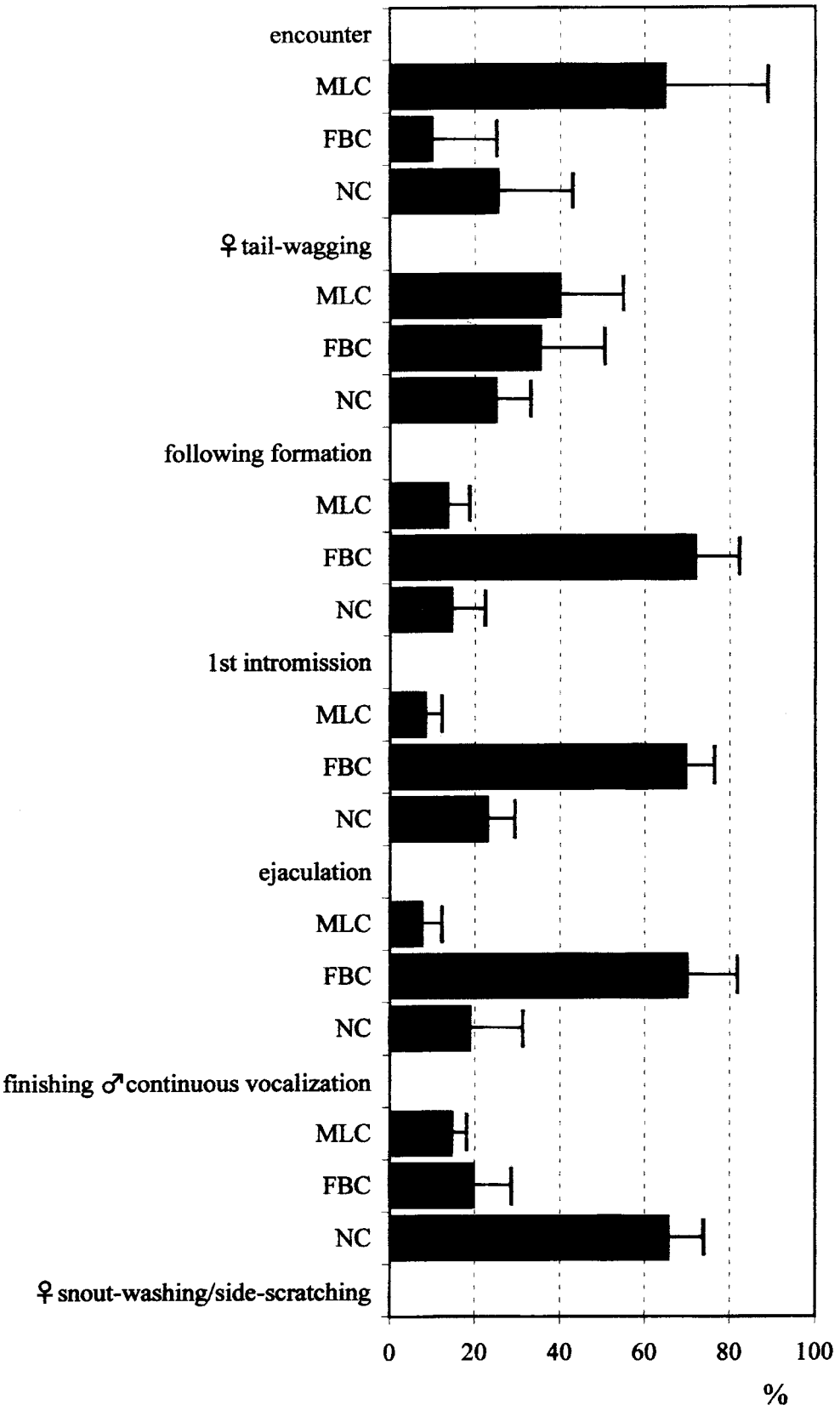

Fig. 1. A graph of Table 1. The vertical axis is a series of conspicuous behaviors and contact manners. The horizontal axis is percentage. The horizontal bars are the mean percentage of the time spent for each type of contact (n=8 trials) and the error bars are SEMs. Abbreviations are as for Table 1.

(1) Type of contact during each period

There were two kinds of contact involved with the following formation: multi-lateral contact (MLC) and front-and-behind contact (FBC). MLC involved one sex touching or moving across the other's flank, back, abdomen or head, including the snout (Figs. 4, 6, 11). Touching occurred all over the body. FBC involved one of the sexes moving behind the other to make a line, i.e. one touched the other from behind (Figs. 7–10; 12–14). During this behavior, one maintained contact with the other's tail, lumbar region, urogenitoanal orifice and its vicinity (hereafter just called 'UO') or heels from behind. FBC occurred just before and during the following formation and was either that the male followed the female (hereafter referred to as 'M to F') or that the female followed the male (hereafter referred to as 'F to M').

Table 1 shows the mean time until the occurrence of each conspicuous behavior and the mean percentage of time spent in MLC, FBC and non-contact (NC) during each behavioral period. Fig. 1 was constructed according to Table 1, and shows the changes in the ratio of the times spent in MLC, FBC and NC during each period.

When the ratios of the times spent in MLC, FBC and NC are compared for each period with the adjacent behavior (Fig.1), it is apparent that the proportion of time spent in FBC increased after following formation and was maintained until the male had finished continuous vocalization, at which time the proportion of NC time increased. The proportion of time spent in NC appeared to be lower than that for MLC and FBC during the period from first encounter to the finish of a male's continuous vocalization (Fig. 1).

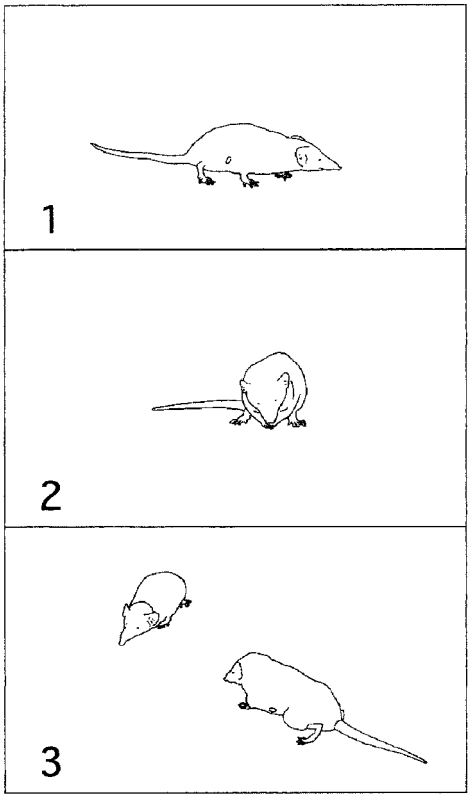

Fig. 2. From female exploration to male approach. 1. an exploring female, 2. a snout-washing female, 3. an orienting female and approaching male.

(2) Exploration and approach (Fig. 2: 1–3)

The rest of the results describe the details of these mating behavior sequences.

When a female was first placed in the tank she sniffed her immediate vicinity. She then moved slowly along the floor, while moving her snout quickly and sniffing (Fig. 2: 1). Three of the eight females engaged in some sort of scent marking. Two females rubbed their flank on the floor and one rubbed her throat in the same manner. Two females also performed UO marking. After exploring the tank for 4–5 min, a female began washing her snout (Fig. 2: 2). At this time, a male was placed in the corner furthermost from the female. In five of the eight trials, the male approached the female who was exploring the tank in the other corner. The female oriented her snout towards the male (Fig. 2: 3). In half of the trials, the female moved a few steps ahead of the male when he approached her, and she turned so that her snout faced his. In the other half of the trials, the female initially avoided the male, although her snout was orientated toward him, but they encountered each other soon afterward.

(3) Encounter and investigation (Fig. 3: 4–10; Fig. 4: 11–13; Fig. 5: 14–20)

In three of the trials, the male vocalized with a sound like that of a chirping bird when he first encountered the female. In two of the trials, the female vocalized when she first encountered the male (a), but the female did not vocalize in the other six trials (b).

(a) The scenario when a female vocalized at the first encounter

When a female vocalized toward the male with her mouth open and teeth bared (Fig. 3: 4), the male turned around, moved away briefly and then carefully approached the female again. When this happened, the female uttered vocal noises that changed from a metallic to a threatening sound. When the male approached her again, the female orientated towards him, moved forward, vocalized and then leaned backward. The male also vocalized. This scenario was repeated two or three times (Fig. 3: 5–6) until the male stopped retreating from the female (Fig. 3: 7). In a subsequent scenario, the male brought his snout close to the female even when the female vocalized (Fig. 3: 8), and in this case the female turned around. As the male touched the female again and again, the female began tail-wagging and moved closer to the male. When the snouts of the pair were close together, the female vocalized (Fig. 3: 9). Alternatively, both sexes vocalized or opened their mouths and bared their teeth at each other (Fig. 3: 10). During the repeated encounters and vocalizations, the pair sniffed each other's snout, face, ear and its vicinity (hereafter just called 'ear'), flank, lumbar region, root of the tail, inguinal region and UO (Fig. 4: 11–13).

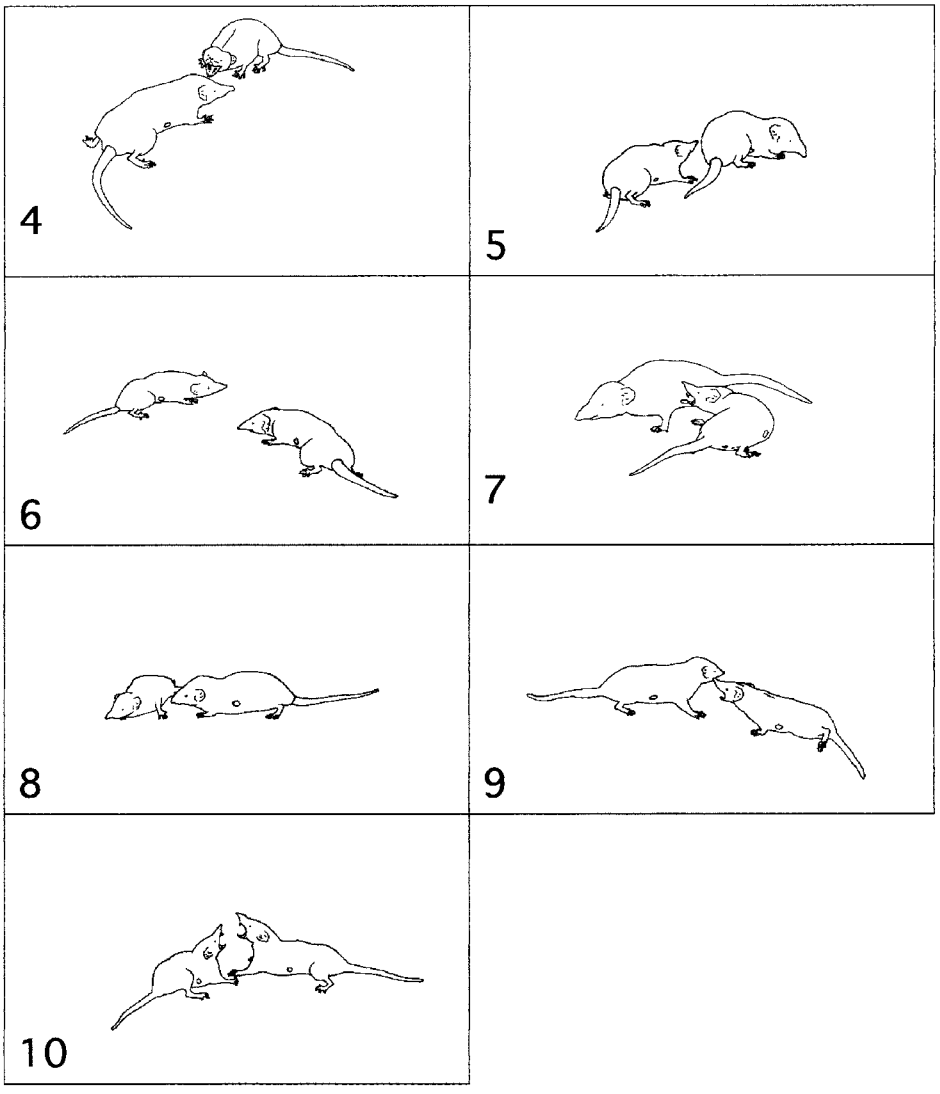

Fig. 3. From encounter to status battle. 4. a vocalizing female (back), 5. a retreating male (right), 6. an approaching male (right) again, 7. a male (back) standing against a vocalizing female, 8. a male (right) moving next to a female who is turning around, 9. a female (right) vocalizing again, 10. status battle.

When the male was frozen by the vocalization of the female (Fig. 5: 14), the female either touched the male (Fig. 5: 15), turned around in front of his snout (Fig. 5: 16), put her snout on his UO (Fig. 5: 17) or rubbed her flank on him (Fig. 5: 18). During these scenarios, the female commenced tail-wagging, or the frozen male wagged his tail, lifted his tail up and the female followed his tail with her snout (Fig. 5: 19). When the pair stayed close together, the female wagged her tail in a squat (Fig. 5: 20).

(b) The scenario when a female did not vocalize at the first encounter (Fig. 6: 21–24)

After the initial encounter, the pair crossed snouts (Fig. 6: 21) and sniffed each other from the neck to the trunk. The contact shifted from their snouts facing each other to their entire bodies crossing each other. One of the pair put their snout on the other's throat (Fig. 6: 22), and then moved it under their throat and along their flank (Fig. 6: 23) or UO (Fig.6: 24). The pair separated, re-approached and sniffed each other repetitively. The female or both sexes began to vocalize after this scenario. There was only one trial out of the eight in which mating occurred without prior vocalization. In this case, as soon as the encounter occurred, the female began tail-wagging and stayed close to the male. In three of the eight trials, the female approached the male. In these cases, the females continued their approaches and retreats without vocalization. When one of the pair approached the other in this scenario, they moved along the wall and encountered the other. Alternatively, the pair orientated as if one had listened to the other's footsteps or sniffed to traced the footmark on the floor.

In the period from the encounter to the female's tail-wagging, more than 80% of the time was spent in either MLC or FBC. More of this time was spent in MLC than in FBC; i.e. they touched each other's entire body more than

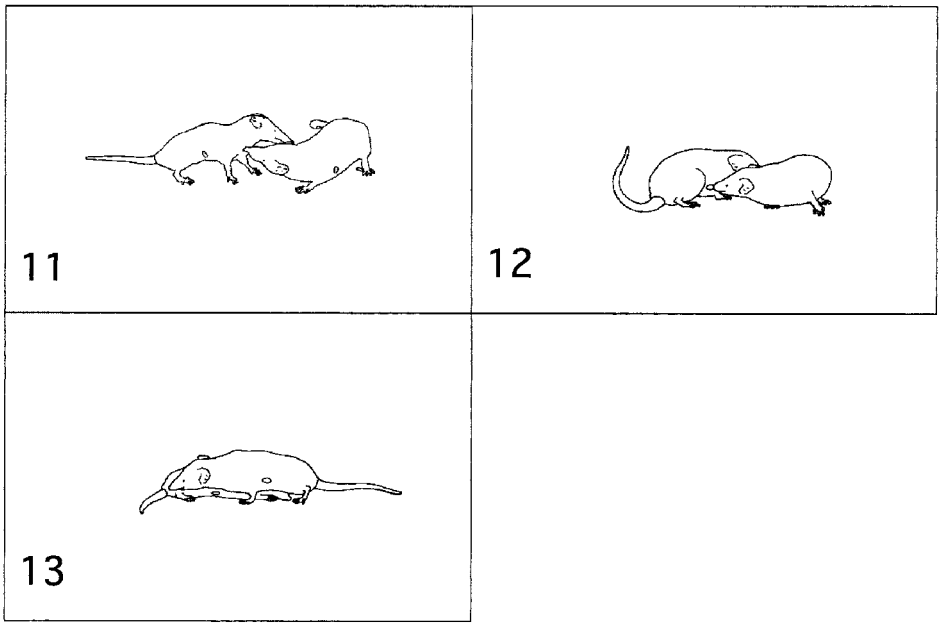

Fig. 4. Mutual investigation. 11. both sexes sniffing the heads of each other, 12. both sexes sniffing the flanks of each other, 13. both sexes sniffing the tail roots of each other.

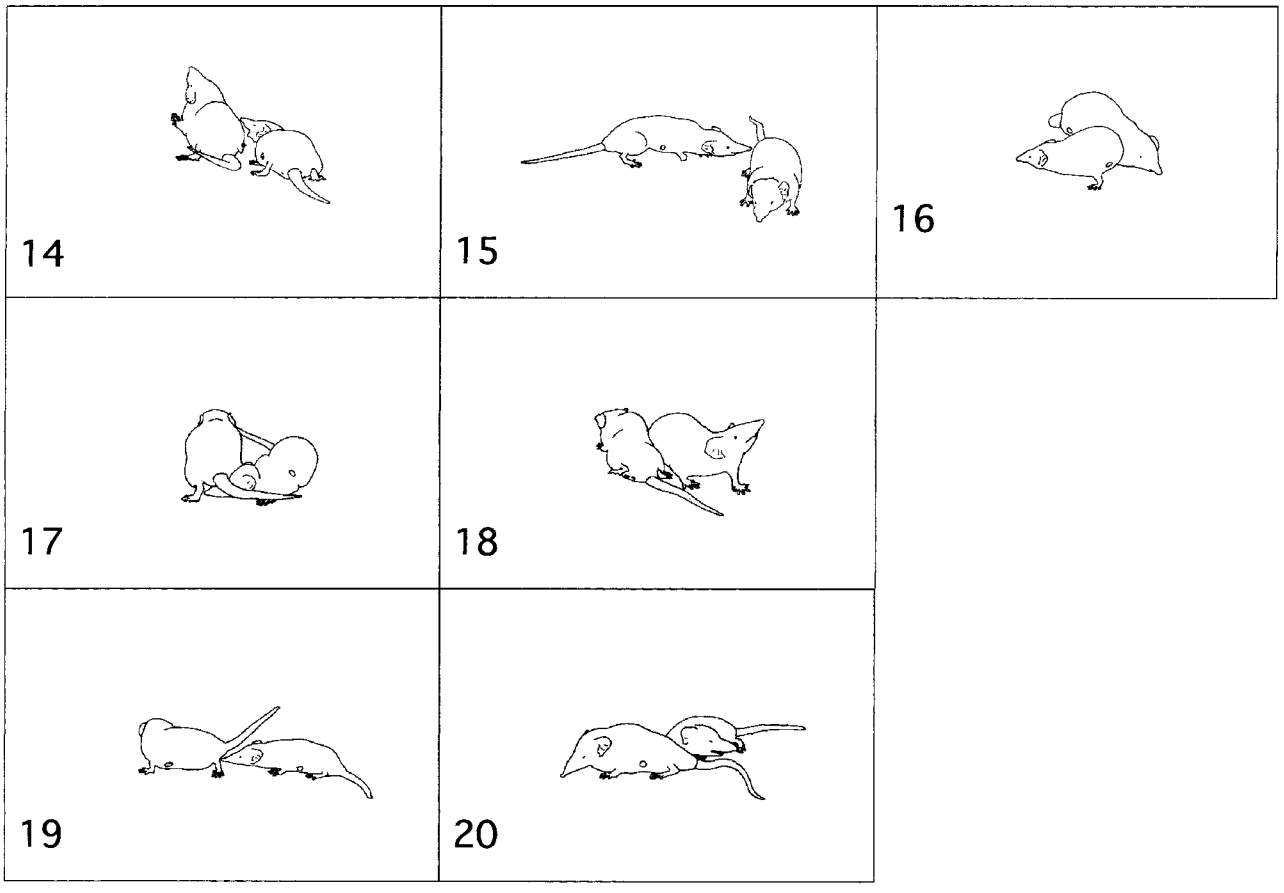

Fig. 5. A female vocalizing during the initial encounter. 14. a vocalizing female (right) and a stationary, frozen male, 15. a stationary, frozen male (right) and a touching female, 16. a female (front) turning around in front of a male, 17. a female (right) putting her snout on a male's abdomen, 18. a female (right) rubbing her flank on a male, 19. a female (left) lifting her tail and a male going after it, 20. a male (back) touching a female while she squats and wags her tail.

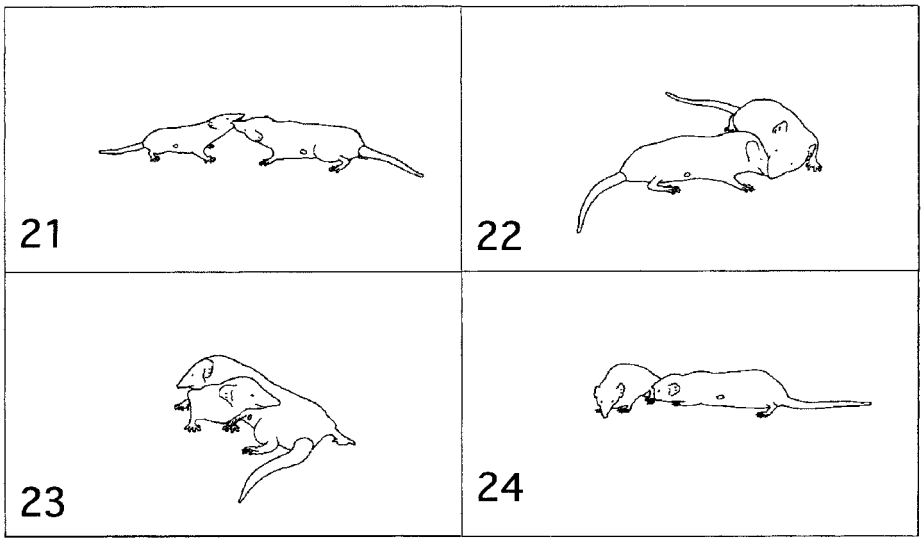

Fig. 6. A female not vocalizing during the initial encounter. 21. a male and female crossing snouts during the encounter, 22. a female (front) putting her snout on a male's throat, 23. a female (left) that had passed under a male's throat and moved close to his flank, 24. a male (right) putting his snout on a female's urogenitoanal orifice.

they specifically touched each other's lumbar region from behind (see Fig. 1).

(4) Tail-wagging to following formation (Fig. 7: 25–31, Fig. 8: 32–34, Fig. 9: 35–41, Fig. 10: 42–45, Fig. 11: 46-56)

Tail-wagging was mostly initiated by the female after the pair had touched and sniffed each other (Fig. 7: 25). When the pair's snouts faced each other, even if the female was tail-wagging in response to touching the male, the female vocalized and/or opened her mouth (Fig. 7: 26) and one or other of them turned around. Alternatively, the female put her snout on, and then under, the male's throat, and then passed her snout along his flank, just as for the encounter without vocalization. When only a female vocalized to the male, the male turned around and approached the female again. When only a male vocalized to the female, the female turned her head away from the male and moved away (Fig. 7: 27).

When a female did not receive the male as a follower, a status battle occurred. The frequency with which the female touched the male just before following formation was significantly higher than just after it (Table 2: $p<0.005$). This means that even if a female threatened a male, she touched him many times before the following formation commenced. The frequency with which a male turned around in the period from tail-wagging to following formation was significantly greater than in both the period from encounter to tail-wagging and the period from following formation to the first intromission (Table 2: $p<0.005$). Females tended to squat while they were tail-wagging (Fig. 7: 28). Nevertheless, when a male touched the female's tail or body, she moved ahead or turned around, both of which directed her lumbar region toward the male's snout. The male went after the female's moving tail (Fig. 7: 29). The female moved with a contracted body and arched back. The female's tail frequently touched the male's face (Fig. 7: 30). When the male's snout approached the root of the female's tail, the female lifted up her tail and the male directed his snout to her UO (Fig. 7: 31). He then touched her UO or inguinal region, including nipples (hereafter just called 'inguinal region'). When the male's snout approached the female's tail, it gradually moved from the tip to the root (Fig. 8: 32–33). Finally, the pair formed a line, with the female moving in front and the male following and touching the female's dorsal lumbar region (Fig. 8: 34).

The frequency with which a male touched a female just before following formation was significantly higher than it was just after it (Table 2: $p<0.05$). The increase in frequency of a male touching a female appeared to promote following formation between the pair.

After the repetition of touching and turning around, the female turned, with her tail touching the male, and began walking with short and straight movements, without vocalization or mouth-opening. This behavior also occurred as soon as the male vocalized or opened his mouth, after which the female turned around and faced the male in response to his touching her lumbar region.

After the following formation started, the tendency of females to squat increased. The male stimulated the squatting female (Fig. 9: 35) by vocalizing into her ear (Fig. 9: 36) and touching her forcefully. He then turned around and moved away from her. Alternatively, he lightly bit the female on her lumbar region or flank (Fig. 9: 37), scratched it (Fig. 9: 38), touched or bit her ear lightly (Fig. 9: 39), or touched her heel, inguinal region or UO (Fig. 9: 40). The female began to move again and the male followed her with his snout touching her lumbar region (Fig. 9: 41), UO (Fig. 10: 42–43), inguinal region (Fig. 10: 44), and/or heel. The male stopped when the female did (Fig. 10: 45) and moved in

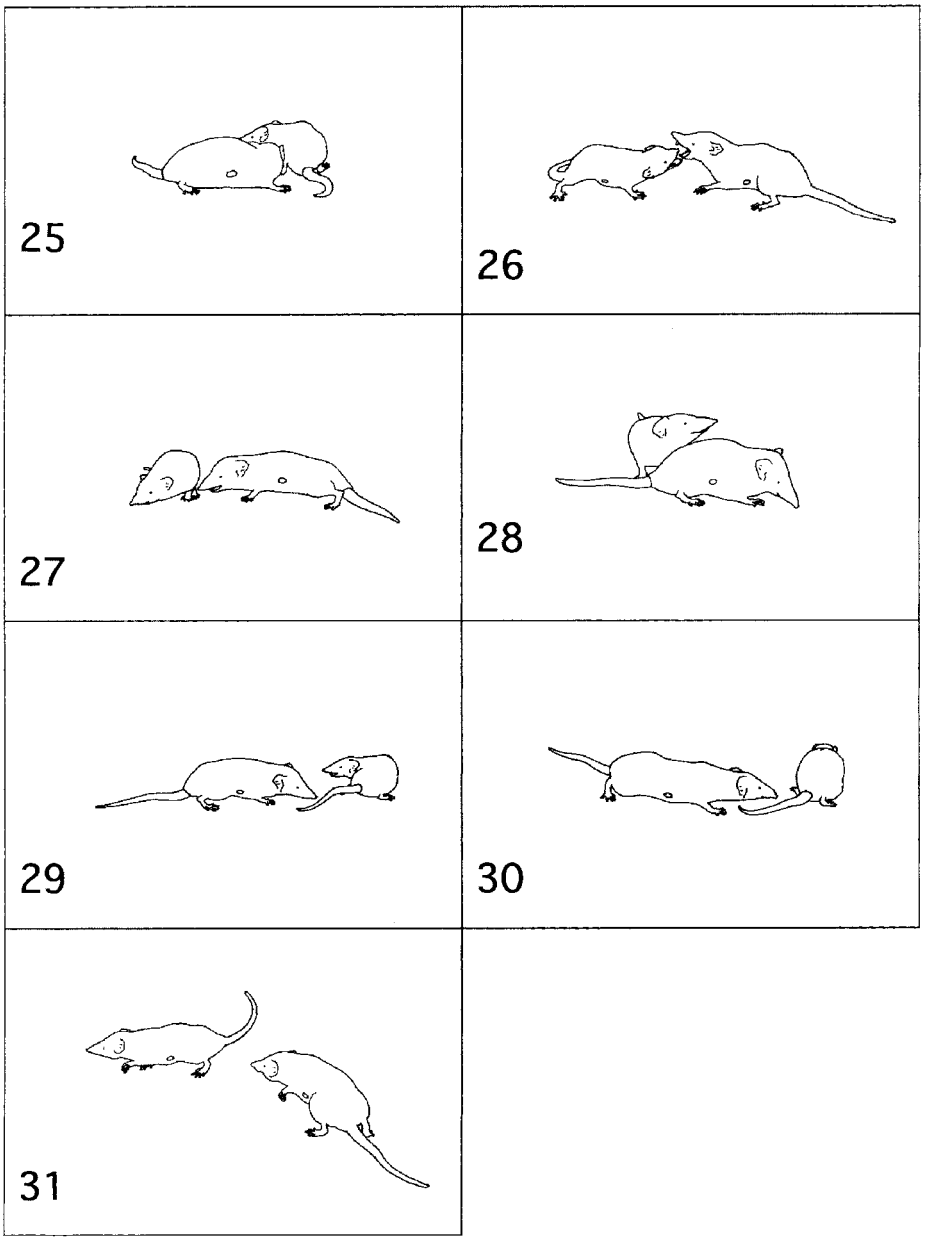

Fig. 7. The commencement of a female's tail-wagging and a male's going after her. 25. a tail-wagging female (back), 26. a status battle, 27. a vocalizing male (right) and a female turning around, 28. a squatting female (front), 29. a male (left) going after a moving female's tail, 30. a female's tail (right) touching a male's face, 31. a female (left) lifting her tail and a male going after her urogenitoanal orifice.

whichever direction she moved. If the female did not start to move again quickly, the male repeated the above stimulation. When the male stopped moving temporarily the female touched him. When they both stopped moving, they stayed in contact and when one started to move it touched the other to stimulate the recipient. When the female touched the male (Fig. 11: 46–47), she turned around in front of his snout, touched him with her tail, then turned her lumbar region toward the male (Fig. 11: 48–49). Alternatively, after turning around, the female (i) slipped through the male's flank from the front to the rear, or vice-versa (Fig. 11: 50), or passed under his body in the same way (Fig. 11: 51) and paused for a moment with her lumbar region in front of his snout, or (ii) touched the male with her tail and went across the front of the male's snout (Fig. 11: 52–56). The male directed his snout toward the female while she was doing this and then they both returned to the following formation again. The frequency with which the female touched the male during the period just before following formation was significantly higher than that just after it (Table 2: $p<0.05$).

Two females touched their males so many times after their encounter that in each case the male turned around and raised his tail, and the female followed the male (F to M) while touching his UO or inguinal region and, finally, his

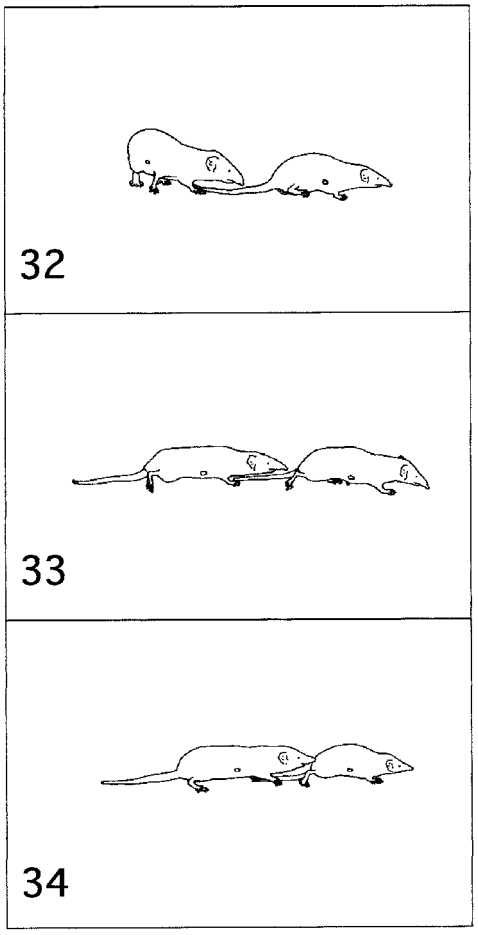

Fig. 8. Following formation. 32. a male (left) touching a female's tail, 33. a male (left) touching a female's tail root, 34. a male (left) following a female while touching her dorsal lumbar region.

dorsal lumbar region. The female wagged her tail before the F to M following formation. Following finished when the male touched the female's UO or inguinal region and, shortly thereafter, the male followed the female.

In the period from the commencement of female tail-wagging to following formation, the proportion of time spent in MLC to that spent in FBC was close to 0.5; i.e. they touched each other's whole body (Fig. 1).

(5) Mounting to intromission (Fig. 12: 57–62)

Sometimes a male quickened his walking pace and mounted the female (Fig. 12: 57). The mean duration between mountings was 91±37 s. When a male mounted the female and thrusted against her, his penis protruded from his UO. The female did not assume a posture of lordosis, even if mounting occurred at the beginning of the following formation. She changed direction and escaped from the male's hold. The male moved his body to the other side and commenced licking his protruded penis until it returned to its normal state (Fig. 12: 58). The female stopped moving in front of the male and squatted a little ahead of him. The male finished genital licking, got back on all fours and vocalized to the female giving a backward glance. The female turned around and the male followed her again. Since mounting had occurred, the female's arched back was sweating. The male repeatedly mounted the female while following her, and the female frequently stopped moving to squat and wag her tail. Then the male stimulated the female, as described in the previous section (vocalization, touching with his snout, scratching and biting lightly). When a squatting female was touched on her face by the male, she occasionally vocalized and pushed him off with her forepaw (Fig. 12: 59). If a female kept squatting, the male left momentarily, re-approached, touched her body, particularly her flank gland, and repeated the stimulation to let her move. If the male left the female and moved independently, the squatting female approached and touched the male. If the female moved, the male followed and mounted her while vocalizing. During the mount, the male occasionally bit the female's back fur (Fig. 12: 60). As the frequency of mounting increased, the female began to assume a posture of lordosis. As soon as the male touched the female's lumbar back or sides with his forepaws, she bent her back downwards. Depending on the individual, the female stopped moving and assumed a posture of lordosis when the male touched her UO.

The male displayed offensive behavior, even after intromission without ejaculation. This behavior involved the male following the female, stepping on her tail and biting her lightly, or scratching the lumbar region of her flank (Fig. 12: 61–62). Furthermore, the male caught up with the female's head as he followed, and he touched or bit her ear lightly. When the snout of the male reached in front of the moving female's ear, she vocalized or opened her mouth and turned her snout toward his. As the following developed, the male also vocalized or opened his mouth as soon as she prepared to give him a backward glance. The female either turned around before the male commenced vocalization or soon afterwards. After this, the female began moving again and the male followed her soon thereafter.

Intromission occurred after a mean mounting frequency of 14.4±2.3 times (range=2 to 22 times).

The proportion of time spent in FBC was greater than that of MLC in the period from following formation to first intromission (Fig. 1).

(6) First intromission to ejaculation (Fig. 13: 63–70)

At intromission, the male thrust his lumbar region forward vigorously and held the female's femurs firmly with his forepaws (Fig. 13: 63). When intromission did not result in ejaculation, the male released the female soon thereafter (Fig. 13: 64). Then the male licked his penis and the female squatted a little ahead of him (Fig. 13: 65). After intromission, the female rubbed her UO on the floor and licked her genital area in the same posture as the male did. The female always finished genital licking first and then approached the male (Fig. 13: 66). The male turned his head toward the female and responded vocally to the female's touching. In response, the female turned around and moved her lumbar region toward the male's snout.

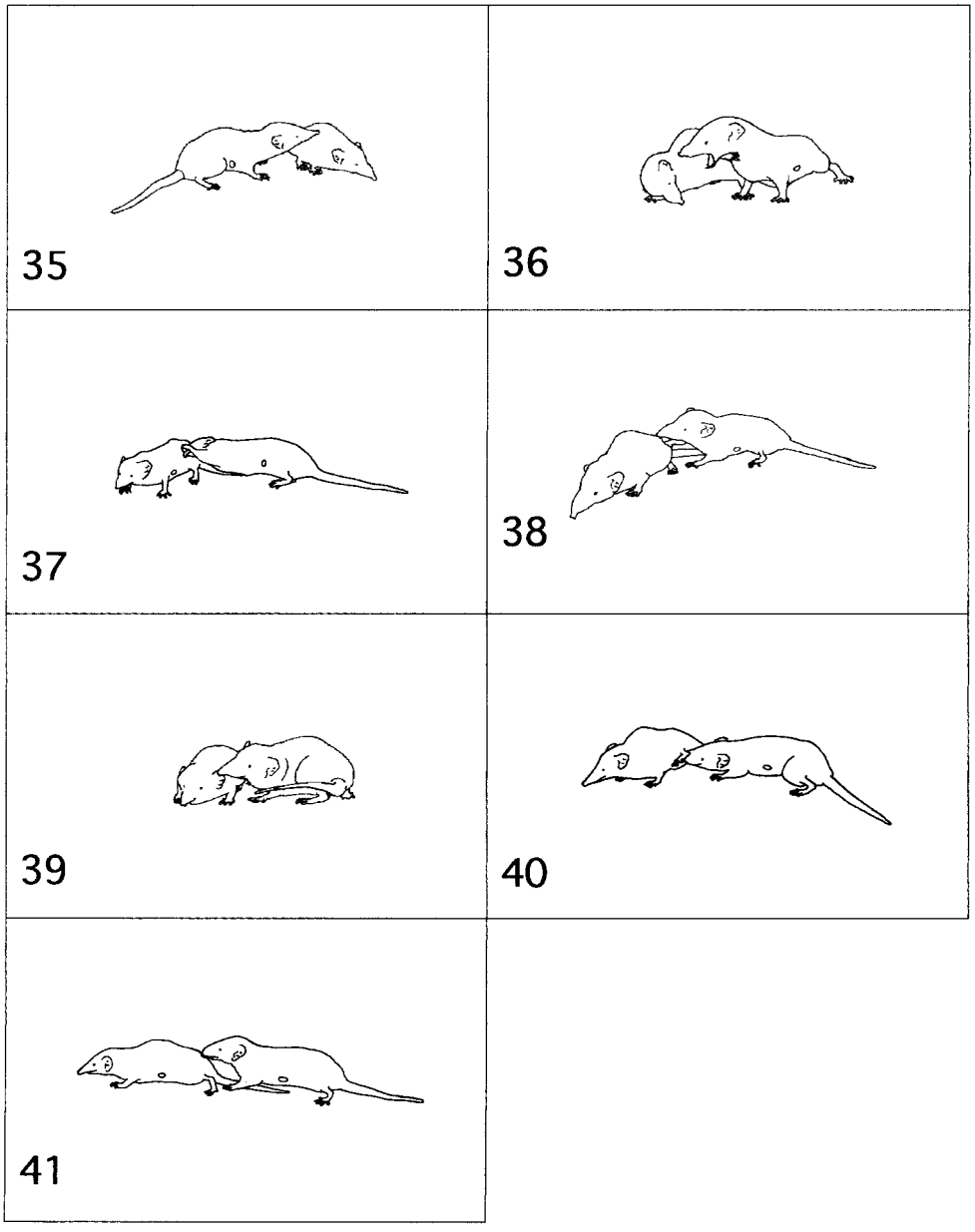

Fig. 9. A male stimulating a squatting female to move. 35. a squatting female (right) and a touching male, 36. a male (right) vocalizing into the ear of a squatting female, 37. a male (right) licking a female's lumbar side, 38. a male (right) scratching a female's lumbar region, 39. a male (right) touching a female's ear, 40. a male (right) touching a female's inguinal region, 41. both sexes forming following again.

Alternatively, the female turned without touching him, and the male turned his head toward the female and vocalized in concert with her footstep. In both cases, the male touched the female's lumbar region, the female moved, and the male commenced following the female again (Fig. 13: 67). The male vocalized and scratched and lightly bit the female before following her.

While the male was following, he continually touched the female to move her from her ongoing squatting behavior. When a female would not move by stimulation to the lumbar region, the male also touched her flank, neck, UO, inguinal region and heel. As soon as the male touched the female, the female gave him a backward glance, the male vocalized (Fig. 13: 68), and the female looked forward and moved ahead. In some trials, the female turned toward the male and vocalized or pushed his face with her forepaw. With continuous male touching, however, the female moved her lumbar region into the male's snout and moved again. The male followed the female while touching her dorsal lumbar region and the female touched his face or body using her tail (Fig. 13: 69). Both sexes continued following in such a manner until the intromission where the male reached ejaculation, (a mean of 3.3±0.4, and a range of 1–5, intromissions) (Fig. 13: 70). At the intromission with ejaculation, the pair

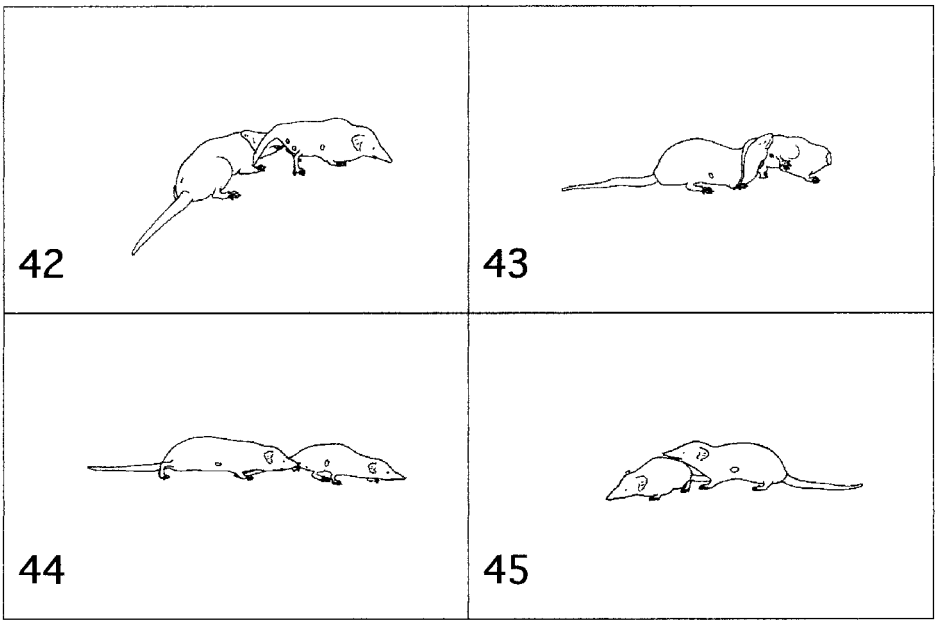

Fig. 10. A male stimulating a female's urogenitoanal orifice (UO) or inguinal region. 42. a male (left) touching a female's UO, 43. a male (left) licking a female's UO, 44. a male (left) touching a female's inguinal region, 45. a stationary female (left) and a male.

kept stationary for 5 to 6 s (mean=5.5±0.2 s). The male would not loosen his hold on the female during ejaculation. The male bit the female's back fur, held her femurs back with his forepaws and thrust his lumbar region forward deeply while his hindpaws were raised. Even if the female pawed the floor, she was unable to separate from the male. The male stood on his tail and the female balanced on her forepaws and abdomen during ejaculation. The pair occasionally lost balance and fell down sideways.

(7) Male offensive behavior after ejaculation (Fig. 14: 71–78)

Following ejaculation, the male shook the female by biting her back fur (Fig. 14: 71). Then the male licked his penis (Fig. 14: 72). The female rubbed her UO on the floor, licked it, and then approached the male. After licking his penis, the male bit and pulled the female's back, lumbar region, flank, tail, hindlimb, neck or ear (Fig. 14: 73–75), or scratched her lumbar region and flank (Fig. 14: 76). His biting was not too hard, as his incisors did not penetrate her skin. Also, while the female moved ahead of him, the male lightly bit her lumbar region, ear and face. When the male followed the female he vocalized continuously except while biting her or licking his genitals. The male's continuous offensive behavior and vocalization ranged from 9 to 168 s (mean=97±20 s). During this behavior, the female moved her lumbar region toward the male, wagged her tail forcefully against him, turned her head forward after a brief backward glance, and continued to move ahead. When the male separated from the female, the female squatted (Fig. 14: 77) and after a while usually approached him again. The male vocalized when the pair's snouts were facing each other (Fig. 14: 78), and the female turned around, wagged her tail and squatted. The male's offensive behavior was persistent and was displayed in preference to following. In six out of eight trials the female received the male's offensive behavior with few counter offensives. In the other two trials, the female bit the male's tail when his offensive behavior began to decline. In response, the male ceased his offensive behavior, wagged his tail and moved forward. In the trials where the female did not display counter-offensive behavior, she began to move independently when the male's offensive behavior subsided, but when the male touched her she continued her tendency to squat. After that, the proportion of continuous contact time between the pair markedly decreased; non-contact (NC) occupied more than 50% of the period from when the male finished continuous vocalization until the female commenced snout-washing/side-scratching (Fig. 1).

(8) Scent marking after ejaculation (Fig. 15: 79–83)

Following the male's continuous offensive behavior, the male rubbed his abdomen (Fig. 15: 79) or UO (Fig. 15: 80) on the floor, or moved backwards and forwards on the wall and floor with his entire flank, including his flank gland. (Fig. 15: 81–83). Conversely, the female rubbed only her UO on the floor, except for one of the eight females who rubbed her entire flank on the wall and floor. Both sexes scratched their sides, washed their snout, licked their genitalia and excreted.

After their scent-marking behavior, the pair moved quickly in a curved line. It looked like strolling in the tank. When the snout of one happened to face the other's, they both let their snout tips meet momentarily and then passed each other. The female continued her tendency of tail-wagging and squatting when the male touched her, and the female occasionally approached the male, touched him and then moved away. Nevertheless, the male didn't follow or

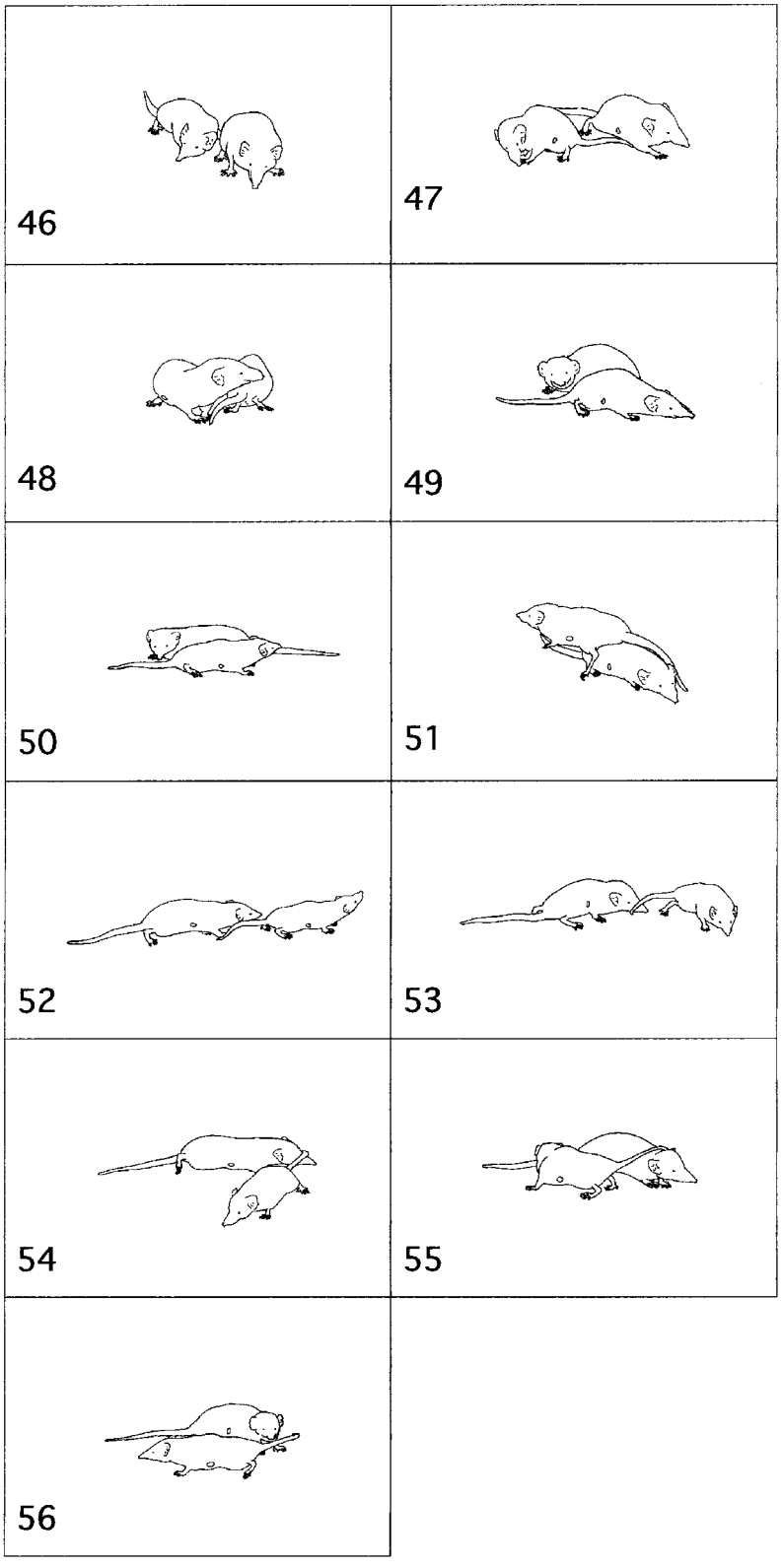

Fig. 11. A female stimulating a stationary male. 46. a female's (left) flank touching a male, 47. a female's (left) tail touching a male, 48. a female (left) turning around in front of a male's snout, 49. a female (front) moving along a male's flank and then leaving his lumbar region, 50. a female (front) slipping along a male's flank, 51. a female (underneath) passing under a male, 52. a female's tail (right) touching a male's neck, 53. a female's tail (right) winding around a male's snout, 54. a female's tail (right) winding around a male's face, 55. a female's tail (left) winding around a male's neck, 56. a female (front) moving away from a male's snout.

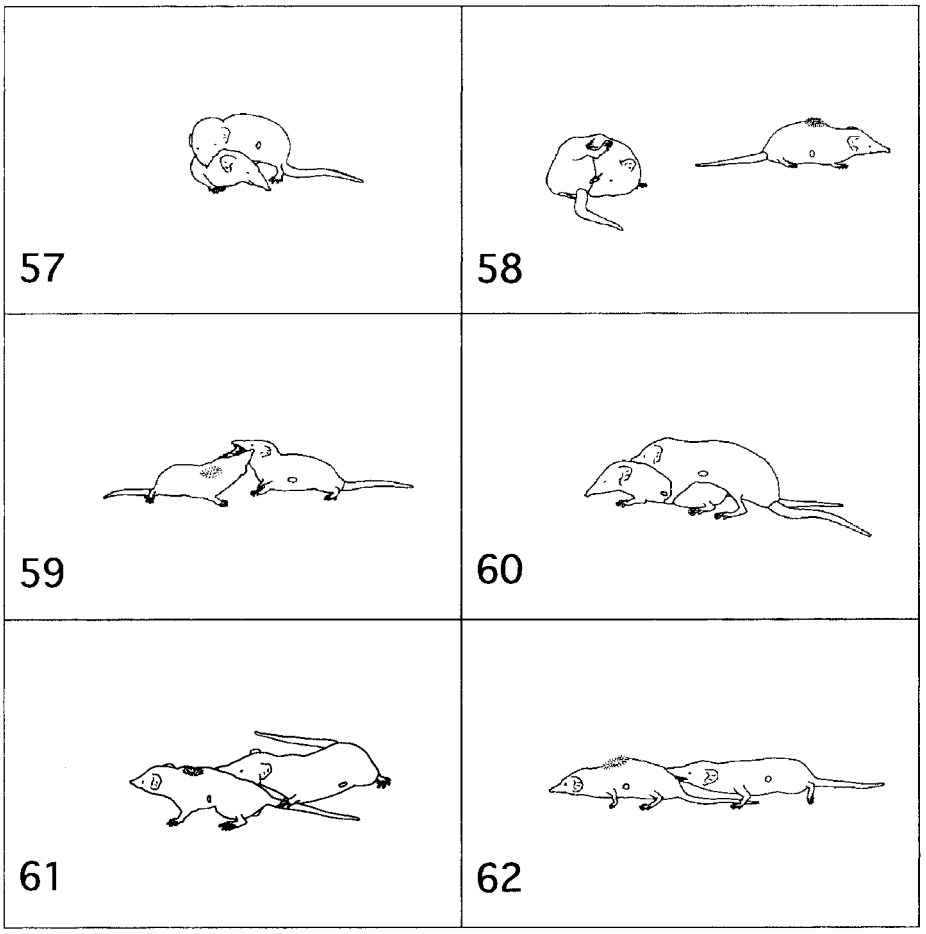

Fig. 12. A first-time mounting male and a female sweating on her back. 57. the first mounting, 58. a male (left) licking his penis and a female squatting in front of him, 59. a female (left) pushing a male's face, 60. a male (upper) biting a female's back fur during mounting, 61. a male stepping on a female's tail (right), 62. a male (right) biting a female's dorsal lumbar fur.

attempt to mount the female any longer.

(9) Subsequent observations (Fig. 16: 84–85)

A male ejaculated only once in a trial. After a male finished post-ejaculatory offensive behavior and scent marking, he tended to remain stationary (Fig. 16: 84). The movement, or lack thereof, of one sex was mostly independent of the other. If the strolling shrew touched or grazed the other, the recipient turned their snout towards the actor (Fig. 16: 85) and followed it, but the pair quickly separated and resumed their independent behaviors. The male did not follow the female any longer and their snout-washing, genital licking and side scratching were performed independently until the observation was over. However, the female strolled toward the male when he was still, or moved around him, sniffing the air.

When the author washed the inside of the tank with hot after each observation, at least two distinctive odors were noticed. The odors adhering to the inside of the glass tank smelled like valeric acid and musk.

DISCUSSION

(1) The timing of touching

The shrew commenced following behavior when a male and female touched each other, and copulation only occurred after continuous following. The MLC subsequent to an encounter was probably the main stimulation that motivated following formation. A hormonal change could have caused an increase in the proportion of FBC after the beginning of female tail-wagging. The adrenal glands maintain female sexual potency or are related to the transition from aggressiveness to receptivity (Rissman *et al*., 1987). Male touching of the female lumbar region, flank, UO, inguinal region and other areas could be one of the important factors promoting hormonal changes in the female.

(2) Encounter to mutual investigation

The behavioral depression of the house musk shrew is considered weak in a novel environment (Tsuji and Naruse, 1985). In the present study, a female moved continuously for four or five minutes when she was first placed into the glass tank. After becoming accustomed to the tank, she washed her snout.

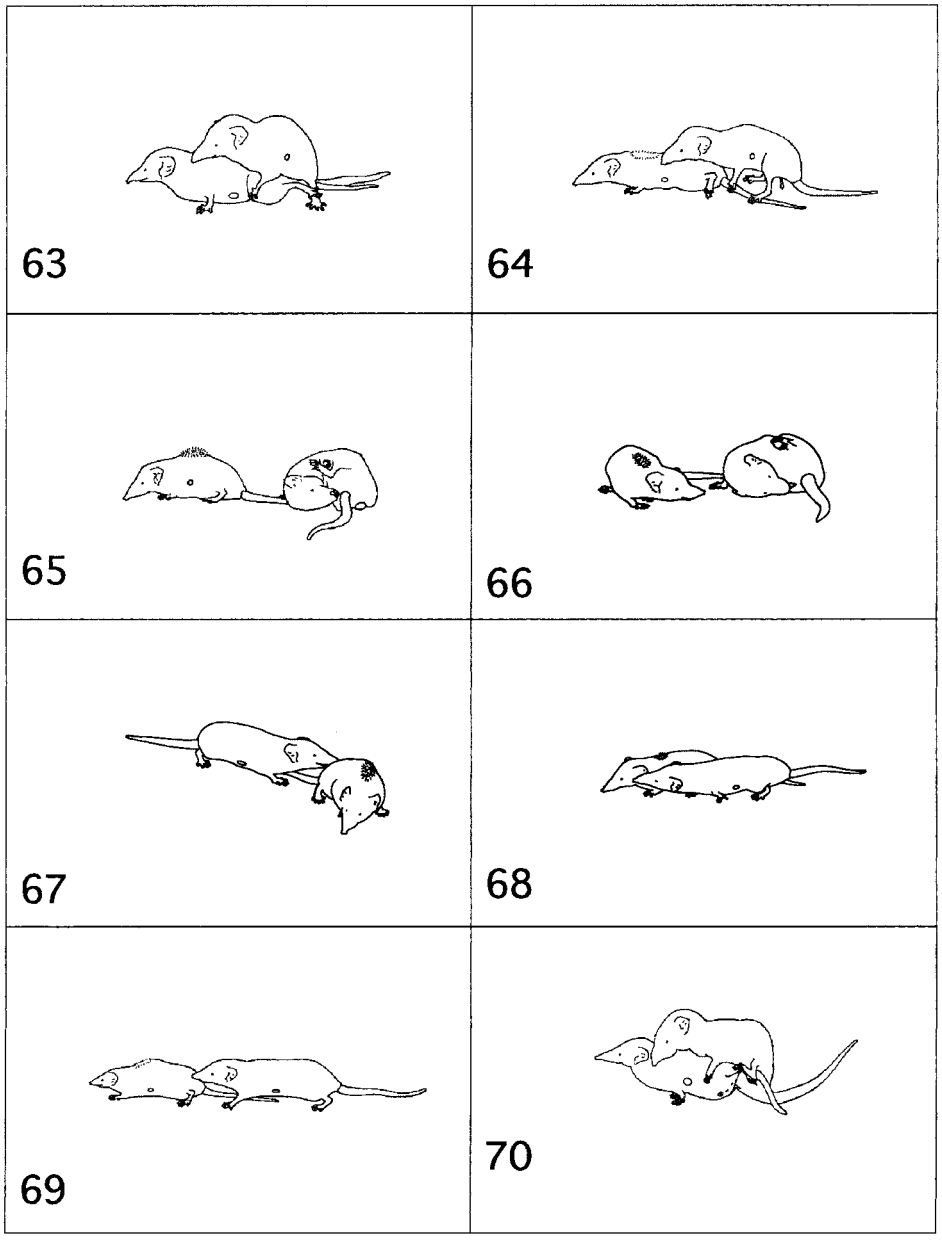

Fig. 13. Intromission to ejaculation. 63. an initial intromission, 64. a male (right) releasing a female soon after intromission, 65. a male (right) licking his penis and a female squatting in front him, 66. a female (left) approaching a male licking his penis, 67. the resumption of following, 68. a male (front) vocalizing to a female who is giving him a backward glance, 69. a female's tail (left) touching a male's chest, and a following male touching the female's dorsal lumbar region, 70. intromission with ejaculation.

(a) When a female vocalized at the initial encounter

Kawano (1992) stated that the house musk shrew regularly displays aggressive behavior in a laboratory setting and that encountering a conspecific in this environment could induce fear. According to Tsuji (1989), the role of male vocalization and tail-wagging is to pacify female aggressiveness. In the present study, a male turned around in front of a female's snout to avoid the female's threatening vocalization.

Kitoh and Ohta (1985) stated that there were sinus hairs on the snout, under-jaw, cheek, and forelimb of house musk shrews. In the present study, it was observed that when a male turned around in front of the female to leave her, or when a female touched a male and then moved away from him, that the former reflexively directed its snout toward the latter. When the pair was close together, the sinus hairs could have touched each other without close body contact. It also appears that when one of the pair moved their snout from the head to the trunk of the other that both were released from the stress by facing each other, and that this touching to the trunk but not the head facilitated the development of the sexual interaction.

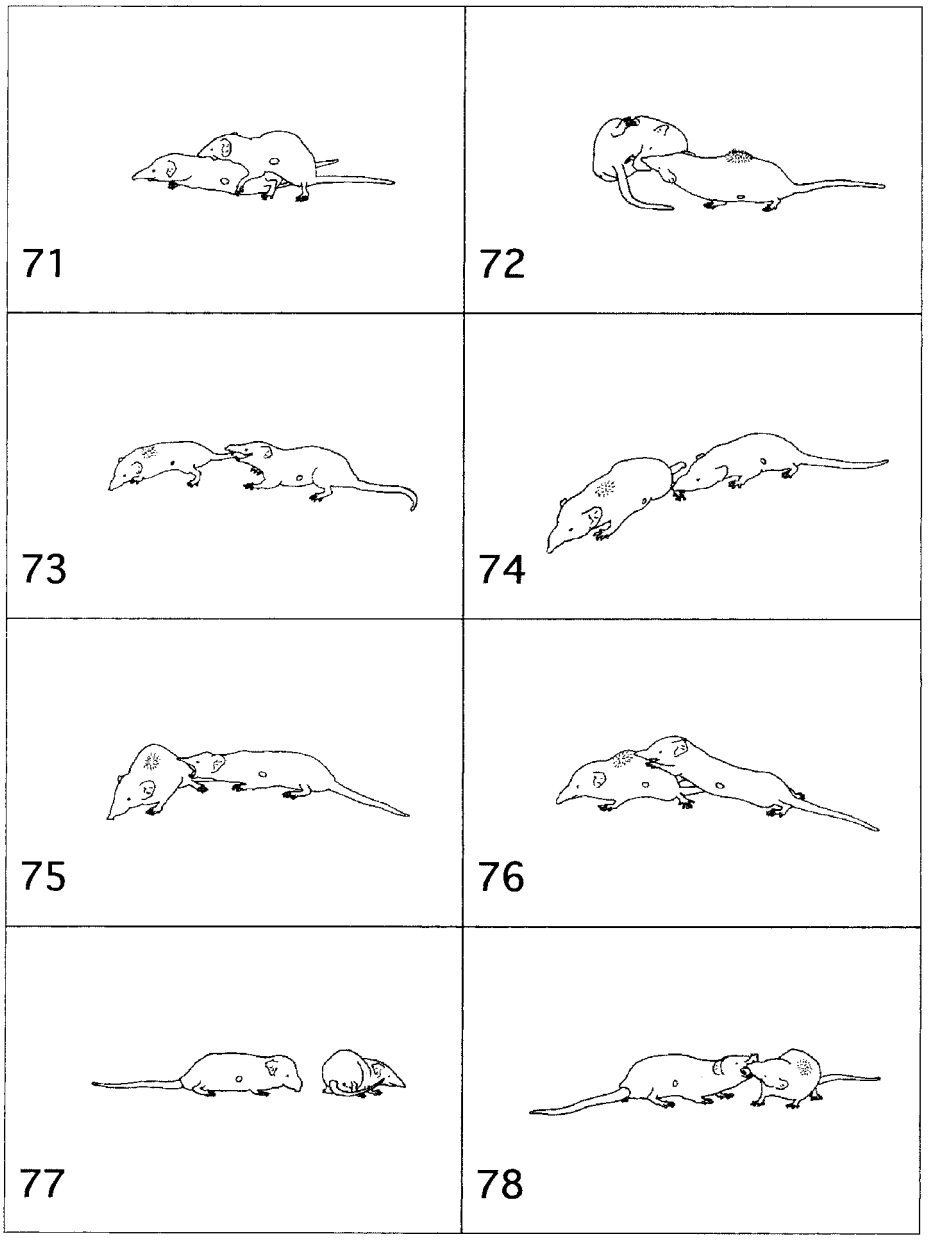

Fig. 14. A male snapping at a female and a female maintaining receptivity. 71. a male (upper) biting a female's back fur and shaking her, 72. a male (left) licking his penis and a female approaching him, 73. a male (right) biting and pulling a female's tail, 76. a male (right) scratching a female's dorsal lumbar region, 77. a male (left) touching a squatting female, 78. a vocalizing male (left) in a moment of the encounter.

(b) When a female did not vocalize at the initial encounter

When one of the pair put its snout on the other's chest it temporarily interrupted the motion of the recipient. The actor could avoid offensive behavior from the receiver and develop the interaction between them with this behavior. When one touched the other's flank, the recipient reflexively turned its snout and tail to the side that the actor touched, and simultaneously curved their trunk to the other side. This action resulted in the pair being in a comma-like position, facing in opposite directions, which probably enabled them to avoid offensive behavior and helped to develop their interaction.

According to Rissman (1987), female tail-wagging is an indicator of her receptivity. Sometimes, however, a male wags his tail, when she is following him, and so tail-wagging could indicate that an individual becomes the front of the line in the following formation.

Smell and touch are probably similarly important for the shrew in developing a relationship with a new mate. When the snout of an individual touches another, they smell and touch each other simultaneously. After the contact of the initial encounter, the pair touch and sniff each other in a comma-shaped arrangement. The snout of each individual touches the other's snout, face, flank, lumbar region, root of

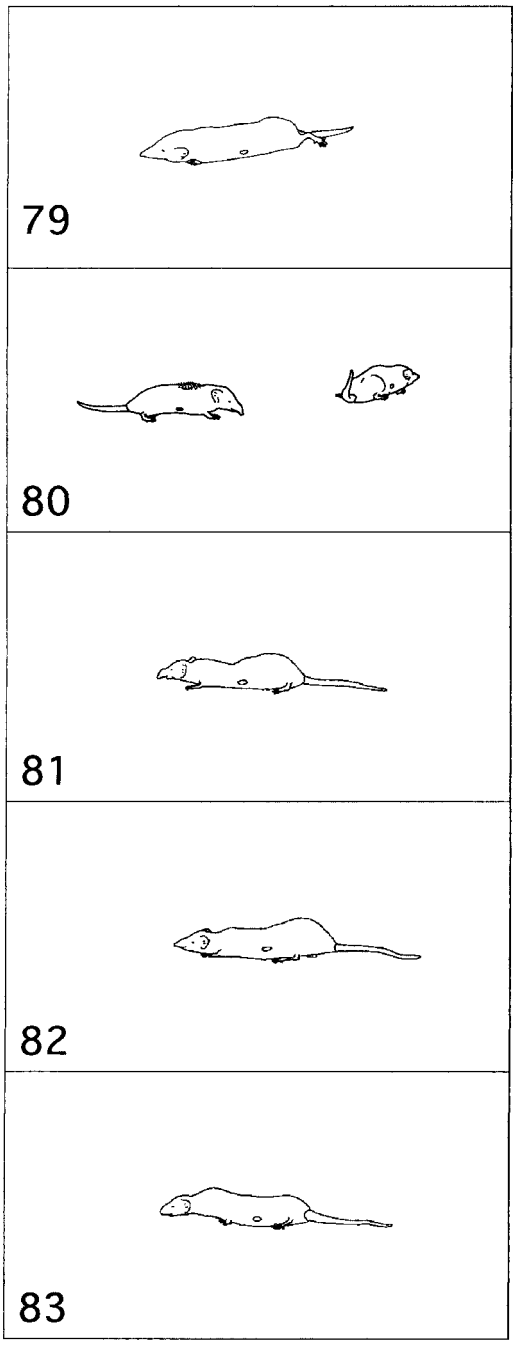

Fig. 15. Male scent marking. 79. a male rubbing his abdomen on the floor, 80. a male (right) rubbing his urogenitoanal orifice on the floor with his tail rolled up, 81. a male rubbing his flank on the wall, 82. a male drawing his body backward with his flank on the wall, 83. a male pushing his body forward with his flank on the wall.

the tail, inguinal region and UO. There are apocrine glands and sebaceous glands on the rear of the ear, and other large sebaceous glands and many sudoriferous (sweat) glands over a musk shrew's body (Dryden and Conaway 1967, Kitoh and Ohta 1985), and these glands could be important olfactory indicators in sexual encounters. Furthermore, four kinds of musk odors have been identified on the

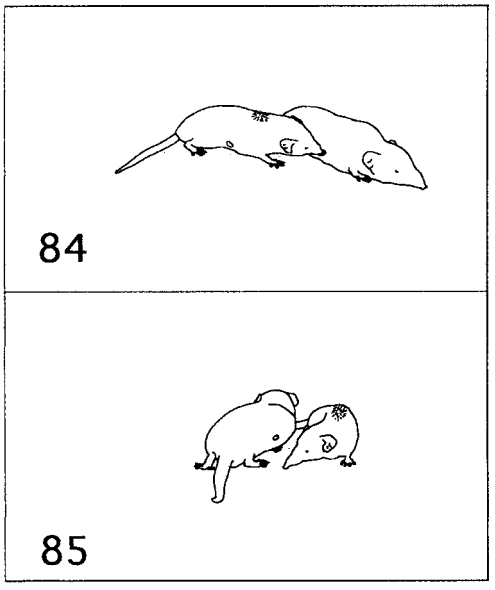

Fig. 16. After a male's scent marking. 84. a stationary male (right), and a female putting her snout tip on the male's flank gland, 85. a female (right) with a backward glance as the pair pass each other.

flank gland of this shrew (Watanabe, 1985) although, according to Dryden and Conaway (1967), the musk odor is not restricted to this gland. Even so, the olfactory organ has a well-developed structure (Kitoh *et al*., 1985). As another example of possible olfactory effects, Rissman (1987) found that a male's soiled bedding reduced the period between an initial encounter and tail-wagging by a female.

As well as smelling, both sexes touched the flank, inguinal region and UO of the other with their snout or mouth. This would not only have physically stimulated the recipient but would also have chemically stimulated the actor via the olfactory, vomeronasal, and gustatory organs. In particular, the extremely quick motion of the snout is associated with the function of the vomeronasal organ (Matsuzaki *et al*., 1993).

Male and female musk shrews probably approach each other from all sides in order to engage their somatic, chemical and auditory senses.

(3) Tail-wagging to following formation

A male's activity appears to be the more prominent during this period because of a female's squatting. However, a female touched a male with her tail in such a way as to encourage him to follow her (Table2).

After a female started tail-wagging, the pair would often vocalize, face each other with their snouts forward and teeth bared, and one or the other would turn around. In this study, this action is termed 'status battle' because it appears that this interaction helps the pair to decide which individual turns around.

The vocalization of the male appears to be an ordering call to let the female be the front of the following formation.

The force driving the mating sequence would act on the two sexes at a time and practice the fixed reproductive plan

of this species.

The M to F following in this study is interesting to note as a behavior of a coitus induced ovulator. This kind of behavior was described by Naik and Dominic (1970) as "male-like mounting", and by Tsuji (1989) and Kawano (1992) as "mating-like behavior". This phenomenon requires further investigation in the house musk shrew.

(4) Mounting to intromission

The frequency that a male touched the female between the following formation and the first intromission was not significantly different from that between the first intromission and ejaculation (Table 2). Nevertheless, the intensity of touching by the male to the female appeared to increase in the latter period.

When the female approached the male, she put her lumbar region in front of his snout, and then she moved away from him. This behavior is also observed in the caravan formation of a mother musk shrew bringing back its offspring to the nest (Tsuji and Naruse, 1984). The caravan formation between a mother and its offspring is not only to care for the offspring, but also to provide the young with early experiences in exploring and extending their environment (Tsuji and Naruse, 1985).

The reflexive response of one individual touching their mate with their snout, and that leading to separation and following, is an effective behavior to promote continued touching.

The proportion of the time spent in FBC between following formation and first intromission was distinctly higher than that of MLC and NC (Fig. 1). This indicates that the contact manner has changed from the multi-lateral to one-sided touching from behind and that the type and region of touching is important for stimulating following. However, the role of touching should be considered in conjunction with continuous olfactory stimulation.

(5) First intromission to ejaculation.

More than 80% of the touching from the first intromission to ejaculation was FBC (Fig. 1), where both sexes primarily touched the caudal region of the other's body. Even when there was a status battle, or threatening or ordering vocalization, turning and FBC facilitated following behavior.

When a male mounted, the female assumed the position of lordosis; she bent backward and raised her head and tail as soon as the male put his forepaws on her lumbar region. It is probably essential for reaching intromission that the female's UO, which is normally set horizontally, becomes vertical instantaneously.

Taking into account that the sebaceous and sudoriferous glands concentrate around the UO (Kitoh and Ohta, 1985), a male's touching of a female's UO with his snout tip or mouth and the male's penis touching the female's UO are probably directly related to the increase of the female's receptivity.

(6) Male offensive behavior after ejaculation

The term "post-ejaculatory attack", coined by Tsuji *et al*. (1999), refers to the same male offensive behavior after ejaculation described in this study. After finishing ejaculation, a male behaved offensively with continuous vocaliza-

Table 2. The differences in contact frequency for conspicuous behaviors according to the development of mating behavior.

contact manner	counting period of contact	CF from ♀ to ♂	significancy	CF from ♂ to ♀	significancy
MLC	encounter → ♀ TW	4.6 ± 2.0		3.6 ± 0.7	
with snout or	♀ TW → FF	14.9 ± 2.8	p<0.025 N.S.	16.9 ± 5.2	p<0.01 N.S.
forepaw	FF → 1st intro	7.3 ± 3.6		36.3 ± 10.3	
FBC with snout	encounter → ♀ TW	1.0 ± 0.8		0.1 ± 0.1	
to UO or	♀ TW → FF	1.3 ± 0.9	p<0.01 p<0.005	6.5 ± 3.4	p<0.005 N.S.
inguinal region	FF → 1st intro	0.0 ± 0.0		4.5 ± 1.7	
TC	encounter → ♀ TW	0.6 ± 0.4		1.1 ± 0.7	
with lumber	♀ TW → FF	8.5 ± 1.6	p<0.05 N.S.	4.1 ± 1.5	p<0.005 p<0.005
region or tail	FF → 1st intro	7.1 ± 2.7		0.5 ± 0.4	
total of every	encounter → ♀ TW	6.0 ± 2.7		4.9 ± 1.0	
kind of contact	♀ TW → FF	25.9 ± 2.3	p<0.01	27.8 ± 5.0	p<0.005
in each period	FF → 1st intro	14.4 ± 5.1	p<0.05 N.S.	41.3 ± 10.4	N.S. N.S.
	1 st intro → ejaculation	3.0 ± 1.0		10.7 ± 2.6	

The contact manner and frequency of conspicuous behaviors, including the encounter, ♀TW, FF, 1st intro and ejaculation are shown. In the transition from the encounter to FF, via ♀TW, the contact manner of both sexes is multi-lateral and CF increases. After FF, CF from ♂ to ♀ is maintained and the female no longer touches the male's UO. Data are means ±SEMs.
♀TW: female tail-wagging, FF: following formation, 1st intro: first intromission, CF: contact frequency, MLC: multi-lateral contact, FBC: front-and-behind contact, UO: urogenitoanal orifice, TC: turning contact; i.e. one individual turns immediately in front of the other's snout with their lumbar region or tail.
p<0.01, 0.05, 0.025, or 0.005: the alpha level used in Wilcoxon signed rank tests
N.S.: not significant

tion to the female and anyone near her in a 'fit of anger'.

When the male approached the female in apparent anger, the female moved forward with vigorous defensive tail-wagging, as also noted by Tsuji (1989), to avoid the offensive behavior and maintain her receptivity, which did not appear to subside with the offensive behavior.

(7) Scent marking after ejaculation

Scent marking by the male is probably a hormonal phenomenon and appears to indicate the finish of mating behavior. It is under control of the genital gland (Balakrishnan *et al*., 1984; Rissman and Bronson, 1987; Tennant *et al*., 1987). Conversely, the female squats after ejaculation and maintains receptivity when the male touches her. Hence, the female is receptive to new mates after the male has ejaculated (Dryden, 1969; Naik and Dominic, 1970).

The secretion from the flank gland adheres to whatever it touches. Therefore, the secretion is probably important both for conspecific recognition and as a guidepost. The excretion of feces and urine is observed frequently before and after mating behavior (Balakrishnan and Alexander, 1976). The excretion might also include components of things in the local environment.

(8) Subsequent behaviors

After scent marking, each sex strolled in the tank, sniffed the surrounding air and/or rested, which might have aided in shifting their efforts away from mating behavior. The odors adhering to the inside of the glass tank smelled like valeric acid and musk, which are quite different from the odor of excretion. These odors were probably emitted from the skin of the animals.

Conclusion

The mating behavior of the domesticated house musk shrew was observed under laboratory conditions. After a series of movements that involved both sexes forming a line, one behind the other, a male mounted the female and reached ejaculation. The role of touching by both sexes in a series of mating behaviors has been discussed.

When a sexually mature conspecific male and female encountered each other, they displayed a fixed repetition of approaching and distancing behavior. In the trials, as soon as one of the pair touched the other and then separated from the receiver, the latter reflexively turned their snout toward the former. This kind of touching action and response continued with one sex following the other. Multilateral contact caused the following formation and one-sided front-and-behind contact maintained the following.

Offensive behaviors, such as vocalization, initiating a status battle and snapping, were also performed by an individual while still touching the other and being responded to. Such a relationship could indeed cause the following formation, and the development of an individual's physiological state in the relationship could maintain the following behavior. In the mating behavior of this species, contact between the sexes after an encounter leads to a following formation and eventually to copulation.

If caravan formation between a mother and her offspring is related to the juveniles' initial experience, such behavior could plant the animal's way of developing a relationship with another conspecific in the offspring. The qualities of following, touching and separation appear in mature individuals. In this sense, one of the sexes could prevent another's deviation from this way of reaching copulation. Simultaneously, these qualities probably make the relationship between individuals closer, as it is a force that drives a series of mating behaviors and ultimately drives reproduction.

When an individual touches another with their snout tip, sniffing also occurs simultaneously. Orientation to steps and specific responses to a mate's vocalization would also involve an auditory response. It is important therefore, that the roles of the olfactory, vomeronasal, and auditory senses of both sexes are considered in further studies.

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REFERENCES

Balakrishnan M, Alexander K M (1976) Hormonal control of scent marking in the Indian musk shrew, *Suncus murinus viridescens* (Blyth). Horm Behav 7: 431–439

Balakrishnan M, Annielet Shelley T, Alexander K M (1984) Role of Progesterone on the Control of Scent Marking in *Suncus murinus viridescens* (Blyth). Physiol Behav 33, 415–419

Dryden G L, Conaway C H (1967) The origin and hormonal control of scent Production in *Suncus murinus*. J Mammal 48: 420–428

Dryden (1968) Growth and development of *Suncus murinus* in captivity in Guam. J Mammal 49: 51–62

Furumura K, Kuriyama T, Ohta K, Yokoyama A (1985) In "*Suncus murinus*: Biology of the laboratory shrew", Ed by K Kondo, Japan Scientific Society Press, Tokyo (In Japanese), pp 126–139.

Kawano K (1992) Aggressive behavior of the domesticated house musk shrew (*Suncus murinus*) in inter-male, inter-female and heterosexed interaction. J Ethol 10: 119–131

Kawano K (1996) Effects of isolation on aggression in the domesticated musk shrew (*Suncus murinus*). J Ethol 14: 77–81

Kitoh J, Sugiura Y, Yoshida M, Kuramoto K, Satoh M (1985) In "*Suncus murinus*: Biology of the laboratory shrew", Ed by K Kondo, Japan Scientific Society Press, Tokyo (In Japanese), pp 295–310

Kitoh J, Ohta K (1985) In "*Suncus murinus*: Biology of the laboratory shrew", Ed by K Kondo, Japan Scientific Society Press, Tokyo (In Japanese), pp 176–184

Kondo K, Oda S (1977) Domestication of a wild species of Insectivora for the laboratory animal. Exp Anim 26: 273–280 (In Japanese)

Matsuzaki O, Iwama A, Hatanaka T (1993) Fine structure of the vomeronasal organ in the house musk shrew(*Suncus murinus*). Zool Sci 10: 813–818

Matsuzaki T, Saito M, Yamanaka M (1984) Planned reproduction of the house musk shrew (*Suncus murinus*). Exp Anim 33: 223–

226
Morita S (1968) On the copulation and ovulation of the riukiu musk shrew, *Suncus murinus*. Sci Bull Fac Lib Arts & Educ, Nagasaki Univ 19: 85–95 (In Japanese with English abstract)
Naik D R, Dominic C J (1970)Observations on the vaginal cell types, sexual receptivity and on the mating behaviour of the musk shrew, *Suncus murinus* L.(Insectivora). Indian Biologist 2: 66–74
Oda S (1985) Collection and transportation. In "*Suncus murinus*: Biology of the laboratory shrew", Ed by K Kondo, Japan Scientific Society Press, Tokyo (In Japanese), pp 97–101
Rissman E F (1987) Social variables influence female sexual behavior in the musk shrew (*Suncus murinus*). J Comp Psychol 101: 3–6
Rissman E F, Bronson F H (1987) Role of the ovary and adrenal gland in the sexual behavior of the musk shrew, *Suncus murinus*. Biol Reprod 36: 664–668
Rissman E F (1989) Male-related chemical cue promote sexual receptivity in the female musk shrew. Behav Neur Biol 51: 114–120
Tennant L E, Rissman E F, Bronson F H (1987) Scent marking in the musk shrew (*Suncus murinus*). Physiol Behav 39: 677–680
Tsuji K, Naruse T (1984) Some observations of the caravaning behaviour in the musk shrew (*Suncus murinus*). Behaviour 90: 167–183
Tsuji K, Naruse I (1985) In "*Suncus murinus*: Biology of the laboratory shrew", Ed by K Kondo, Japan Scientific Society Press, Tokyo (In Japanese with English summary), pp 459–475
Tsuji K (1989) Modification of early behaviour and reproductive behaviour in the process of domestication. The Report for the Grant-in-Aid for Scientific Research (In Japanese)
Tsuji K, Ishii K, Matsuo T, Kawano K (1999) The house musk shrew *Suncus murinus* as a new laboratory animal for use in behavioural studies. Jpn J Anim Psychol, 49: 1–18
Watabe I (1985) In "*Suncus murinus*: Biology of the laboratory shrew", Ed by K Kondo, Japan Scientific Society Press, Tokyo (In Japanese), pp166–168

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