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Laboratory experiments on spatial use and aggression in three sympatric species of shrew in Hokkaido, Japan

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Abstract. Aggression and the use of vertical and horizontal space in the presence of con- or hetero-specific individuals were investigated in laboratory for *Sorex unguiculatus*, *S. caecutiens*, and *S. gracillimus* in Hokkaido, Japan. *S. unguiculatus* frequently used the below floor strata of experimental cages or subterranean burrows as their main area of activity, whereas *S. caecutiens* and *S. gracillimus* mainly used the cage floor or the ground surface. The presence of con- or hetero-specific individuals led to no changes in any of the three species in the use of space, or in behavioral patterns (active/inactive; underground/resting/ moving on the ground surface). When two individual shrews were introduced into two interconnected cages, they tended to remain in separate cages, with the exception of *S. gracillimus* with a conspecific. Dominance rank was highest in *S. unguiculatus*, intermediate in *S. caecutiens*, and lowest in *S. gracillimus*. *S. caecutiens* attacked *S. gracillimus* most frequently and *S. gracillimus* received attacks from *S. caecutiens* most frequently. The implication of this research is that severe interference competition may occur in the field between *S. caecutiens* and *S. gracillimus*.

Key words: coexistence, interference competition, niche shift, surface activity, underground activity.

Sorex unguiculatus, *S. caecutiens*, and *S. gracillimus* are three common species of shrew occurring throughout Hokkaido. When *S. caecutiens* and *S. gracillimus* occur together, they are never the two most abundant species (Ohdachi and Maekawa 1990a, Ohdachi 1995a). Ohdachi (1995b) confirmed that *S. caecutiens* and *S. gracillimus* share a greater similarity in their diets than do either of these species and *S. unguiculatus*. These findings indicate that interspecific competition is likely to be more severe between *S. caecutiens* and *S. gracillimus*. Further, *S. unguiculatus* is a much stronger burrower than either of the other two species (Ohdachi 1995c). It is suspected, therefore, that severe interference for space exists between *S. caecutiens* and *S. gracillimus*.

There is the potential for a niche shift by one species, when in the presence of the other, that could influence the outcome of competition. If both species exhibit interference competition, but neither of them changes any of its niche dimensions, then the physically superior individual or species may exclude the inferior individual or species from good habitat or a good position (*e.g.*, Hardin 1960, Schoener 1975, Werner and Hall 1976, Holbrook 1979, Parker and Sutherland 1986, Alatalo and Moreno 1987, Arthur 1987). In such cases, aggressive behavior and physical superiority are essential keys for guild formation, and thus make it interesting to investigate whether individuals change their use of space (or niche) in the presence of other individuals.

For cryptic species whose life histories are poorly known, such as the shrews of Hokkaido, it is difficult to carry out extensive field studies of space use and interactions. Ohdachi (1992) described the home ranges of sympatric shrews in Hokkaido, but was only able to present limited information about interspecific interactions because of the difficulties in observing them directly. Therefore, the alternative means of investigating direct interactions in the laboratory was chosen for this study. Although the reality of simulated situations, particularly in the scaling of time and space, is questionable (Bennett 1990), the results obtained from laboratory experiments can, nevertheless, complement those from field studies (Diamond 1986, Hairston 1989, Keddy 1989).

This paper serves to describe: (1) interspecific differences in the use of space, (2) interspecific interactions such as aggressive behavior, and (3) the impact of the presence of another individual on the use of activity space and on behavioral patterns, in *S. unguiculatus*, *S. caecutiens*, and *S. gracillimus* in Hokkaido. For these purposes, two different laboratory experiments were conducted.

MATERIALS AND METHODS

1. Experiment 1

The first experiment was designed mainly to examine the effects of the presence of con- or hetero-specific individuals on vertical space use. Animals used in this experiment were nine *S. unguiculatus* (5 young males, 4 young females), eight *S. caecutiens* (1 adult male, 4 young males, 3 young females), and five *S. gracillimus* (3 young males, 2 young females), which were captured in Yufutsu Moor (Tomakomai-shi) during 14-18 June 1992 and in a wind-shelter belt near the Teshio Experimental Forest of Hokkaido University (Horonobe-cho) during 25 June to 27 August 1992. Basically, sexually immature individuals were used in experiments in order to lessen the potential effect of sexual behavior on space use. Shrews were kept under a 16-hr light and 8-hr dark photoperiodic cycle at 20±2°C. The light intensity was maintained at 1420 lux during the light period and at 12 lux during the dark period (as measured at the center of laboratory floor; See Ohdachi 1994, 1995c for details). Each experiment was conducted throughout the 8-hr dark period, from 11 October 1992 to 6 January 1993.

Each observation cage contained 20 levels and the floor surface, and was fitted with two staircases (Fig. 1). Each of the boards separating the levels

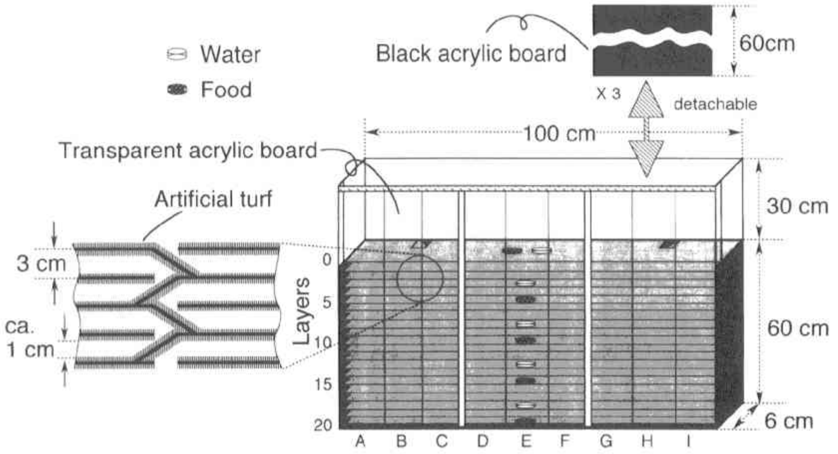

Fig. 1. The experimental device for Experiment 1. Black boards were removed just before an experimental session.

was covered on both sides with artificial turf so that shrews were always in physical contact with this surface while moving about between levels. Pieces of tissue paper, which simulated ground litter, were located on the cage floor. Trays of the mixed paste diet and water were located as shown in Fig. 1. Black acrylic boards were attached in front of transparent cage walls, so as to exclude light before observation periods.

Either one or two animals were released simultaneously onto the cage floor thirty minutes before the onset of the dark period. The black masking boards were gently removed immediately after the light was turned off. The location and behavior of each shrew were then recorded every fifteen minutes using a weak red spot-light. After finishing an experimental session, the animals were removed and the cages were washed with ethanol and kitchen detergent and then dried out.

The vertical location of a shrew was assigned to one of five categories: surface level (0), levels 1-5, 6-10, 11-15, and 16-20. Utilization of each level by an individual was obtained by averaging the percent frequencies for the level among several experimental sessions under the same experimental treatment. Seventy experimental sessions were used for analysis.

The dominance relationship between two individuals was defined as follows: the "loser" was the individual which avoided, escaped, or fled from its "opponent" when two animals encountered or fought, while the opponent under these circumstances was a "winner". If the number of wins and losses observed were the same, the two animals were judged to be "even". When no direct contact was observed, this was defined as "no match".

2. Experiment 2

The second experiment was designed to investigate aggressive behavior and the effect of the presence of con- or hetero-specific individuals on the use of space use (especially horizontal use) and behavioral patterns. Animals used in this experiment included ten *S. unguiculatus* (1 adult female, 5 young males, 4 young females), three *S. caecutiens* (2 young male and 1 young female), and five *S. gracillimus* (2 adult females, 1 young male, and 2 young females), which were captured in wind-shelter belts near the Teshio Experimental Forest of Hokkaido University during 6–22 August 1993, and one adult female *S. caecutiens* that was captured in Yufutsu Moor in July 1992. Laboratory conditions were the same as in Experiment 1. Each experiment was conducted throughout the dark period, from 30 August to 24 November 1993.

Two animals were released separately into experimental cages (Fig. 2) one day before an experiment, with both sides of the connecting tube being closed by rubber plugs. The rubber plugs were removed five minutes before the onset of the dark period. As a control experiment, an empty cage was connected to a cage where a single shrew was introduced. The first cage into which a shrew was introduced, prior to the cages being connected for the experiment, is hereafter referred to as the "home" cage, while the other is referred to as the "away" cage.

Shrew behavior was recorded using a video camera recorder (in the twilight vision mode) throughout the dark period, and sampled every 5 minutes while replaying the video tapes. Behavior was ascribed to one of three categories: "underground activity" (shrews were underground or digging), "in

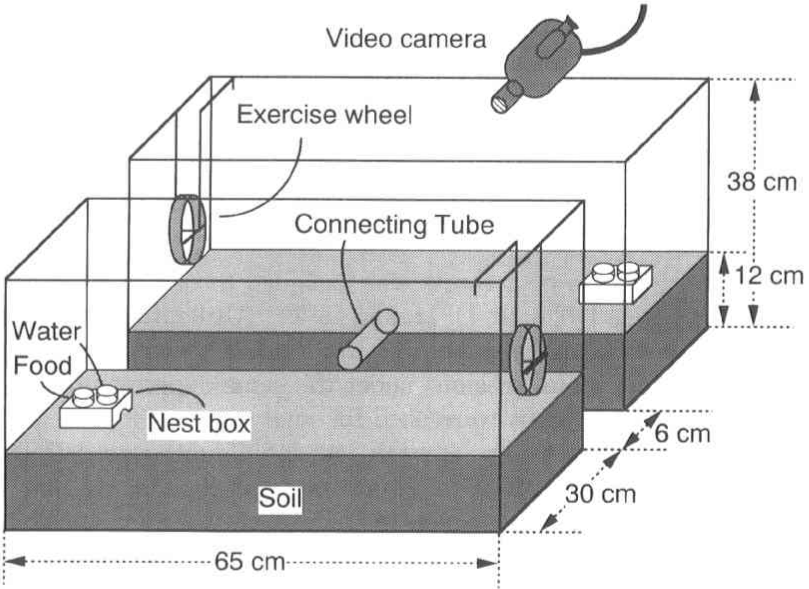

Fig. 2. The experimental device for Experiment 2. A connecting tube is plugged until an experimental session is started. Note that the bottom of a nest box was open to the ground surface.

action on the ground" (shrews were in nest boxes or resting on the ground surface), and "moving on the ground" (shrews were walking or running on the ground surface, or whirling exercise wheels). Other behaviors, such as eating, drinking, or self-grooming, were usually too brief to be recorded by the 5-minute-interval sampling method. Behavior below ground and in nest boxes could not be observed in this experiment. Because *S. unguiculatus* usually constructed burrows in its "home" cage and some entrances of the burrows opened under its nest box, it was impossible to distinguish "underground activity" and "inaction on the ground" when it was in its nest box. According to preliminary observations, however, *S. unguiculatus* usually entered burrows under its nest box instead of staying on the ground surface when in its nest box. Therefore, unless it was possible to verify that the shrew did not enter a burrow, the case in which *S. unguiculatus* was in a nest box was classified as "underground activity". Preliminary observations revealed that *S. caecutiens* and *S. gracillimus* usually stayed on the ground surface under the nest box of *S. unguiculatus*, and that they were usually inactive there. Thus, when *S. caecutiens* or *S. gracillimus* was in the "away" nest box of *S. unguiculatus*, this was classified as "inaction on the ground", except when they obviously entered burrows under the nest box.

The frequency of each behavioral category for an individual was obtained by averaging the observation frequencies of the category across several experimental sessions under the same experimental treatment. Sixty-two experimental sessions (496-hour observation in total) were used for the analysis.

The number of attacks and the dominance relationship between individuals were determined by continuous scanning of the video tape throughout the 8-hr experimental session (complete observation). Attacking behavior includes chasing, biting body or tail, and wrestling. Attacks interrupted for more than 10 seconds was counted separately. The criteria for "win", "lose", and "no match" were the same as in Experiment 1. In this experiment, however, "even" was defined as follows: frequent counterattacks were observed or an individual did not escape from the opponent even when it was attacked often.

RESULTS

1. Experiment 1

Sorex unguiculatus was more subterrestrial than either *S. caecutiens* or *S. gracillimus*. *S. caecutiens* used the surface level significantly more frequently than *S. unguiculatus* during its active phase (ANOVA with arcsine transformation by Scheffe's method, $\alpha = 0.05$), but utilization of the other levels did not differ significantly between these two species (Fig. 3). *S. gracillimus* appeared to frequently use the surface level as did *S. caecutiens*, although its surface activity was not statistically different from that of either *S. unguiculatus* or *S. caecutiens* (Fig. 3).

Vertical space use did not differ significantly between the experimental treatments in each of the three species (Fig. 3). The dominance relation also

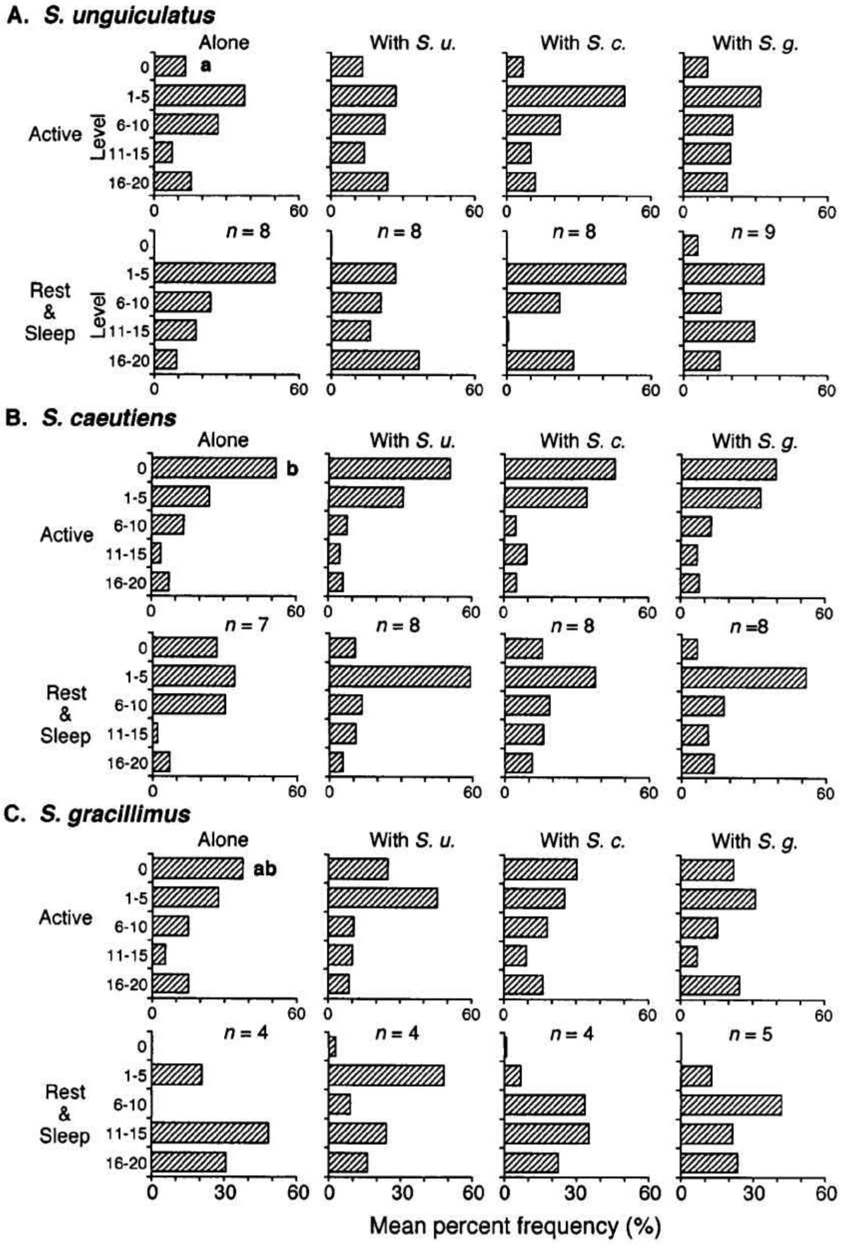

Fig. 3. Vertical spatial use of shrews when they were alone and with con- or hetero-specific individuals (mean percent frequency). The same bold letters (a, b) indicate non-significant difference in mean percent frequency for the floor surface (0) between species when shrews were "alone" ($\alpha = 0.05$, ANOVA, arcsine transformation, Scheffe's method; the sequential Bonferroni correction among levels, Rice 1989). There was significant difference neither among species for the other levels when alone nor among experimental treatments for each level within species.

Table 1. The ratios of "active" and "rest & sleep" phases in three shrew species observed in Experiment 1 (mean percent frequency ± *SD*). Mean percentages in the "alone" column differed significantly between any two of the three species ($\alpha=0.05$, ANOVA, arcsine transformation, Scheffe's method). The different letters indicate significant differences. The mean percentages did not differ significantly among the experimntal treatments within species.

Experimental treatment	Alone	With		
		S. u.	*S. c.*	*S. g.*
S. unguiculatus	a			
Active	33.0±10.9	38.7±15.5	39.2±12.8	41.4±17.1
Rest and Sleep	67.0	61.3	60.8	58.6
(*n*)	(8)	(8)	(8)	(9)
S. caecutiens	b			
Active	70.6±12.1	73.3±17.9	65.5±25.0	68.6±8.2
Rest and Sleep	29.4	26.7	34.5	31.4
(*n*)	(7)	(8)	(8)	(8)
S. gracillimus	c			
Active	50.0±10.4	60.5±12.4	50.8±6.2	53.8±12.2
Rest and Sleep	50.0	39.5	49.2	44.2
(*n*)	(4)	(4)	(4)	(5)

had no apparent effect on vertical space use ; there were no significant differences for almost all comparisons.

The percentages of active and non-active phases did not differ significantly between the exrimental treatments (alone and with con- or hetero-specific individuals) in any of the three species (ANOVA with arcsine transformation by Scheffe's method, $\alpha=0.05$, Table 1). Interspecific differences in activity when animals were "alone" were, however, significant. *S. caecutiens* was most active, *S. unguiculatus* was least active, and *S. gracillimus* was intermediate between them. Dominance relationships between two individuals (win, even, lose, or no match) also had no effect on activities of shrews.

2. Experiment 2

The use of "home" or "away" cage did not differ significantly among species when shrews were "alone" (ANOVA, $\alpha=0.05$). *S. unguiculatus*, however, tended to stay in its "home" cage more than either of the other two species (Table 2). The experimental treatments (alone and with con- or hetero-specific individuals) also had no effect on the use of "home" and "away" cages for any of the three species (Table 2). The dominance relationships tended not to influence the use of either the "home" or "away" cage in the three species ; there were no significant differences for almost all comparisons.

When two individuals were introduced into two interconnected cages, they tended to stay in separate cages (Table 3). The mean percentage of time spent in a single cage or separate cages did not differ significantly among the experimental treatments.

Table 2. The utilization of "home" and "away" cages by three shrew species observed in Experiment 2 (mean percent frequency ± *SD*). The mean percentages differed significantly neither between the experimental treatments within species nor between species when shrews were "alone" ($\alpha = 0.05$, ANOVA, arcsine transformation, Scheffe's method).

Experimental treatment	Alone	With		
		S. u.	*S. c.*	*S. g.*
S. unguiculatus				
Home	70.7±28.3	76.9±20.5	64.2±36.5	72.1±29.1
Away	29.3	23.1	35.8	27.9
(*n*)	(10)	(10)	(10)	(10)
S. caecutiens				
Home	50.7±31.9	52.0±26.6	36.3±11.6	49.6±23.2
Away	49.3	48.0	63.7	50.4
(*n*)	(4)	(4)	(4)	(4)
S. gracillimus				
Home	56.5±29.7	68.0±7.9	48.2±29.4	48.2±18.5
Away	43.5	32.0	51.8	51.8
(*n*)	(4)	(4)	(5)	(4)

S. unguiculatus remained underground or dug soil significantly more frequently ($\alpha = 0.05$) than did either *S. caecutiens* or *S. gracillimus* when they were in their "home" cages (Fig. 4). The mean frequencies of the three behavioral categories, however, did not differ significantly among the three species when they were in "away" cages (Fig. 4).

S. unguiculatus was "active underground" significantly more frequently in its "home" cage than it was in the "away" cage under each of the experimental

Table 3. Occupation of cages by two shrews in Experiment 2 (mean percent frequency ± *SD* of staying in the same cage and separate cages). The means did not differ significantly between any comparisons ($\alpha = 0.05$, ANOVA, arcsine transformation, Scheffe's method). *n*: number of experimental sessions examined.

	With		
	S. unguiculatus	*S. caecutiens*	*S. gracillimus*
S. unguiculatus			
Same	35.9±19.9	35.6±17.3	24.2±14.3
Different	64.1	64.4	75.8
(*n*)	(5)	(10)	(10)
S. caecutiens			
Same	-	33.9±19.6	38.4±15.0
Different	-	66.1	66.3
(*n*)		(5)	(9)
S. gracillimus			
Same	-	-	54.8±10.7
Different	-	-	45.2
(*n*)			(4)

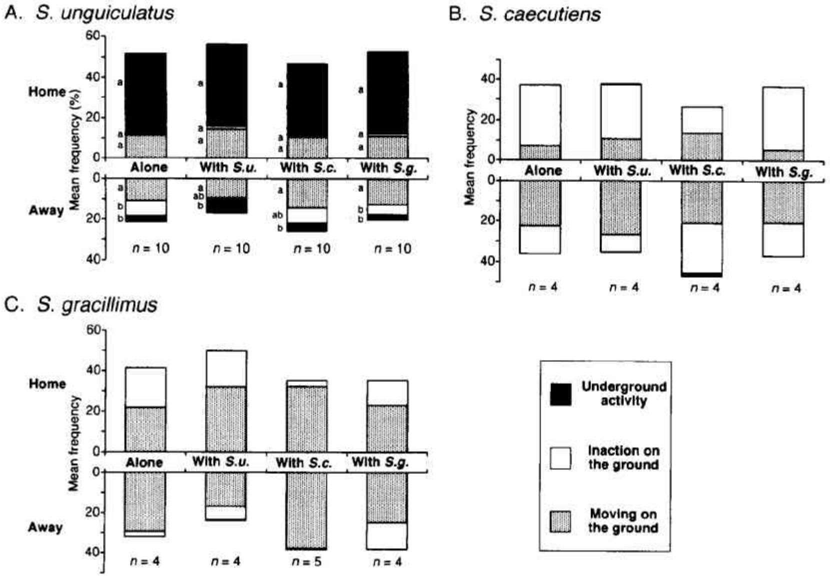

Fig. 4. The effects of con-or hetero-specific individuals on the behavior of shrews (mean percent frequency). The same letters indicate non-significant difference in mean frequency of each behavior category among the experimental treatments and between "home" and "away" cages within experimental treatment ($\alpha = 0.05$, ANOVA, Scheffe's method). In *S. caecutiens* and *S. gracillimus*, any significant difference in behavioral category was not found among the experimental treatments nor between "home" and "away" cages.

treatments (Fig. 4-A). In contrast, the mean frequency of each behavior in *S. caecutiens* and *S. gracillimus* did not differ significantly between the "home" and "away" cage situations (Fig. 4-B, C). The experimental treatments (alone and with con- or hetero-specific individuals) also had no effect on the behavioral patterns for any of the three species (Fig. 4).

The relationship between the mean frequencies of the behavioral categories and the dominance relation was not fully analyzed because of small sample size. However, behavioral patterns appeared not to be affected by the dominance relationship.

3. Dominance relationships and attacks

Among the three species, *S. unguiculatus* was most dominant and *S. gracillimus* was most submissive in terms of physical superiority. *S. unguiculatus* was seldom defeated by *S. caecutiens* and never defeated by *S. gracillimus* (Table 4). Furthermore, "no match" was the major result between conspecific individuals of *S. unguiculatus* in Experiment 2, but this result might be an artifact of the observation method that underground behaviors could not be observed. *S. caecutiens* beat *S. gracillimus* in most combats.

S. unguiculatus showed no significant difference in the number of attacks

Table 4. Dominance relations between two con- or hetero-specific individuals in Experiments 1 and 2 (numbers of individuals of four kinds of the relation). Results of different experimental sessions for an individual were treated as diffrent counts.

		Opponent		
		S. u.	*S. c.*	*S. g.*
Experiment 1				
S. unguiculatus	win	4	6	6
	even	4	4	1
	lose	4	0	0
	no match	0	2	3
S. caecutiens	win	0	5	4
	even	4	4	2
	lose	6	5	1
	no match	2	0	2
S. gracillimus	win	0	1	2
	even	1	2	4
	lose	6	4	2
	no match	3	2	0
Experiment 2				
S. unguiculatus	win	1	6	8
	even	0	1	0
	lose	1	1	0
	no match	8	2	2
S. caecutiens	win	1	5	7
	even	1	0	0
	lose	6	5	0
	no match	2	0	2
S. gracillimus	win	0	0	4
	even	0	0	0
	lose	8	7	4
	no match	2	2	0

Table 5. Mean numbers of attacks (±*SD*) between two individuals in Experiment 2. The same letters indicate non-significant difference ($\alpha = 0.05$, Mann-Whitney's *U*-test, the sequential Bonnferroni correction, Rice 1989). The first letters before comma indicate the results of between-columm comparisons and the second letters are those of between-rows. Numbers parentheses are those of observations examined.

	Against		
	S. u.	*S. c.*	*S. g.*
S. unguiculatus	0.5±0.7 (2) a, a	1.2±1.6 (8) a, a	5.6±9.3 (8) a, a
S. caecutiens	1.0±1.4 (8) a, a	6.4±8.9 (10) a, a	27.4±16.6 (7) b, b
S. gracillimus	0.0±0.0 (8) a, a	0.6±0.5 (7) b, a	0.9±1.4 (8) ab, a

against other individuals (Table 5). *S. caecutiens* attacked *S. gracillimus* significantly more frequently than it did *S. unguiculatus* or other *S. caecutiens*. *S. gracillimus* attacked other individuals less frequently than did either of the other two species. *S. gracillimus* was attacked more often by *S. caecutiens* than by *S. unguiculatus* or by conspecifics (Table 5)

DISCUSSION

S. unguiculatus was frequently active underground, whereas *S. caecutiens* mainly used the ground surface (Figs. 3 and 4). *S. gracillimus* showed an intermediate vertical use of space in Experiment 1, but it was primarily a ground-surface dweller (Fig. 4) in Experiment 2, which was deemed to simulate natural conditions more realistically than Experiment 1.

The interspecific differences in use of space were consistent with those in burrowing habits (Ohdachi 1995c) and in dietary constituents (Abe 1968, Inoue and Maekawa 1990, Ohdachi 1995b) : *S. caecutiens* and *S. gracillimus*, which are poor burrowers and mainly eat small epigeal arthropods, showed more surface activity than did *S. unguiculatus*, which was a superior burrower and a heavy consumer of earthworms.

The presence of a con- or hetero-specific individual or their dominance relationships affected neither the space utilization nor the mean frequencies of behaviors (active/inactive and underground/resting/ground surface activity) in each of the three shrew species. *S. unguiculatus* was intrinsically different in its use of space (especially vertically) from *S. caecutiens* and *S. gracillimus*. It is, therefore, likely that direct interaction or interference over space is less frequent between *S. unguiculatus* and either of *S. caecutiens* or *S. gracillimus* than between the latter two species.

A dominance order among the three species was evident (Table 4) and seemed to correspond with the shrews' body size. The strongest *S. unguiculatus* weighs on average approximately twice as much as the second-ranked *S. caecutiens*, and *S. caecutiens* is 1.5 times as heavy as the weakest *S. gracillimus* (Ohdachi and Maekawa 1990b). The correlation between fighting ability and body size has also been reported from some other insectivorous or carnivorous vertebrates (*e.g.*, Persson 1985, Alatalo and Moreno 1987, Dickman 1988, Erlinge and Sandell 1988, Ducey *et al.* 1994, Nakano and Furukawa-Tanaka 1994).

Each of the three shrew species exhibited antagonistic behavior whenever two con- or hetero-specific individuals encountered, although *S. gracillimus* were least likely to attack. It may have been this tendency that led them to remain in whichever cage was not occupied by its opponent (Table 3). Many other soricine species also show antagonism against con- or hetero-specific individuals (Crowcroft 1957, Olsen 1969, Hawes 1977, Martin 1981, Barnard and Brown 1982, Churchfield 1990, Ellenbroek 1990, Dickman 1991, Ellenbroek and Hamburger 1991, Krushinska and Rychlik 1993). However, some species, such as *Neomys anomalus* and *Cryptotis parva*, are tolerant towards conspecifics

(Broadbooks 1952, Conaway 1958, Mock 1982, Krushinska and Pucek 1989, Krushinska and Rychlik 1993). Krushinska and Pucek (1989) reported that acquaintance reactions, such as warning and nasal contact, were observed in *N. anomalus* when two individuals met. In their study, shrews gradually avoided direct conflict by learning their place of the dominance rank. In the present study, such acquaintance behaviors were not observed; shrews suddenly attacked other individuals (or were attacked) throughout experiments. The lack of acquaintance behavior in the present study might have resulted from the brevity of experiments which might have led to their intolerance of other individuals.

Although *S. unguiculatus* was strongest of the three species (Table 4), it attacked other two species less frequently (Table 5). In the present study, attacks could only be observed among animals on the ground surface, which might thus underestimate the attacking frequency of *S. unguiculatus*. Under natural conditions, however, attacks by *S. unguiculatus* against *S. caecutiens* and *S. gracillimus* are also probably rare, because the latter two species use subterranean space less frequently and presumably rarely encounter *S. unguiculatus*.

Soricids usually establish intraspecific territories or exclusive home ranges, especially among individuals of the same sex (Ingles 1961, Shillito 1963, Buckner 1966, 1969, Croin-Michielsen 1966, Platt 1976, Hawes 1977, Pernetta 1977, Inoue 1988, 1991, Ohdachi 1992, Ivanter *et al.* 1994, Moraleva and Telitzina 1994, Stockley *et al.* 1994). Such territoriality seems to be maintained by aggressive behavior and odor marking (Crowcroft 1957, Hawes 1976). Two types of interspecific spatial relationships are known among soricine shrews. In the first type, territories overlap between species, as between *S. araneus* and *S. minutus* (Croin-Michielsen 1966, Pernetta 1977, Ellenbroek 1980). In the second type, there is interspecific territoriality as between *S. cinereus* and *S. vagrans* (Spencer and Pettus 1966) and between *S. vagrans* and *S. obscurus* (Hawes 1977). In Hokkaido, *S. unguiculatus* and either of *S. gracillimus* or *S. caecutiens* appear to have overlapped territories (Ohdachi 1992). The occurrence of overlapped territories might be explained by the interspecific difference in vertical space use: *S. unguiculatus* appears only rarely to encounter either *S. gracillimus* or *S. caecutiens* in the field. In contrast, inferring from the results of the present study (Figs. 3 and 4), it is plausible that *S. caecutiens* and *S. gracillimus* maintain interspecific territories when in symtopy, because both species are ground-surface dwellers and they do not shift their space of activity even when they co-habituate.

S. caecutiens tenaciously attacks *S. gracillimus*, and the latter seldom beats *S. caecutiens*. The similarity in space use and the physical inferiority of *S. gracillimus* could lead to its exclusion from habitats where *S. caecutiens* occurs. Moreover, recipients of aggressive behavior may experience reduced fitness in general (King 1973). This could partly explain the relative abundances of the two species in a given habitat (Ohdachi and Maekawa 1990a): *S. caecutiens* and *S. gracillimus* do not occur together as the first and second most abundant species. However, if *S. caecutiens* were to always exclude *S. gracillimus*, then *S. gracillimus* would be unable to occur in Hokkaido. In reality, *S. gracillimus* outnumbers *S. caecutiens* and *S. unguiculatus* in some habitats (Ohdachi and Maekawa 1990a). This might be attributed to interspecific differences in habitat preference. *S. gracillimus* is the most abundant species in moor and uplands, especially, in northern Hokkaido, whereas *S. caecutiens* tends to outnumber other species in habitats with sandy- or volcanic ash-soils (Ohdachi and Maekawa 1990a), which implies that each species prefers particular environments. Furthermore, competitive (interference) capabilities may vary in relation to such environmental variables as temperature, humidity, or soil type, and the result of competition depends on environmental conditions. Such phenomena are known in fish (Dunson and Travis 1991, De Staso and Rahel 1994), planktons (Hessen *et al.* 1995), and beetles (Park 1954). Also, the distribution pattern of soricids in Hokkaido is probably determined by a combination of both competitive ability and environmental conditions. In order to understand community organization or distribution pattern of the shrews in Hokkaido, further investigations of the effect of environmental conditions on competitive ability are recommended.

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