Home ranges of sympatric soricine shrews
in Hokkaido, Japan

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Ohdachi S. 1992. Home ranges of sympatric soricine shrews in Hokkaido, Japan. Acta theriol. 37: 91 – 101.

Home ranges of sympatric shrews, *Sorex unguiculatus* Dobson, 1890 *S. gracillimus* Thomas, 1907 and *S. caecutiens* Thomas, 1907 were studied by a mark-receapture method during the non-snow covered seasons in northern Hokkaido, 1988 and 1989. Home range size of *S. unguiculatus,* the largest species (15.1 g for adult males), was not significantly different from that of *S. gracillimus*, the smallest species (4.4 g for adult males). Both *S. unguiculatus* and *S. gracillimus* had more exclusive home ranges within species than between species. Tolerance of home range overlap may be related to the reduction of dietary overlap. No reliable information of home range for *S. caecutiens* was obtained in this study.

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Introduction

The influence of interspecific competition in shaping guild structure can be reflected in the partitioning of resources between species, including differences in use of space (Hill and Lein 1989, Murray 1971, Schoener 1968, 1986; Wiens 1989), although some authors insist that experiments be needed to establish its importance (Connell 1983, Schoener 1983a). Further, comparison of interspecific relationships of resource use between different guilds may yield instructive insights into the influence of interspecific competition on guild structure.

Eighty six species of soricine shrews (subfamily *Soricinae*) are wide-spread throughout the temperature and boreal zones in the northern hemisphere (Macdonald 1984), where they occur in multi-species assemblages or guilds. In Europe, Siberia, and North America, the ecology of shrews is well studied in comparison to Asia, and interspecific relationships of spatial and food resource utilization are known for some species. However, in Hokkaido, northern Japan, there have been only a few ecological studies on shrews (e.g. Abe 1968, Inoue 1988, 1989), although there are four species of *Sorex* (*S. unguiculatus* Dobson, 1980;

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S. caecutiens Thomas, 1907; *S. gracillimus* Thomas, 1907; and *S. minutissimus* Thomas, 1906) and *Crosidura dsinezumi* Temminck, 1844 (Abe 1967) and the former three species of *Sorex* are the most abundant ones in the small mammalian fauna (pers. obs.).

In this paper, I examine home range size and overlap within and between species for two sympatric *Sorex* shrews in Hokkaido (*S. unguiculatus* and *S. gracillimus*) and give supplemental information of home range for *S. caecutiens*. Then I relative home range overlap and size to food habits and discuss how the shrews partition space, comparing it with some other soricid guilds.

Materials and methods

Study area

The survey was carried out in Horonobe (45° N, 142° E), northern Hokkaido, from September to November 1988, and from April to October 1989. Temperatures in the study area range approximately from −35 to 35°C during a year, and the annual average temperature is 5°C (data from the office of Teshio Experimental Forest, Hokkaido University). Mean annual precipitation is 1,200 mm. Snow depth is approximately 1,000 mm in lowlands (ca. 40 – 100 m altitude) and 2,000 mm in high mountainous areas (ca. 100 – 500 m alt.). Snow cover usually exists from early December to the middle of April in lowlands, and from late November to early May in the mountainous areas.

The main native vegetation types are *Picea glehnii* forest in the serpentine zones and the mixed forests of conifers (*Picea jesoensis* and *Abies sachaliensis*) and deciduous trees (such as *Quercus mongolica*, *Tilia japonica*, *Betula* spp., *Acer* spp., and *Ulmus* spp.). The forest floors are covered with dense Sasa bamboo (*Sasa kurilensis*). Most of the plain areas and some of the hills are cultivated into
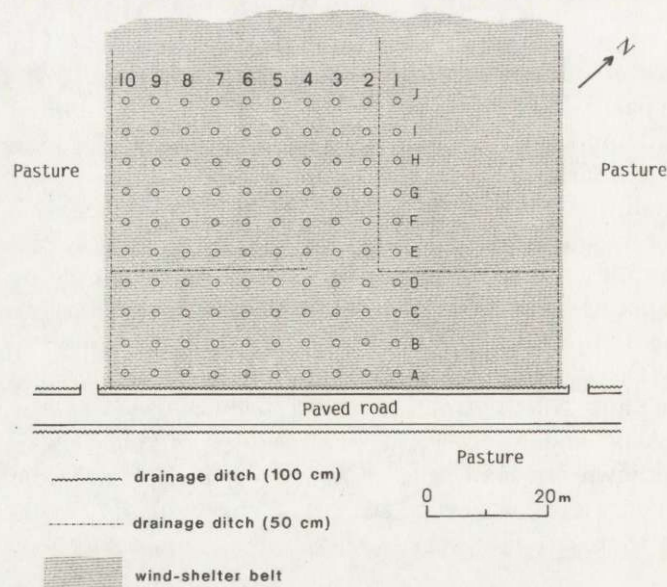

Fig. 1. Permanent trapping grid of a mark-recapture study of shrew species in northern Hokkaido, Japan, 1988 and 1989. Small circles are the fixed points of the trap grid.

pastures and ranches, and wind-shelter belts of *Fraxinus mandshrurica* are constructed among them. The forest floor of the wind-shelter belt is covered with dense *Sasa senanensis,* sparse tall herbs such as *Polygonum sachaliense* and *Senecio cannabifolius,* and ferns (*Pteridium aqurinum*).

In addition to the three species of *Sorex* examined in this study, *S. minutissimus* also occurs in the study area but is seldom caught (Ohdachi 1990, Ohdachi and Maekawa 1990a). Four species of rodents (*Clethrionomys rufocanus bedfordiae, C. rutilus, Apodemus argenteus,* and *A. speciosus*) coexist with the shrews; however, population density of each rodent species is lower than that of *S. unguiculatus* or *S. gracillimus* (Ohdachi 1990).

Trapping procedure

To investigate the home ranges of shrews, a mark-recapture program was carried out in a wind-shelter belt once a month. One hundred polyethylene pit-fall traps (16 cm diameter at the opening and 20 cm depth) were set in a permanent 10– by 10–grid at 5 m intervals (Fig. 1). However, in November 1988 and on 28 September 1989, only 50 traps (from A–1 to E–10; Fig. 1) were used due to snow and heavy rains, respectively. The locations of 10 – 20 traps arbitrarily chosen from the 100 traps were moved within a 1.5 m radius of the fixed points of the grid before daily surveys in order that shrews did not habituate traps. There are small ditches across the trap grid, but they contain no water except just after snow melt in spring. The trap grid was not enclosed by barriers, although a paved road ran along trapline 'A' and pasture expanded outside line '10' (Fig. 1).

Census was conducted for 3 – 5 (usually 5) days each month, but a census was interrupted when it rained heavily. Traps were checked four or five times a night at 2 hour intervals from 16 September 1988 to 26 July 1989 and at 1.5 hour intervals from 27 July to 26 October 1989. Traps were opened 1.5 or two hours prior to the first check of each daily survey, and were first checked around sunset (2000 h from April to July, 1930 h in August, 1830 h in September, and 1800 h in October and November). The final checking of traps was begun around midnight or early morning (2300 – 0230 h), and wood plates or twigs were put into all traps so that shrews could escape from the traps. Irregularly, a single census was carried by day (1200 – 1800 h) on 24 October 1988. To reduce mortality from starvation, small amounts of minced meat (chicken or pork), dried herring, kamaboko (a kind of fish sausage), or frozen silk worm larvae were placed in the traps.

Capture point, time, species, identification number, age (young or overwintered), sex, and body mass were recorded for each specimen captured. Toe-clipping was used to identify individuals; one digit from a forefoot and one from a hindfoot were cut off. Age determination was based on body mass and pelage (Abe 1958). For *Sorex* in Hokkaido, except *S. minutissimus,* no young individuals become mature untill the next spring and all overwintered individuals are mature (Abe 1968, Inoue 1989, Ohdachi and Maekawa 1990b). Therefore, for overwintered individuals, males were easily determined by descended testes and females by enlarged mammae. I did not determine the sexes of young individuals, except ones which were accidentelly killed in traps and dissected later.

Home range calculation

Home range size of individuals was estimated as the maximum observed length between capture points, and as the area determined by the convex polygon (minimum area) method (Stickel 1954). Home range size was calculated for 'residents' which had more than three different capture points, with no more than one of these in traps in row '1' or column 'J' (Fig. 1); I assumed that shrews did not move beyond traps in row '10' and column 'A' since there was a wide paved road or pasture outside these trap lines. I defined 'residents' as shrews which were captured in the trap grid in more than two monthly surveys. I used all capture points during the whole study period for the estimation of the home range size. This procedure of home range estimation is appropriate at least for *S. unguiculatus,* because the home range of the residential individuals do not change largely between months (Inoue 1989).

Home range overlap (maximum overlap percentage) of an individual was calculated by the formula: $100 \times (O / H)$, where H was the area of home range for an individual of interest, and O was the maximum overlapping area with co-occuring individual(s) over the whole study period.

Results

The total numbers of captured individuals was 37 for *S. unguiculatus*, 28 for *S. gracillimus*, and 10 for *S. caecutiens* over the whole study period (including those found dead in traps). The total numbers of residents was 10 for *S. unguiculatus*, 5 for *S. gracillimus*, and one for *S. caecutiens*. One male *S. unguiculatus* (No. 004) was the only individual captured in both 1988 and 1989. It was first captured on 16 September 1988, and last captured on 28 April 1989.

The accidental death rate in traps was highest in *S. gracillimus*. The death rate was 2.7% (2 dead shrews found in traps / 74 total capture times) for *S. unguiculatus*, 8.3% (1/12) for *S. caecutiens*, and 13.3% (6/45) for *S. gracillimus* over the whole study period. Examinations of stomachs showed that they probably died from starvation. Thus, *S. gracillimus* appears to have the least tolerance of food deprivation among the three species.

Table 1. The maximum length between capture points and home range area based upon the convex-polygon method for residents in *Sorex unguiculatus*, *S. gracillimus*, and *S. caecutiens* in the non-snow covered season in northern Hokkaido, 1988 and 1989. Results in parentheses are supplemental information for individuals that did not satisfy the conditions for the calculation of home range size. Y – young, OW – overwintered (mature), M – male, F – female, UK – sex unknown.

Species	No.	Age	Sex	Max. length (m)	Area (m^2)
S. unguiculatus	002	Y	UK	36.5	175.0
	004	OW[a]	M	36.2	295.6
	022	OW	F	15.0	37.5
	(033	Y	UK	11.2	–)
	035	Y	UK	36.3	499.0
	036	Y	UK	25.5	173.8
	(037	Y	UK	20.0	–)
	039	Y	UK	15.7	12.5
	044	Y	UK	28.3	125.0
			mean[b]	27.6	188.3
S. gracillimus	020	OW	M	38.0	408.5
	026	OW	M	25.4	62.5
	(027	OW	F	15.8	25.0)
	(053	Y	UK	35.3	235.6)
	061	Y	UK	42.5	298.2
			mean[b]	35.3	259.4
S. caecutiens	(051	Y	UK	10.0	–)

[a]Young in 1988, [b]Excluding the data in parentheses.

Table 2. The maximum home range overlap percentage within- and between-species for resident *Sorex unguiculatus* and *S. gracillimus* during the non-now covered seasons in northern Hokkaido, 1988 and 1989. The formula for calculating maximum overlap percentage is given in methods.

Species	No.	VS. *S. unguiculatus*					VS. *S. gracillimus*				
		No.	Mon[a]	N[b]	Overlapping %	Overlapping m²	No.	Mon[a]	N[b]	Overlapping %	Overlapping m²
S. unguiculatus	002	004	Sep	2	1.6	2.8	none	–	0	0.0	0.0
	004	002	Sep	1	1.0	2.8	020	Apr	3	54.2	160.3
	022	none	Apr	2	0.0	0.0	none	Apr	3	0.0	0.0
	035	036+044	Jun (Jul)	7	17.1	85.3	020	Jun	1	36.4	181.8
	036	035	Jun (Jul)	7	29.3	51.0	020	Jun	1	67.9	118.0
	039	none	Jun (Jul)	7	0.0	0.0	none	Aug	2	0.0	0.0
	044	035	Jun (Jul)	7	27.4	34.3	020	Jun	1	29.8	37.8
	mean				10.9					30.9	
S. gracillimus	020	035+036+044	Jun	7	70.1	286.5	none	Apr (May)	3	0.0	0.0
	026	none	Apr	2	0.0	0.0	none	Apr (May)	3	0.0	0.0
	061	035	Aug	5	29.9	89.2	none	Aug (Sep)	2	0.0	0.0
	mean				33.3					0.0	

[a,b] Month and number of coexisting residents in the study area when an individual had the maximum overlapped home range, respectively. When the individual overlapped with no shrews, they are the month and number when the number of coexisting residents is greatest.

The mean home range size for *S. grasillimus* and *S. unguiculatus* was not significantly different ($U = 5$, $p > 0.05$ for the maximum length; $U = 7$, $p > 0.05$ for the area; two tailed Mann-Whitney's test), although the former species showed larger mean size (Table 1). No *S. caecutiens* statisfied the conditions for the calculation of home range size. *S. unguiculatus* and *S. gracillimus* had more exclusive home ranges within species than between species (Table 2), although statistical analysis (simulation analysis) could not be conduced due to insufficient sample size.
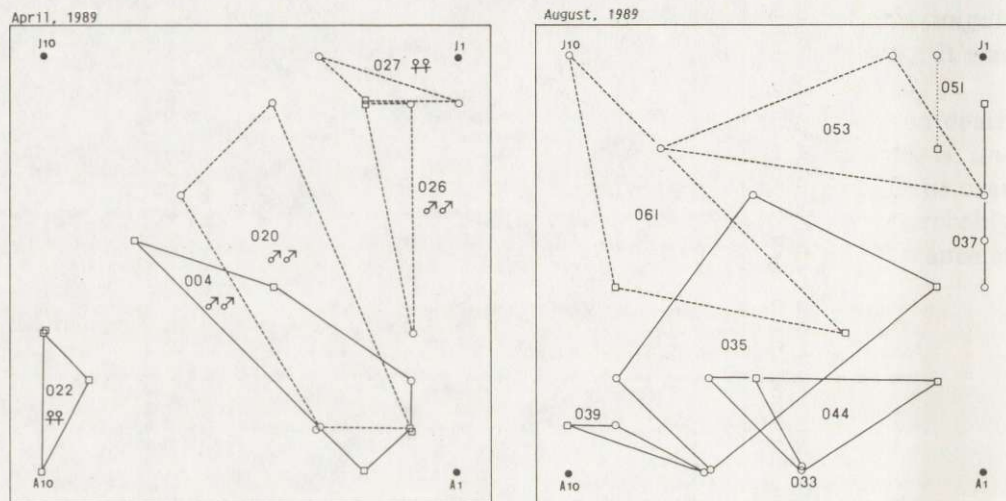
Fig. 2. Representative maps of shrews' home ranges in northern Hokkaido, Japan. Solid line – *Sorex unguiculatus*, broken line – *S. gracillimus*, dotted line – *S. caecutiens*. All capture points of each individual are used for drawing of the home range. Capture points are plotted with squares and circles; squares denote the capture points for the month in which home range of a shrew is drawn, and circles denote the points for the other months. Numbers within polygons are individual identification numbers of shrews.

Discussion

Home range size

Home range size of shrews was not positively related to body size among species. Home range size did not differ significantly between *S. unguiculatus* and *S. gracillimus*, although the former species has a much larger mean body size than the latter; e.g. mean body weight for overwintered males is 15.1 g ($n = 143$) in *S. unguiculatus*, and 4.4 g ($n = 22$) in *S. gracillimus*. I obtained no reliable information on home range size for *S. caecutiens*, whose mean body weight of overwintered males is 7.4 g ($n = 70$). Instead, the mean home range size of *S. caecutiens* in central Hokkaido is 225.0 m^2 ($n = 3$) (K. Maekawa, pers. comm.), which is intermediate between the values for *S. unguiculatus* and *S. gracillimus*

in the present study (Table 1). However, more samples are necessary to confirm the relationship between body mass and home range size for the shrews in Hokkaido.

Negative relationships between home range and body sizes have been reported for some sympatric shrews in Europe and North America, and the difference in home range size seems to be related to shrews' foraging behaviour and energy requirements. *S. araneus* has a smaller home range than the smaller *S. minutus* in Europe (Croin-Michielsen 1966, Dickman 1988, Shillito 1963), and *Blarina brevicauda* has a smaller home range than the smaller *S. cinereus* and *S. arcticus* in North America (Buckner 1957, 1966). The large species (*S. araneus* and *B. brevicauda*) are semi–fossorial foragers and feed heavily on earthworms, whereas the smaller ones (*S. minutus*, *S. cinereus*, and *S. arcticus*) are epigeal foragers and prey mainly on small terrestrial invertebrates (Aitchison 1987a, Babcock 1914, Butterfield *et al.* 1981, Churchfield 1980, 1982; Dickman 1988, Ellenbroek 1980, Ellenbroek and Hamburger 1991, Grainger and Fairley 1978, Michielsen 1966, Pernetta 1976a, Rudge 1968, Hamilton 1930, Whitaker and Mumford 1972). Generally speaking, costs of foraging are higher in burrowing species than wandering species (e.g. Vleck 1979), and therefore a burrower should not have a large foraging range if the cost is higher than energy gain per unit surface area. Furthermore, smaller shrews have higher energy requirements per unit body mass than larger ones (Aitchison 1987b, Genoud 1988, Pernetta 1976b). This suggests that the smaller species have to search for food more frequently if habitat quality is same for both species, or over larger areas if habitat quality is lower for the smaller species (e.g. Dill 1978, McNab 1963, Schoener 1983b, Simon 1975). Additionally, in Hokkaido, *S. unguiculatus* is regarded as a semi-fossorial forager, while *S. gracillimus* and *S. caecutiens* are regarded as epigeal foragers (Ohdachi 1990, Yoshino and Abe 1984), and the difference of home range size among these species might be explained by their foraging habits and body mass as in European and North American shrews.

Home range overlap

S. gracillimus showed exclusive home ranges or territories within species. In general, soricine shrews, except *Cryptotis parva* (Mock 1982), have exclusive territories within species; e.g. *S. araneus* and *S. minutus* (Buckner 1969, Croin-Michielsen 1966, Ellenbroek 1980, Pernetta 1977, Shillito 1963), *S. vagrans* and *S. obscurs* (Hawes 1977, Ingles 1961), *S. cinereus* and *S. arcticus* (Buckner 1966), *S. unguiculatus* (female–female overlap; Inoue 1988, 1989), and *B. brevicauda* (Platt 1976). *S. gracillimus* in northern Hokkaido followed this general pattern of apparent intraspecific territoriality; data for *S. caecutiens* were too few to analyze.

Territoriality of shrews is generally maintained by direct fighting and odor marking (Crowcroft 1957, Dickman 1991, Hawes 1976, Platt 1976). In the present study, I sometimes found that two *S. unguiculatus* in the same traps were aggressive to one another, suggesting that the territoriality for this species is also

maintained by aggressive behavior. In addition, it might be warthy to note that two *S. gracillimus* (male No. 026 and female No. 0.27) which had exclusive home ranges were trying to copulate in a trap (I–3) on April 27, 1989.

Four out of seven *S. unguiculatus* showed exclusive intraspecific home ranges but the remaining three had considerable overlap with conspecific individuals (Table 2). Thus, mean overlaps of *S. unguiculatus* in the present study was greater than that of other shrews mentioned earlier (Buckner 1966, 1969; Croin-Michielsen 1966, Ellenbroek 1980, Hawes 1977, Ingles 1961, Inoue 1988, 1989; Pernetta 1977, Platt 1976, Shillito 1963). Inoue (1989) reported that home range overlap of *S. unguiculatus* was considerably great, as in the present study, between male individuals although females had strictly exclusive home ranges each other. Therefore, the large overlaps in the present study might be those between male individuals.

I obtained no information on the home range relationships between *S. caecutiens* and the other two *Sorex* species in the present study. However, one *S. unguiculatus* has been observed to overlap with the home ranges of three *S. caecutiens* in central Hokkaido (K. Maekawa, pers. comm.), suggesting that *S. caecutiens* also has tolerance of home range overlap with *S. unguiculatus*.

The overlap of home ranges is probably related to interspecific differences in diets and foraging habits. The main foods of *S. unguiculatus* are earthworms whereas those of *S. gracillimus* and *S. caecutiens* are small terrestrial invertebrates (Abe 1968, Inoue 1983, Inoue and Maekawa 1990, Ohdachi 1990). Therefore, interspecific competition for food might be higher within species than between *S. unguiculatus* and either *S. gracillimus* or *S. caecutiens*.

In other guilds of soricine shrews, interspecific differences in spacing may also be related to food habits. Two interspecific spacing relationships are known in shrew guilds. In one, territories overlap between species, as in *S. araneus* and *S. minutus* (Croin-Michielsen 1966, Pernetta 1977, Ellenbroek 1980) the other involves interspecific territoriality, as in *S. cinereus* and *S. vagrans* (Spencer and Pettus 1966) and *S. vagrans* and *S. obscurus* (Hawes 1977). *S. araneus* mainly eats earthworms whereas *S. minutus* eats small epigeal invertebrates, which they obtain from different vertical strata (Butterfield *et al.* 1981, Churchfield 1980, 1982; Croin-Michielsen 1966, Ellenbroek 1980, Grainger and Fairley 1978, Pernetta 1976a, 1977; Rudge 1968). On the other hand, the principal foods of *S. cinereus* and *S. vagrans* are the same small invertebrates (Buckner 1966, Clothier 1955, Hamilton 1930, Whitaker and Mumford 1972), and *S. vagrans* and *S. obscurus* also have similar life history patterns (Hawes 1977).

There is no information on the spacing relationships between *S. gracillimus* and *S. caecutiens* in Hokkaido. However, inferring from the other shrew guilds mentioned above, we can predict that *S. gracillimus* and *S. caecutiens* will show interspecific territoriality as in *S. cinereus*/*S. vagrans* and *S. vagrans*/*S. obscurus*, because the two species in Hokkaido consume similar food items (Ohdachi 1990) and thus may compete for food resources. Furthermore, *S. gracillimus* and

S. caecutiens do not co-occur as the dominant and the second most dominant shrew species in various habitats and regions in Hokkaido (Ohdachi and Maekawa 1990a), suggesting that they compete more severely than either does with *S. unguiculatus*. This finding also suggests that they may have exclusive territories.

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