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Diets and Abundances of Three Sympatric Shrew Species in Northern Hokkaido

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Abstract. The diets and abundances of three sympatric shrew species (*Sorex unguiculatus, S. gracillimus*, and *S. caecutiens*), food resource conditions, and environmental characteristics were investigated in three habitat types (riparian forest, wind-shelter belt, and spruce forest), during seasons without snow-cover in northern Hokkaido, Japan. *S. unguiculatus* outnumbered *S. gracillimus* in both the riparian forest and wind-shelter belt, and *vice versa* in the spruce forest. *S. caecutiens* was rare in the study area. Abundances of *S. unguiculatus* and *S. gracillimus* seemed to be unrelated to those of their principal foods. The main prey of *S. unguiculatus* was earthworms, whereas *S. gracillimus* and *S. caecutiens* mainly consumed small terrestrial arthropods. *S. unguiculatus* tended to consume more earthworms in the spruce forest than in the other habitat types. The earthworm consumption appeared to directly reflect their availability per capita. Food consumption by *S. gracillimus* tended to be constant regardless of the habitat type.

Key Words: dietary niche; abundance; *Sorex*; food availability; guild structure

Soricine shrews (Insectivora, Soricinae) are distributed throughout boreal regions of the northern hemisphere, where their assemblages often consist of morphologically and ecologically "equivalent" species (Abe 1983, Hanski 1989). In some European shrews, interspecific competition is a major determinant of the spatial and numerical relationships of syntopic species (e. g., Croin-Michielsen 1966, Ellenbroek 1980, Dickman 1988, 1991, Neet and Hausser 1990, Churchfield 1991). Fox and Kirkland (1992) demonstrated non-random patterns in species assemblages of North American soricids and suggested that the non-random patterns should be attributed to interspecific competition (see also Kirkland 1991). Thus, interspecific competition appears to play an important role in structuring some shrew guilds in Europe and North America. In the northeastern Asiatic region, where up to nine soricine species coexist (Dolgov 1985), however, only a few studies of shrews have focused on interspecific relations (e. g., Okhotina 1974, Yoshino and Abe 1984, Inoue and Maekawa 1990, Ohdachi 1992).

This study was focused on an investigation of the diets and abundances of three sympatric *Sorex* species (*Sorex unguiculatus* Dobson, *S. gracillimus* Thomas, and *S. caecutiens saevus* Thomas) during seasons without snow-cover in northern Hokkaido. Food resource conditions and environmental variables in three habitat types (riparian forest, wind-shelter belt, and spruce forest) were also examined. The factors that may influence shrew abundance and food consumption are discussed, and finally, the shrew assemblage in Hokkaido is compared with those in other regions.

Materials and Methods

Study Area and Habitat Types

The study area was located in the Teshio Experimental Forest of Hokkaido University and in adjacent areas in northern Hokkaido, Japan. A general description of the study area was given elsewhere (Ohdachi 1992). The study was carried out in riparian forest, wind-shelter belt, and spruce forest during seasons without snow-cover (April to November) in 1988-1990. The environmental characteristics of the three habitat types are summarized in Table 1.

Trapping of Shrews

Trapping of shrews was conducted in the three habitat types once a month from May to November 1988, April to November 1989, and May to July 1990. Polyethylene pit fall traps (16 cm diameter at the opening and 20 cm deep) were

Table 1. Environmental conditions of three habitat types in northern Hokkaido.

	Riparian forest	Wind-shelter belt	Spruce forest
1. Altitude	40 m	40 m	500 m
2. Topography	flat	flat	slope
3. Period of snow cover	mid-December to mid-April	mid-December to mid-April	late November to early May
4. Maximum snow depth	1 m	1 m	2 m
5. Main tree species	*Salix* spp. *Alnus japonica* *Fraxinus mandshurica*	*F. manshurica* *Betula platyphylla* *Hydrangea paniculata*	*Picea glehnii* *Betula ermanii*
6. Undergrowth	tall herbs *Sasa kurilensis*	*Sasa senanensis* tall herbs, ferns	*Sasa kurilensis*
7. Litter layer	broad leaves+herbs	broad leaves+*Sasa*	*Sasa*+*Picea*
8. Soil type	clay	clay-loam	clay-loam (serpentite)
9. Soil structure	massive	granular	massive
10. Soil hardness	3.00 kg/cm^2	1.57 kg/cm^2	1.36 kg/cm^2

used from May to November 1988, in April 1989, and from May to July 1990. Twenty traps were set in two parallel lines each of 10 traps with a 5m interval between both traps and lines. As a rule, trap lines were set at different sites each month. No baits were used, and water was poured 10cm deep into the traps to kill shrews quickly. Trapping sessions lasted 2−4 (usually 3) nights, and animals were removed every day. From April to November 1989, smaller vinyl pit fall traps (8 cm diameter at the opening and 13.5 cm deep) were also used for trapping shrews. These traps were the same ones that were used for collecting terrestrial arthropods (see next section for trapping procedure). Shrews were collected every day, whereas arthropods were collected on the last day. Abundance of shrews was expressed as the number of animals captured per 100 trap-nights (No./100TN). One *S. minutissimus* was captured in the study area, but omitted from the present study.

Chi-square tests were employed to compare relative abundances of shrews between the habitat types (H_0 : the relative abundance does not differ between habitat types) and the abundances of each species among the three habitat types (H_0 : a shrew species was evenly distributed among the three habitat types). The expected values of the latter test were proportional to the sampling effort (trap-nights). The sequential Bonferroni technique (Rice 1989) was applied where necessary.

Food Resource Conditions

The biomass of earthworms (Megascolecidae and Lumbricidae) in the soil of each habitat type was estimated from samples obtained from April to November 1989. Three soil cores (30 by 30 cm^2 in area and 20 cm deep without litter layers) were taken monthly from each habitat type. Earthworms were collected from the soil cores manually and preserved in 70% ethanol. Later, they were dried in an oven at 60 °C for 24 hours and weighed to the nearest 0.1 mg.

The activity of small arthropods on the ground surface was investigated from April to November 1989. Arthropods were collected using the vinyl pitfall traps described in the previous section. A solution of 1% formalin and 1% kitchen detergent was poured 2−5 cm deep into the traps. Twenty pitfalls were set in two lines each of 10 traps with a 1m interval and were deployed over 3−5 nights at each plot. As a rule, trap sites were changed each month. In the riparian forest, however, traps were set at nearly the same sites after May 1989 since alternative trap sites were destroyed by logging.

Arthropods were collected along with sediments on the last day of each survey. These samples were sieved through a 2 mm wire-mesh sieve. Then, arthropods were manually segregated from the sediments and preserved in 70% ethanol. Later, arthropods were sorted into major taxonomic groups (usually at the family level), and the number of individuals of each taxon was recorded. Arthropods less than 1 mm in maximum length, which were not sieved out, were ignored. The activity (or relative abundance) of arthropods was expressed by the number of arthropods captured per 100 trap-nights (No./100TN).

Wilcoxon's signed rank tests were employed to compare earthworm biomasses and the activity of arthropods between habitat types. The sequential Bonferroni technique (Rice 1989) was applied to the analyses.

Dietary Analysis of Shrews

Three hundred and two *S. unguiculatus*, 122 *S. gracillimus*, and 33 *S. caecutiens* were used for the dietary analysis. Entire digestive tracts, from stomach to rectum, were removed and preserved in 70% ethanol or 10% formalin. Each digestive tract was dissected in a glass vessel and all contents were extracted. The contents were strained through a plankton net, and all the remains were placed into another vessel. Then, a piece of glass slide was placed over the remains with water or 70% ethanol so that all content items were evenly distributed. Each item of the contents was identified under a binocular microscope, compared with reference specimens. Then, the number of unit squares of the ocular lens ruler (20 by 20 squares, 1 × 1 cm) which a specific item occupied was counted at ×7 magnification.

Digestive tract contents were divided into 12 categories: earthworms (Megascolecidae and Lumbricidae), snails and slugs (Gastropoda), larval lepidopterans, adult coleopterans, larval coleopterans, adult ants (Formicidae), other insects, spiders and harvestmen (Araneae and Opiliones), centipedes (Chilopoda), other arthropods, plants, and other materials.

Food items were quantified by the percent frequency of occurrence ($F\%$), by percent volume index ($V\%$), and by average volume index per capita (AVI). They were calculated as follows:

$$F\%_j = (n_j/N) \times 100,$$

$$V\%_j = \left(\sum_i^N V_{ij}\right) \Big/ \left(\sum_i^N \sum_j^S V_{ij}\right) \times 100,$$

$$AVI_j = \left(\sum_i^N V_{ij}\right) \Big/ N,$$

where $F\%_j$ = the percent frequency of occurrence for item j, $V\%_j$ = the percent volume index for food item j, AVI_j = the average volume index of food item j, V_{ij} = the number of unit squares of the ocular lens ruler occupied by item j in the digestive tract of individual i(= volume index), N = the total number of shrews examined, S = the number of food categories, and n_j = the number of individuals which contained item j. The percent volume index ($V\%$) was used for the comparison of food item volume among species, and the average volume index (AVI) for the comparison of food consumption within species among habitat types.

The similarity of food consumption between shrew species was calculated as follows (after Schoener 1970):

$$C_{kh} = 1 - 1/2 \sum_j^S \left| (V\%_{kj} - V\%_{hj})/100 \right|,$$

where C_{kh} = the similarity of food consumption between species k and h, $V\%_{kj}$ = the volume index percentage for food item j of species k, and $V\%_{hj}$ = that of species h. Note that C_{kh} is zero when species k and h share no food items and 1.0 when they have identical food consumption.

Dietary niche breadth (B) was calculated as follows (after Levins 1968):

$$B = 1/\sum_{j}^{S}(V\%_j/100)^2$$

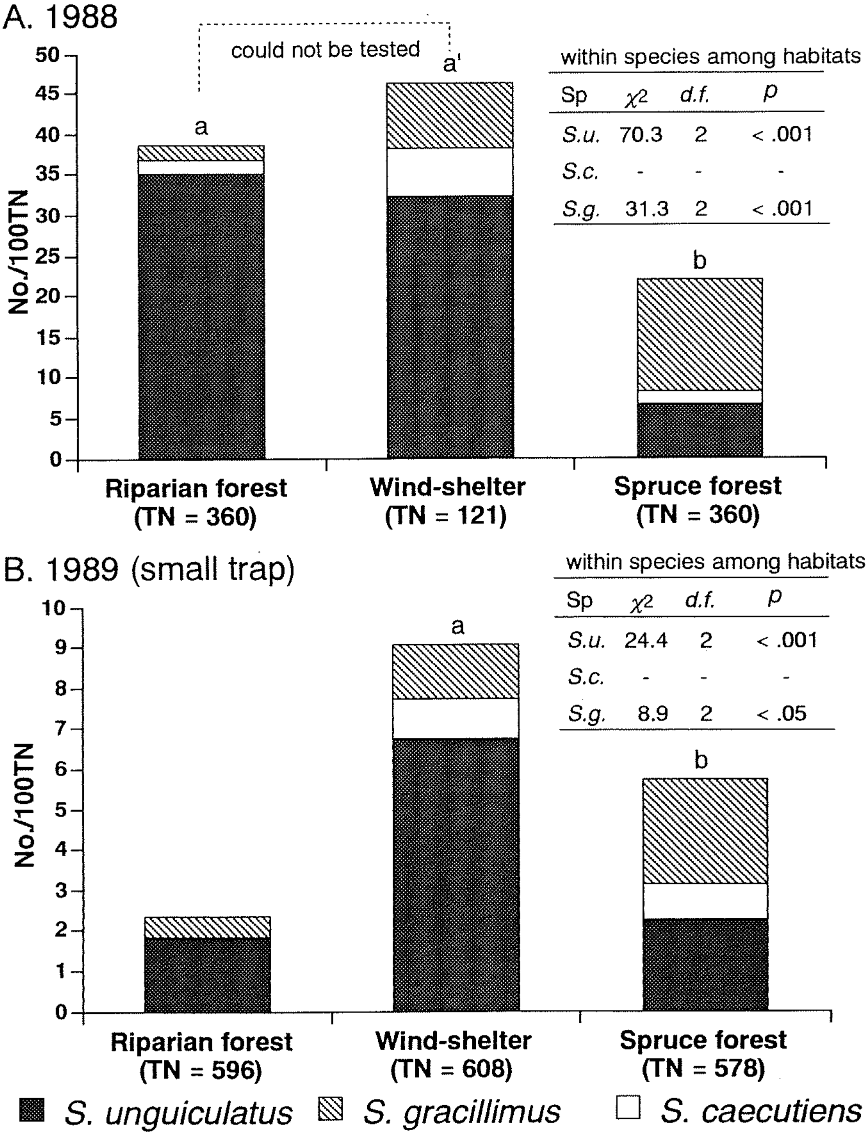
Chi-square tests were used to compare the proportion of frequency occurrence of each food category between habitat types (H_0: proportion of frequency occurrence of each food category does not differ between habitat types) and the frequency occurrence among the three habitat types for each food category (H_0: shrews used a food category evenly among the three habitat types). The expected values in the latter test were proportional to the total number of digestive tracts examined. The sequential Bonferroni technique (Rice 1989) was applied where necessary. Analysis of variance (Scheffé's method) was used to compare the average volume index between the habitat types for each food category.

Results

Abundance of Shrews

In 1988, the relative abundances of the shrew species differed significantly among the three habitat types ($p < 0.05$). In addition, *S. unguiculatus* was numerically most dominant in the riparian forest and wind-shelter belt whereas *S. gracillimus* was most dominant in the spruce forest (Fig. 1-A). *S. caecutiens* was least abundant in all three habitat types. The numerical relationship among the three species in 1989 was similar to those in 1988 (Fig. 1), although statistical tests could not be conducted between the riparian forest and the other two types due to insufficient data.

In 1988, the abundance of *S. unguiculatus* differed significantly ($p < 0.01$) among the three habitat types. Additionally, *S. unguiculatus* was more abundant in the riparian forest and wind-shelter belt than in the spruce forest (Fig. 1-A). In 1989, the abundance of *S. unguiculatus* differed significantly ($p < 0.01$) among the three habitat types, though it was more abundant in the wind-shelter belt than in either of the other two types (Fig. 1-B). The reduced abundance in the riparian forest, however, may have resulted from over-trapping, as alternative trapping sites were no longer available (see Materials and Methods). *S. gracillimus* differed significantly in abundance among the three habitat types in both 1988 ($p < 0.01$) and 1989 ($p < 0.05$), and was most abundant in the spruce forest in both years (Fig. 1). The abundance of *S. caecutiens* could not be tested statistically among habitat types because the sample size was too small.



within species among habitats

Sp	χ^2	*d.f.*	*p*
S.u.	70.3	2	< .001
S.c.	-	-	-
S.g.	31.3	2	< .001

within species among habitats

Sp	χ^2	*d.f.*	*p*
S.u.	24.4	2	< .001
S.c.	-	-	-
S.g.	8.9	2	< .05

Fig. 1. Abundances of *Sorex unguiculatus*, *S. gracillimus*, and *S. caecutiens* in three habitat types in northern Hokkaido in 1988 and 1989. Letters above bars indicate a significant difference ($\alpha = 0.01$) according to χ^2 tests (H_0 : the proportion of the three species does not differ between habitats) ; the same letters indicate non-significant differences. Note that statistical tests could not be made between either the riparian forest and wind-shelter in 1988, or between the riparian forest and the other two habitats, due to insufficient sample sizes. Tables in the figure indicate the result of one-sample χ^2 tests for the abundance of shrews between habitats in each species (H_0 : the abundance of a shrew species does not differ among the three habitats). Note that different kinds of pitfall traps were used in 1988 and 1989, and thus the number of shrews captured per 100 trap-nights could not be compared directly between the two years.

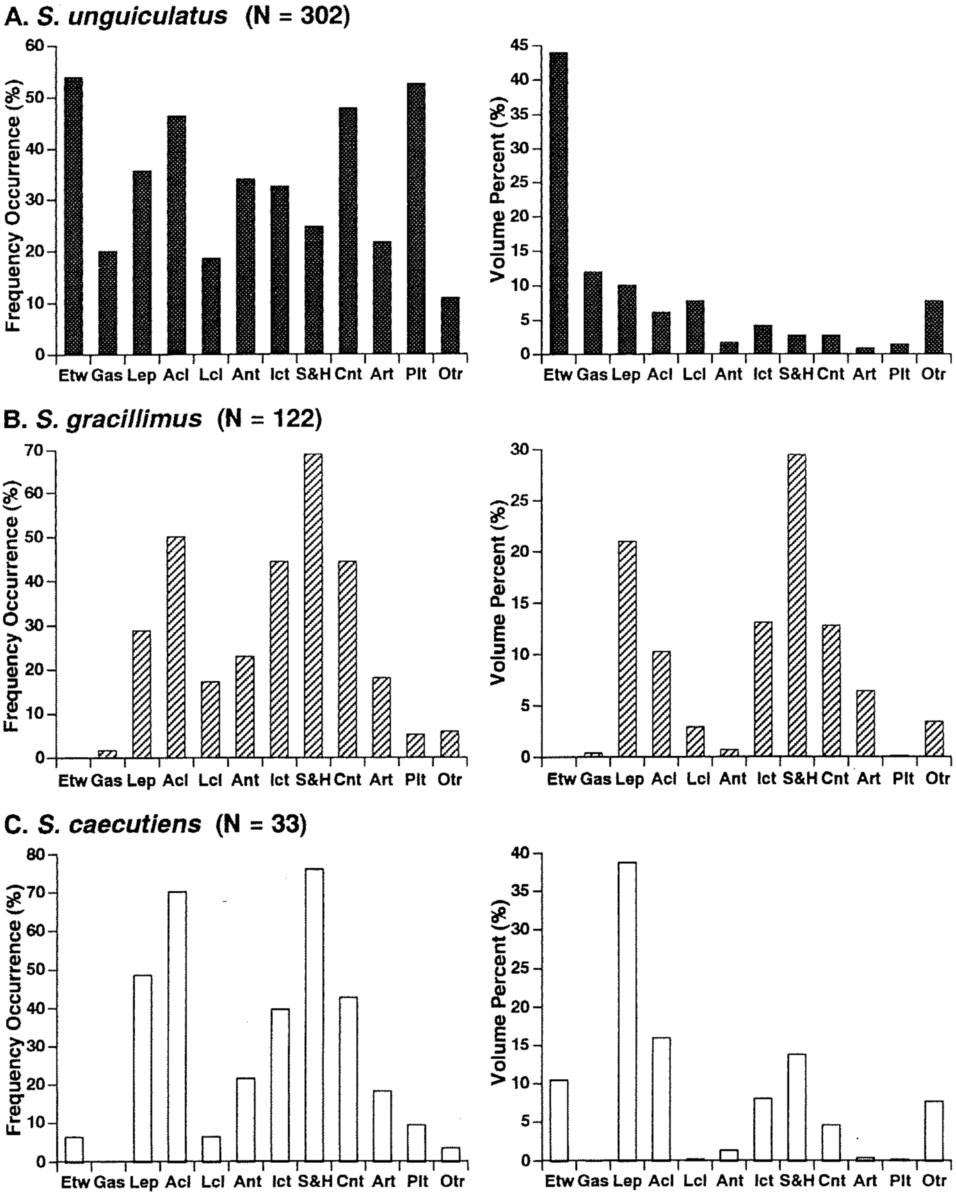


Fig. 2. Interspecific differences in diet use (percent frequency of occurrence and percent volume index) among *Sorex unguiculatus*, *S. gracillimus*, and *S. caecutiens* in northern Hokkaido. Etw=earthworms; Gas=snails and slugs; Lep=larval lepidopterans; Acl=adult coleopterans; Lcl=larval coleopterans; Ant=adult ants; Ict=other insects; S&H=spiders and harvestmen; Cnt=centipedes; Art=other arthropods; Plt=plants; Otr=other food items.

Dietary Analysis of Shrews

The diets of *S. unguiculatus* and *S. gracillimus* differed considerably, while that of *S. caecutiens* was intermediate between the other two species though more similar to *S. gracillimus* (Table 2). Earthworms and gastropods (slugs and snails) were the major constituents in the diet of *S. unguiculatus* (Fig. 2). This shrew also consumed small epigeal arthropods such as insects, spiders and harvestmen, and centipedes, although their volume index percentages were small. In contrast, *S. gracillimus* did not eat earthworms at all and consumed few slugs and snails (Fig. 2). The main prey items of *S. gracillimus* were small arthropods, such as spiders and harvestmen, centipedes and insects. The main prey of *S. caecutiens* was also epigeal arthropods, especially larval lepidopterans (Fig. 2). In addition, this species consumed earthworms. The dietary niche was broadest in *S. gracillimus* and narrowest in *S. unguiculatus* (Table 2), although the number of food categories eaten by the latter species was greater than the former. The narrower niche breadth of *S. unguiculatus* was due to its intensive consumption of earthworms.

Table 2. The breadth and similarity of the dietary niches for *Sorex unguiculatus*, *S. gracillimus*, and *S. caecutiens* in northern Hokkaido. Calculations are given in the text. Twelve food categories (earthworms, snails and slugs, larval lepidopterans, adult coleopterans, larval coleopterans, ants, other insects, spiders and harvestmen, centipedes, other arthropods, plants, and other foods) were used for the calculations.

Species	N	Breadth	Similarity	
			S. unguiculatus	*S. gracillimus.*
S. unguiculatus	302	4.27		
S. gracillimus	122	5.56	0.34	
S. caecutiens	33	4.61	0.45	0.62

Foods consumed by *S. unguiculatus* varied among habitat types (Fig. 3-A). The proportion of frequency occurrence for each food category differed significantly ($p<0.01$) between riparian forest and wind-shelter belt. Within each category, the frequencies of larval coleopterans and other insects varied significantly among habitat types. The average volume indices of earthworms and larval lepidopterans differed significantly among habitat types. The dietary niche breadth varied among the habitat types in *S. unguiculatus*, being narrowest in the spruce forest (Table 3). This reflected the high consumption of earthworms there.

In *S. gracillimus*, the proportion of the frequency occurrences of seven food categories did not vary significantly ($p\geq0.05$) among the three habitat types (Fig. 3-B). In addition, no frequency occurrence of an individual food category differed significantly ($p\geq0.05$) among habitat types. Only the average volume index of adult coleopterans varied significantly among habitat types. The niche breadth of *S. gracillimus* tended to be constant among the habitat types, in contrast to *S. unguiculatus* (Table 3).

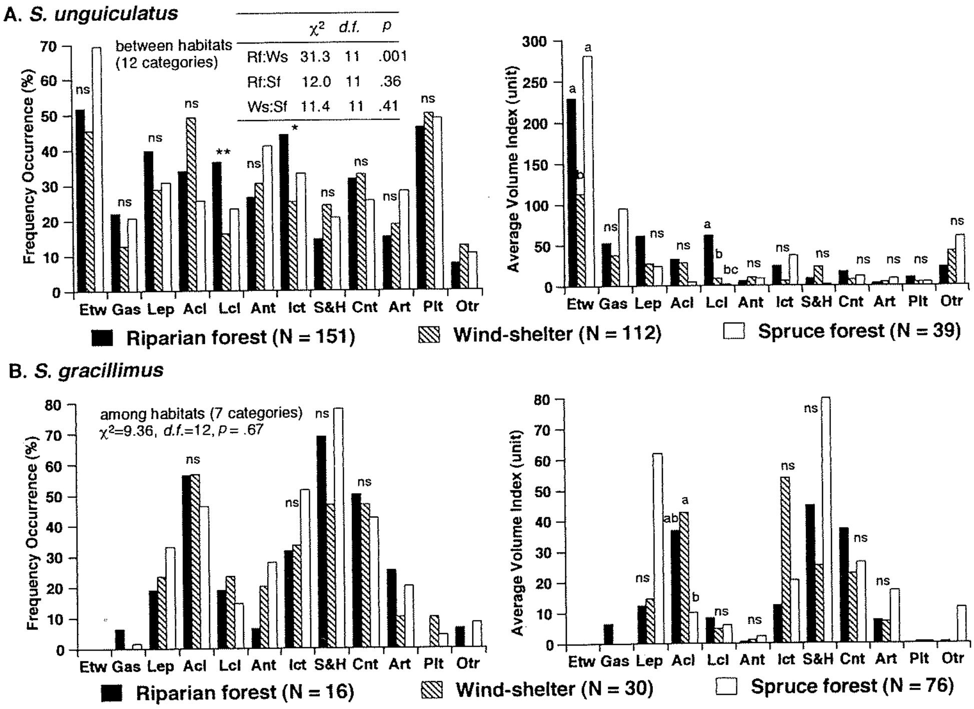


Fig. 3. Differences in diet use (percent frequency of occurrence and average volume index per capita) among three habitats in *Sorex unguiculatus* and *S. gracillimus* in northern Hokkaido. Letters above bars of the frequency occurrence graphs are the results of one-sample χ^2 tests (H_0 : the frequency of a food category does not differ among the three habitat types) ; $** = p < 0.01$, $* = p < 0.05$, ns$= p \geq 0.05$. Letters above bars of the average volume index graphs indicate a significant difference ($\alpha = 0.05$) according to ANOVA using Scheffé's method (H_0 : the average volume index for a food category does not differ significantly among the three habitats). When the same letters are included between habitat types, the difference is not significant. The tables within the frequency occurrence graph shows the result of χ^2 tests (H_0 : the proportion of frequency occurrence does not differ between habitat types. Etw, Gas, Lcl, Plt, and Otr were omitted for analysis in *S. gracillimus*). See Fig. 2 for abbreviations.

Table 3. Changes in the dietary niche breadths and similarities of *Sorex unguiculatus* and *S. gracillimus* among the three habitat types in northern Hokkaido.

Habitat types	Riparian forest	Wind-shelter belt	Spruce forest
Breadth			
S. unguiculatus	4.15	5.04	3.00
S. gracillimus	5.25	4.77	4.64
Similarity	0.32	0.33	0.22

The differences in the dietary use of *S. caecutiens* could not be statistically compared among the three habitat types, owing to the small sample sizes. I just note that earthworms were only consumed by this species in the wind-shelter belt.

Food Resource Conditions

The biomass of earthworms was significantly greater in the riparian forest than in either the wind-shelter belt or the spruce forest, but did not differ significantly between the latter two habitats (Fig. 4). Similarly, the capture (No./100TN) of arthropods was also significantly greater in the riparian forest than in the other two habitat types (Fig. 4). In addition, the captures of adult small coleopterans and ants were obviously greatest in the riparian forest, whereas that of centipedes was greatest in the wind-shelter belt. Other arthropods did not show clear differences in their relative abundances between the habitat types.

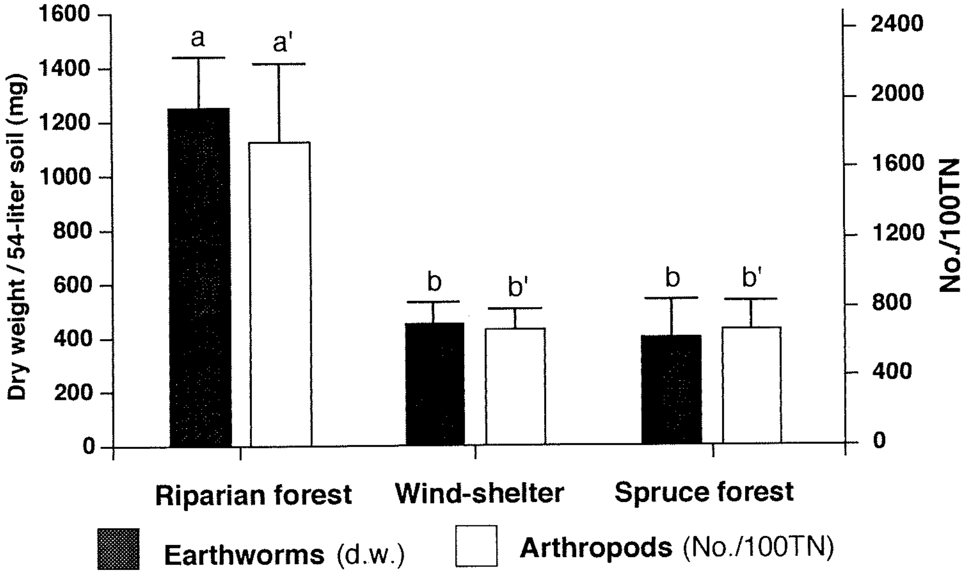


Fig. 4. Numbers of arthropods (mean No./100TN + *SE*) and biomass of earthworms in the soil (mean dry weight per 54liter soil + *SE*) in three habitat types in northern Hokkaido, 1989. The same letters above bars indicate non-significance difference ($p \geq 0.05$) between habitat types according to Wilcoxon's signed rank tests.

Earthworm Availability and Consumption by S. unguiculatus

The biomass of earthworms was high in the riparian forest and low in both the wind-shelter belt and the spruce forest, while the earthworm availability per individual *S. unguiculatus* was highest in the spruce forest and lowest in the wind-shelter belt (Table 4). The average volume index for earthworms was positively related to the availability per individual shrew. On the other hand, earthworm consumption by the *S. unguiculatus* population was highest in the riparian forest, which reflected the greater earthworm biomass there.

Table 4. Biomass in the soil, relative availability, and relative consumption of earthworms by *S. unguiculatus* in three habitat types during periods without snow-cover in northern Hokkaido. Numbers in parentheses are relative values when that in the spruce forest is 1.0.

	Riparian forest	Wind-shelter belt	Spruce forest
Total earthworm biomass (mg/594liter soil)	9,995.1 (3.17)	3,571.8 (1.13)	3,157.2 (1)
No./100TN of *S. unguiculatus* in 1988	35.00 (5.25)	32.23 (4.83)	6.67 (1)
1. Relative availability	285.6 (0.60)	110.8 (0.23)	473.3 (1)
2. *AVI* for earthworms (unit)	229.1 (0.82)	112.4 (0.40)	279.9 (1)
3. Relative consumption by shrew population	8,018.5 (4.30)	3,622.7 (1.94)	1,866.9 (1)

1 Biomass/(No./100TN).

2 Average volume index per individual *S. unguiculatus* for earthworms.

3 (No./100TN)×(*AVI* of earthworms).

Discussion

The abundance of three sympatric shrew species in northern Hokkaido did not appear to be determined solely by food abundance in their various habitats (as determined by the biomass of earthworms and the surface activity of arthropods) during seasons without snow-cover. If an animal population is at equilibrium, food abundance may determine the equilibrium abundance of that animal (e. g., Brown 1969). Under such conditions, shrews should be abundant in habitats where their principal prey is abundant. In fact, Butterfield *et al.* (1981) and Yalden (1981) showed that abundances of *S. araneus* and *S. minutus* in Europe were related to the abundance of their principal prey. If this also holds true for the shrews of Hokkaido, both *S. unguiculatus* and *S. gracillimus* should be most abundant in the riparian forest and less abundant in the wind-shelter belt and spruce forest, since earthworms and small epigeal arthropods were much more abundant (or more active) in the former habitat type than in the latter two (Fig. 4). These predictions, however, were not confirmed in the present study (Fig. 1; except for the result of *S. unguiculatus* in 1989 because there seemed to be sampling bias; see Materials and Methods for details). Thus, the biomass of earthworms and the soil surface activity of arthropods did not determine the abundances of *S. unguiculatus* and *S. gracillimus*.

What, therefore, does determine the shrews' abundance? One factor might be abiotic environmental conditions of habitats. *S. unguiculatus* tended to be more abundant and *S. gracillimus* less abundant in the riparian forest and wind-shelter belt than in the spruce forest (Fig. 1, except for the data in 1989). Common abiotic conditions shared by the riparian forest and wind-shelter belt are altitude, snow-covered periods, and snow depth (Table 1). These conditions differed markedly between the spruce forest and the other two habitat types (Table 1, see also Fujiwara *et al*. 1994). Furthermore, distributional survey of shrews in Hokkaido shows that *S. gracillimus* tends to outnumber *S. unguiculatus* at higher altitudes and in wet lands (Ohdachi and Maekawa 1990) and the abundance of the former species tends to be greater in northern regions than in central and southern regions in Hokkaido (personal observation). It is, therefore, feasible that abiotic environmental conditions may have affected the abundances of *S. unguiculatus* and *S. gracillimus* in the study area.

The dietary niche of *S. unguiculatus* was very narrow in the spruce forest (Table 3), which was attributed to the high earthworm consumption there (Fig. 3). This may in turn have resulted from the greater availability of earthworms per capita in the spruce forest. Factors other than prey abundance, such as temperature and snow depth, may have limited the abundance of *S. unguiculatus* there. As a result, the low density of *S. unguiculatus* would reduce intraspecific competition for earthworms, thereby leading to a high availability of earthworms per capita (Table 4). This would promote the high consumption of earthworms.

The potential interspecific relationships between *S. caecutiens* and the other two species also merit discussion. *S. caecutiens* was the rarest of the three main shrew species occurring in the study area (Fig. 1), though it is numerically dominant in some other parts of Hokkaido (Ohdachi and Maekawa 1990). *S. caecutiens* and *S. gracillimus* tend not to occur together as the numerically dominant and second dominant species in Hokkaido (Ohdachi and Maekawa 1990), which suggests the existence of a negative ecological relationship between them. Furthermore, *S. caecutiens* has a dietary niche that is more similar to that of *S. gracillimus* than to that of *S. unguiculatus* (Table 2 ; see also Abe 1968, Inoue and Maekawa 1990). The observed numerical relationship between *S. caecutiens* and *S. gracillimus* in Hokkaido may well be related to the similarity in their diets. Interspecific competition may thus be more severe between *S. caecutiens* and *S. gracillimus* than between *S. caecutiens* and *S. unguiculatus*.

Finally, guild structure of soricids is compared among some regions of the world to find a general pattern of the guild organization. A common structure of soricid guilds among Europe, eastern North America, and Hokkaido is to have one earthworm specialist plus one or more species which feed principally on epigeal arthropods. In western and northern continental Europe and Great Britain, *S. araneus* and *S. minutus* coexist. The former species eats earthworms, slugs, and small arthropods, while the latter eats mainly small arthropods but few earthworms (Rudge 1968, Pernetta 1977, Grainger and Fairley 1978, Butterfield *et al*. 1981, Bauerová 1984, Churchfield 1984). Hence, *S. araneus* and *S. minutus* appear ecologically "equivalent" to *S. unguiculatus* and

S. gracillimus in Hokkaido, respectively. *S. caecutiens* also coexists with *S. araneus* and *S. minutus* in northern Europe but tends not to be abundant in syntopy with *S. minutus* (Hanski 1986). In central Siberia, however, *S. caecutiens* tends to be more abundant than *S. minutus* (Sheftel 1989, Shvarts and Demin 1994). The numerical relationship between *S. caecutiens* and *S. minutus* in Europe and central Siberia is also similar to that between *S. caecutiens* and *S. gracillimus* in Hokkaido (Ohdachi and Maekawa 1990).

In eastern North America, *Blarina brevicauda* eats mainly earthworms and slugs (Babcock 1914, Whitaker and Mumford 1972). In various regions, epigeal soricine species whose main prey is small arthropods coexist with *B. brevicauda*, for example *S. cinereus* in Michigan (Getz 1961), *S. cinereus* and *S. arcticus* in Manitoba (Buckner 1957, 1966), and *S. cinereus* in Indiana (Whitaker and Mumford 1972). It seems that *B. brevicauda* and the smaller epigeal species are ecologically equivalent to *S. unguiculatus* and *S. gracillimus*/*S. caecutiens* in Hokkaido, respectively. Thus, there exists a similarity in the guild structure of soricids in Europe, East Asia, and North America.

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