Ann. Zool. Fennici 26:339–348. 1989

Distribution and habitat selection of shrews in Finland

Ilkka Hanski & Asko Kaikusalo

Hanski, I. & Kaikusalo, A. 1989: Distribution and habitat selection of shrews in Finland. — Ann. Zool. Fennici 26:339–348.

This paper outlines the main ideas and hypotheses that are relevant for the understanding of the geographical distribution and habitat selection of shrews in Finland. Three of the six species (*Sorex araneus*, *S. minutus* and *Neomys fodiens*) occur throughout Finland, while the three species belonging to the Siberian faunal type (*S. caecutiens*, *S. idoson* and *S. minutissimus*) have more restricted distributions. The larger and competitively superior species are most abundant in the more productive habitats, while the smaller species find a refuge in the less productive habitats or habitat patches, where they may survive because of their low per capita food requirements. Species richness of shrews first increases but then decreases with decreasing latitude in Finland. We suggest that this pattern is related to the size-dependent asymmetry in habitat selection, and to the increasing productivity of habitats from north to south.

I. Hanski, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki, Finland.
A. Kaikusalo, Finnish Forest Research Institute, Ojajoki Field Station, SF-12700 Loppi, Finland.

1. Introduction

Six species of soricine shrews are known from Finland, *Sorex araneus*, *S. caecutiens*, *S. isodon*, *S. minutus*, *S. minutissimus* and *Neomys fodiens*. The species belonging to the European faunal type (*S. araneus*, *S. minutus* and *N. fodiens*) have been correctly identified for a long time, but the presence, correct identity and distribution in Finland of the remaining species belonging to the Siberian faunal type have been discovered only gradually, and the present faunistic knowledge was not achieved until the 1950s (Hanski & Pankakoski 1989). This may seem surprising for a group of mammals in a country in northern Europe, where intensive faunal surveys have a tradition going back some 200 years. There are two explanations for the slow accumulation of knowledge on soricine shrews. First, *Sorex* shrews are deceptively similar in their morphology, in spite of substantial size differences, and second, the trapping techniques commonly used for rodents do not work well with especially the smaller species of shrew. The least shrew, *Sorex minutissimus*, the juveniles of which weigh less than 2 g, is so light that it is not normally caught in ordinary snap-traps. The best technique for catching shrews, whether alive or dead, is pitfall trapping.

In this paper we first outline, in Sections 2 and 3, the main population ecological ideas that are relevant for the understanding of the geographical distribution and habitat selection of shrews in Finland. Section 4 summarizes our current knowledge about the actual distribution of the six species in Finland, three of which seem to be absent in the most southern and western parts of the country. In Section 5 we review data on habitat selection. In the final section we attempt to identify the unifying factors in the geographical distribution and habitat selection of shrews in Finland.

2. Theories of geographical distribution

2.1. Climate and other physical factors

Climate and other physical factors often limit the geographical distribution of mobile animals only indirectly, for instance, via their effects on food availability and foraging efficiency (Brown & Gibson 1983). In soricine shrews, like in many other animals, the northern distribution limit is more likely to be affected by physical factors than the southern one, owing to the increasing severity of the climate with increasing latitude. However, it should be recognized that the subnivean environment occupied by shrews in winter provides considerable protection against extreme climatic conditions. The various behavioural, physiological and anatomical adaptations of shrews to winter conditions in boreal regions are discussed by Aitchison (1984, 1987) and Merritt (1986).

Winter mortality in boreal shrews is not generally correlated with weather conditions (Dokuchaev 1989, Henttonen et al. 1989, Sheftel 1989) but depends primarily on food availability (Dokuchaev 1989). However, exceptional weather in the autumn and in the spring may dramatically increase mortality (Sheftel 1989).

2.2. Food resources

Soricine shrews are highly opportunistic predators, which mostly consume arthropods, and they are unlikely to be much affected by the availability of any particular food type. Two apparent exceptions are earthworms (Lumbricidae), which are much used by many of the larger species of shrew (Rudge 1968, Okhotina 1974, Pernetta 1976), and larch seeds, which constitute an important food source for shrews in North-East Siberia (Dokuchaev 1989).

The level of food availability in general may limit the distribution of shrews at the highest latitudes and at high elevations. Aitchison (1987) suggests that the absence of large invertebrates, such as lumbricids, diplopods and isopods, may explain the absence of large shrews in arctic and alpine areas. The species of shrew with the most northern geographical distribution tend to be small (Aitchison 1987 and references therein), contrary to Bergmann's rule and the general pattern in mammals (Zeveloff & Boyce 1988).

The dominance of small species of shrew in East Siberia (*Sorex caecutiens*, Dokuchaev 1989) and in most of boreal North America (*S. cinereus*) is probably due to the relatively low level of food availability in these areas, in comparison with Europe and West Siberia, where the shrew assemblages are dominated by *S. araneus*, a large species (Hanski 1990).

2.3. Other biotic factors

The three interspecific interactions that may affect species' geographical distributions are competition, predation and mutualism (Brown & Gibson 1983). The latter two are not known to play any significant role in restricting the distribution of soricine shrews, but competition with crocidurine shrews may be of some importance in setting the southern distribution limit of some soricine species.

The two subfamilies of Soricidae, Soricinae and Crocidurinae, have evolved separately since the Oligocene, in the Paleotropical and Holarctic regions, respectively (Repenning 1967). Genoud (1988) discusses the various adaptations in Soricinae and Crocidurinae to warm (tropical) and cold (boreal) climates, respectively. In Europe, the two subfamilies have largely complementary distributions, suggesting broad-scale competitive exclusion (Poitevin 1984). Apart from competition with crocidurine species, an important factor limiting the southern distribution of soricine shrews may be their exceptionally high basic metabolic rate, a definite advantage in boreal regions but a handicap in warm climates, where high BMR may lead to overheating and a water deficit (Genoud 1988).

2.4. History

Any species present in northern Europe today has had to spread there some time since the last glaciation. Some insight into the spreading of shrews to Finland may be gained by examining the geographical distribution of the different chromosomal races of the common shrew *Sorex araneus*.

Sorex araneus is well known for its exceptionally profuse and rapid chromosomal evolution. Halkka et al. (1987) have divided the Finnish populations into six groups according to the basic chromosome arm combinations of the metacentric chromosomes. The different chromosomal races occupy non-overlapping areas, and their present distributions primarily reflect the postglacial dispersal of the species to Finland, and the old water barriers to dispersal (Fig. 1), though some translocations have probably also occurred in Finland during the past 10 000 years (Halkka et al. 1987). The key point for the remaining species is that the dispersal route from the east, crucial for the Siberian species, has been open for a long time.

2.5. Dispersal barriers

Shrews have an exceptionally high mass-specific metabolic rate (Vogel 1976, 1980, Hanski 1984) and small body energy reserves, which means that shrews have short starvation times and that they are consequently relatively poor dispersers. Shrews may dis-

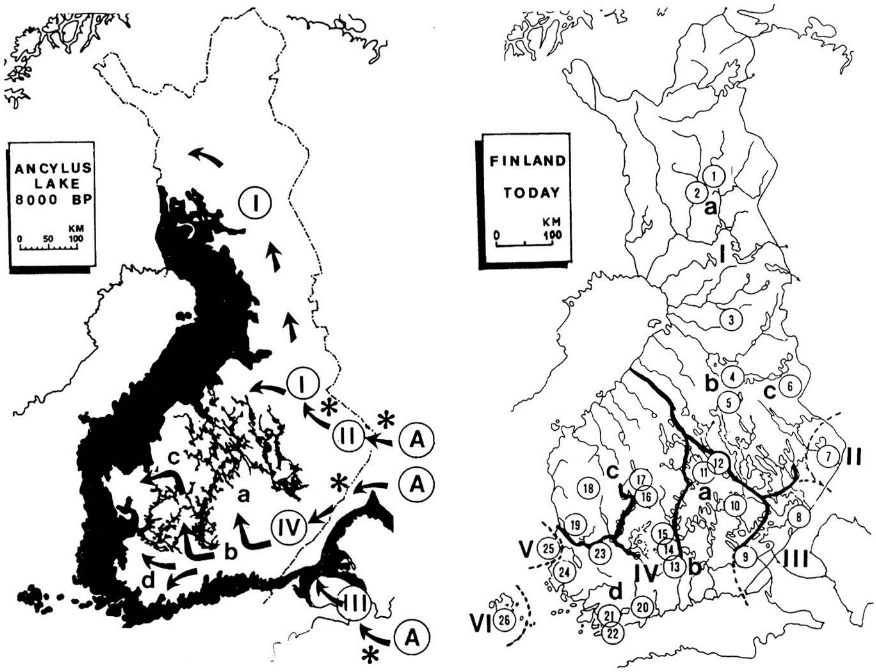

Fig. 1. Hypothetical postglacial migration routes of the chromosomal races of *Sorex araneus* to Finland during the late Ancylus Lake Stage (about 8000 BP). Asterisks indicate steps of reciprocal translocations. The map on the right shows the locations of 26 populations for which data are available and the observed or proposed borders (black lines) between the chromosomal races and racial subgroups, mostly coinciding with the backbones of the postglacial Ancylus Lake gulf systems (from Halkka et al. 1987). Recently, a population from Kilpisjärvi, NW Finnish Lapland, has been found to represent the race reported from North Sweden and has been found to be different from the race present in the rest of North Finland.

perse some kilometres across water by swimming (Skarén 1980, Hanski 1986) and they may run across ice in winter (Tegelström & Hansson 1987), but any greater expanses of open water or ice present severe dispersal barriers to shrews. Newfoundland, which is separated by 25 km of water from Labrador, did not have any shrews before *Sorex cinereus* was introduced there in 1958 to control the outbreaks of the larch sawfly *Pristiphora erichsonii* (Buckner 1966, Warren 1970). For the dispersal to and the distribution of shrews on the large islands in northern Europe, see Peltonen et al. (1989).

2.6. Habitat patchiness

The theory of metapopulation dynamics (Levins 1969, 1970, Hanski 1989) predicts that a species becomes regionally extinct if the average size of the habitat patches is smaller and/or their average isolation is greater than a threshold value. If the average size of the habitat patches decreases or their average isolation increases along a geographical gradient, the distribution of a species may end abruptly where the threshold value is reached (Levins 1969, Carter & Prince 1981).

3. Theories of habitat selection

In this paper we are concerned with the macrohabitat selection of shrews — their occurrence in different types of forest, or patches of forest, meadows, etc. At a smaller spatial scale, at the scale of the home ranges of single shrews, coexisting species show differences in their use of different microhabitats (Saarikko 1989). For instance, while the larger species spend much time foraging underground, the smaller species move more between the forest litter and the soil surface (Okhotina 1974, Hanski 1990). As there is no sharp distinction between microhabitat and macrohabitat selection, both of which are affected by partly the same factors, our choice of coverage is somewhat arbitrary.

3.1. Food availability

The average level of food availability must exceed a threshold value, dependent on individual food requirements and foraging efficiency, to allow survival and reproduction in a particular habitat. As the per capita food requirement is about twice as high in the large species of shrew (*S. isodon* and *S. araneus*) as it is in the smallest species (*S. minutissimus* and *S. minutus*; Hanski 1984), the smaller species may potentially occur in a range of habitats that are too unproductive for the larger species.

Apart from the average, variance in food availability may also influence habitat selection (Hanski 1989). Large species have longer starvation times than small species, and they are hence potentially able to use habitats with greater variance in food availability (Hanski 1985). For risk-sensitive (micro)habitat selection in *S. araneus,* see Barnard & Brown (1985) and Barnard et al. (1985).

3.2. Resource competition

Assuming that population dynamics are density-dependent, as they most certainly are in soricine shrews (Kaikusalo & Hanski 1985, Henttonen et al. 1989), and that the habitats vary in their intrinsic suitability, the range of habitats occupied is expected to depend on population density. In the ideal free habitat distribution, habitats are occupied in the order of decreasing intrinsic suitability, the less suitable habitats not being occupied until increasing density in the more suitable habitats has sufficiently suppressed the fitness of individuals (Fretwell & Lucas 1970).

Rosenzweig (1981, 1985) has extended the single-species theory of ideal free habitat selection to two competing species. His main result is that, depending on the relative suitabilities of two habitats to two species, they may exclusively specialize in different habitats, or one or both species may be present in both habitats. In particular, an inferior competitor may exclusively select a poor habitat because of competition with a stronger competitor (Pimm et al. 1985).

3.3. Interference competition with other species

Large body size is an advantage in interference competition in vertebrates in general, and in shrews in particular (Crowcroft 1957, Saarikko 1989). Therefore, the absence of a species from a particular habitat may be due to interference competition with one or more larger species.

In this section, we shall examine a model of coexistence of competitors based on habitat selection. The model includes the influence of habitat productivity (food availability) and interference competition (Hanski 1990, modified from Lande 1987), and it will be developed for two species, though it can be generalized for several competitors. We assume that one of the species is larger, and hence superior in interference competition to the smaller species. The large species may exclude the small one from the most productive habitat patches, but the small species finds a refuge in the less productive habitat patches due to its lower per capita food requirement. The question of interest is: under which conditions may the two species coexist regionally, in a system of habitat patches?

Assume that the environment is divided into discrete patches of three different qualities, in which all of the patches are the size of individual territories. The worst patches (fraction u_1 of all patches) are unsuitable for both species, the best patches (fraction h) are suitable for both species, while the remaining patches (fraction u_2) are suitable for species 2 (smaller species) but unsuitable for species 1 (larger, dominant species). Competition is asymmetric: species 2 can only establish itself at a patch in the absence of species 1, but species 1 can always replace an individual of species 2. Dispersing juveniles are able to search for m patches before perishing, unless they find an unoccupied, suitable patch and establish a territory. Denoting by p_1 the fraction of patches occupied by species 1 ($0<p_1<1$), Lande (1987) shows that, at equilibrium,

$$(1-(u_1+u_2+p_1h)^m)R_0' = 1, \qquad (1)$$

and

$$p_1 = 1-(1-k_1)/h, \qquad (2)$$

where R_0' is the net lifetime production of female offspring per female, conditional on the mother's finding a suitable territory (for details see Lande 1987), and $k_1 = (1-1/R_0')^{1/m}$. The equilibrium fraction of patches occupied by species 2 is

$$p_2 = 1-(1-k_2)/[u_2+(1-p_1)h]. \qquad (3)$$

Fig. 2 shows that, depending on the structure of the environment, in other words the values of u_1, u_2 and h, neither species can maintain a population in the system of habitat patches, species 1 or 2 will occur alone,

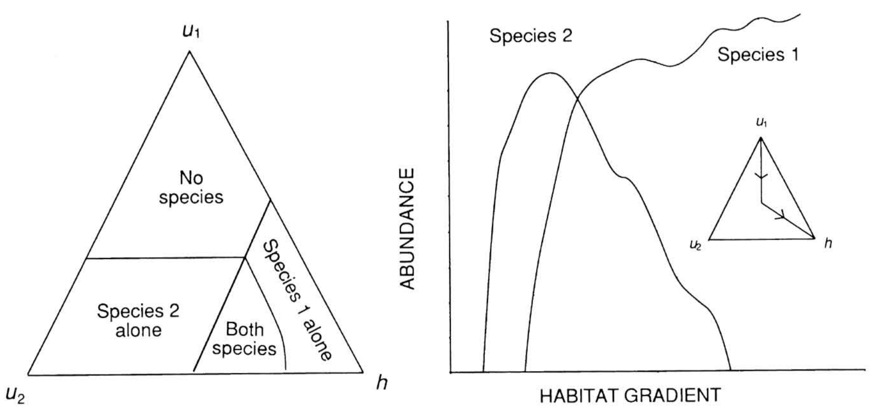

Fig. 2. A model of habitat selection. u_1, u_2 and h are the proportions of habitat patches that are not suitable for any species (u_1), are suitable for species 2 (an inferior competitor) but unsuitable for species 1 (a superior competitor; u_2), and are suitable for both species (h). The figure on the left gives an example of how environments with different values of u_1, u_2 and h are expected to have no species, species 2 alone, species 1 alone, or both species 1 and 2. The figure on the right gives an example of varying relative abundances of species 1 and 2 along a gradient of increasing productivity (as indicated in the insert).

or the two species may coexist. Extrapolating the model to multispecies assemblages, species diversity is first expected to increase but eventually to decrease with increasing habitat productivity. Abramsky & Rosenzweig (1984) have reported such a humped species richness curve for desert rodents (though their explanation of this pattern is different from the one suggested here).

3.4. Predators and parasites

There is no evidence that predation or parasitism would affect the habitat selection of soricine shrews. See Korpimäki & Norrdahl (1989) and Haukisalmi (1989) for comprehensive reviews of the predation and parasitism of shrews.

4. Distribution of shrews in Finland

Of the six species of shrew known from Finland, three species occur throughout the country from the Åland islands to northern Lapland: *Sorex araneus*, *S. minutus* and *Neomys fodiens*. Peltonen et al. (1989) describe their occurrence in the Åland islands and other large islands and island groups in northern Europe. There are no known gaps in their distributions, apart from small islands in the sea and in lakes. These absences are undoubtedly due to isolation and the small size of the islands, which decrease the rate of colonization and the time of persistence of small populations (Hanski 1986). In the case of the water shrew *N. fodiens*, many absences may be due to lack of suitable habitat on smaller islands (Peltonen et al. 1989).

The remaining three species, *Sorex isodon*, *S. caecutiens* and *S. minutissimus*, belong to the Siberian faunal type and have a more restricted distribution in Finland. The maps in Fig. 3 show all known records of these species that have been accumulated since the 1950s, including our own records, records from the literature and museum collections, and unpublished records by other individuals (see the Acknowledgements). The observations have been recorded on 10 by 10 km^2 Atlas grids. Black dots represent records confirmed by a specimen, while open circles are records obtained from diet analyses of birds of prey. Most of the latter records are from Mikkola (1972) and from K. Huhtala's unpublished studies (Department of Zoology, University of Oulu), mostly originating from samples collected at nests and hence probably representing local prey populations. *Sorex caecutiens* has the widest distribution of the Siberian species in Finland. It was previously considered to be restricted to the east and the north, but it appears to be entirely absent only from the archipelagoes surrounding the Baltic coast (Fig. 3). *Sorex caecutiens* is however scarce and its distribution may be patchy in southern and western Finland, while it is most abundant in the eastern part of Finland, and especially in Lapland; in parts of eastern Lapland it is the numerically dominant species (Peltonen et al. 1989).

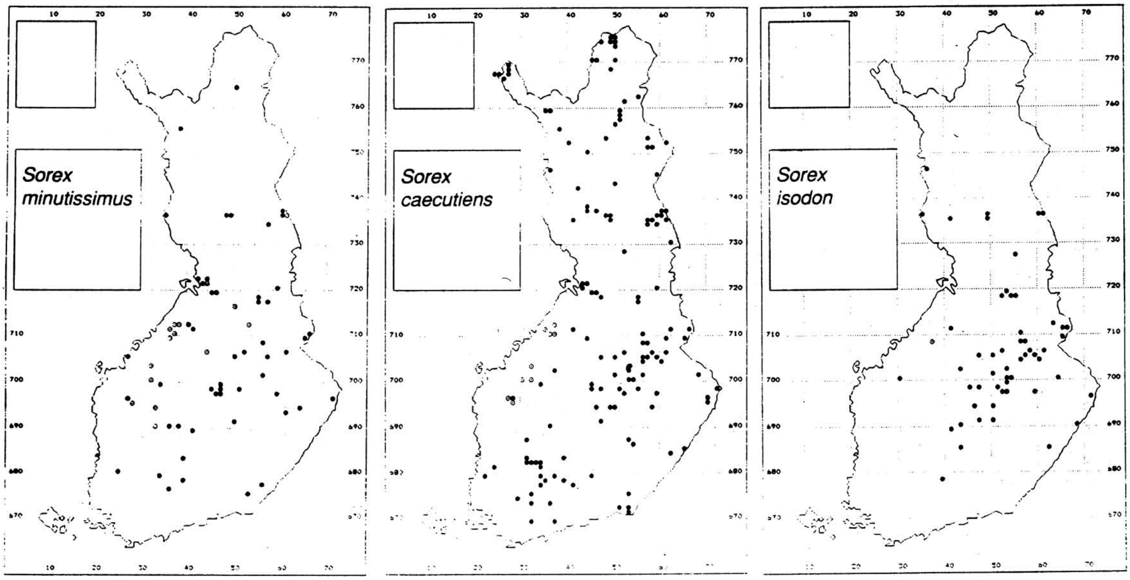

Fig. 3. Distribution of *Sorex minutissimus*, *S. caecutiens* and *S. isodon* in Finland. The black dots represent records confirmed with specimens, while the circles are records based on bones recovered from the nests of birds of prey.

Sorex isodon, the largest *Sorex* in Finland, occurs in the central and eastern parts of the country, including the southern fringes of forest Lapland (Fig. 3). This species has never been caught during long-term and intensive trapping studies in northern Lapland (Kilpisjärvi, Pallasjärvi and Inari area) or on the south coast (Helsinki and Hamina), and it is apparently entirely absent in most of Lapland and in the most southern and western parts of Finland (Fig. 3). How patchy the distribution of *S. isodon* in Central and eastern Finland is is not known, but the most southern (Lammi) and western (Kauhava) records seem to be isolated.

Sorex minutissimus, the smallest shrew in Finland and in all of boreal Eurasia, is also the rarest one: no one has ever found and reported a "local population" of this species, in other words a place where one could predictably find at least some individuals whenever wanted. To what extent the rarity of *S. minutissimus* is only apparent, due to difficulty of trapping it, is not known. *Sorex minutissimus* is generally caught only in pitfalls.

Taking into account the real or apparent rarity of *S. minutissimus*, it appears to have the same distribution as *S. caecutiens*, in other words most of Finland, excluding the Åland islands and possibly the very north of Lapland (though in Siberia *S. minutissimus* occurs even in the tundra; Judin 1962).

5. Habitat selection

Tables 1 and 2 and Fig. 4 present data on habitat selection of Finnish *Sorex*. The key pattern is the higher frequency of the larger species in the more productive habitats. The largest species, *S. isodon*, is most abundant in patches of the most luxuriant spruce forest on deep soils; in abandoned fields with thick grass cover; and in natural wet meadows by lakes and rivers. The common factor characterizing these habitats is deep, fertile soils with high biomass of soil arthropods, including the lumbricids, a key food resource for large shrews.

The smaller species are absolutely or relatively more abundant in less productive habitats with often shallow or barren soils, for example pine forests on sandy soils and bogs. The shift towards less productive habitats with decreasing body size is especially

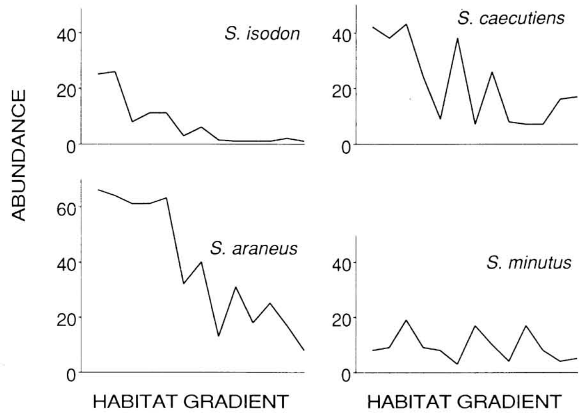

Fig. 4. Habitat selection of *S. isodon*, *S. araneus*, *S. caecutiens* and *S. minutus* in the Soviet Union. The horizontal axis gives 13 different habitat types arranged in an order of decreasing pooled density of *Sorex*, which is well correlated with the productivity of the habitat. The vertical axis gives the average density of the species in the different habitats in tens of studies from different parts of the Soviet Union (B. Sheftel & I. Hanski unpubl.).

clear amongst the three species *isodon*, *araneus* and *caecutiens*, which are very similar in ecology and morphology apart from their size differences. *Sorex minutus* and especially *S. minutissimus* are generalists and occur relatively evenly in most habitat types. We suggest that habitat selection in the large (*isodon*, *araneus* and *caecutiens*) and small species (*minutus* and *minutissimus*) is based on partly different factors, related to differences in their microhabitat and food selection, especially in their use of below and above ground microhabitats. The water shrew *Neomys fodiens* is the most extreme specialist, largely confined to the vicinity of small bodies of water.

6. Discussion

Habitat selection in boreal shrews supports the combination of habitat productivity (food availability) and the interference competition hypotheses: the larger species are most frequent in the most productive habitats, whereas the smaller species are relatively or absolutely more numerous in barren habitats. The model described in Section 3 assumed interspecific territoriality, which has been reported for shrews in North America (Hawes 1977) and Siberia (Moraleva 1987). There are no studies on territoriality of shrews in Finland, but we might expect interspecific

Table 1. Habitat selection of *Sorex* shrews in Soviet Karelia (from Ivanter 1981). The figures show the number of individuals per 100 trap-nights in a large set of data. The species are *S. isodon*, *araneus*, *caecutiens*, *minutus* and *minutissimus*.

Habitat type	*iso*	*ara*	*cae*	*min*	*mss*
Dry pine forest	–	56	10	19	–
Pine forest	1	46	17	19	1
Spruce forest	1	83	11	20	1
Mixed forest	1	37	13	7	3
Deciduous forest	2	112	6	20	1
Clear-cut	1	32	2	1	1
Meadows	1	71	4	11	1
Edge of bog	–	87	1	10	–

Table 2. Habitat selection in *Sorex* shrews: percentage of individuals caught from barren forest types in six studies. As the distinction between barren versus more fertile forest types varied between the studies, as did the sampling effort in different forest types, only the rank order of the species can be fairly compared between the studies. All the localities, except Petrozavodsk in Soviet Karelia (Ivanter 1981), are in Finland.

Localities	*iso*	*ara*	*cae*	*min*	*mss*
Loppi (AK)	–	31	49	11	–
Evo (IH)	–	31	48	43	–
Kuhmo (IH)	3	13	20	17	75
Petrozavodsk	11	34	61	49	47
Sotkamo (AK)	22	24	45	22	88
Kilpisjärvi (AK)	–	38	60	37	–

Table 3. Shrew populations before and after clear-cutting of an old spruce forest in Sotkamo, eastern Finland. The figures show the number of individuals per 100 trap-nights (snap-traps). Trapping was conducted in the autumn (A. Kaikusalo unpubl.).

	Before (average 1966–70)	After				
		1971	1972	1973	1974	1975
S. araneus	2.9	0.2	3.2	1.5	1.6	1.9
S. isodon	0.9	–	–	–	–	–
S. caecutiens	0.7	–	0.2	–	–	–
S. minutus	0.4	–	–	–	0.2	–

territoriality amongst *isodon*, *araneus* and *caecutiens*. Interspecific territoriality does not occur between *araneus* and *minutus* (Croin Michielsen 1966), but it is still possible that the larger *araneus* reduces the numbers of *minutus* in the habitat patches where the former is abundant (Malmquist 1985, Dickman 1988).

The smaller species are not entirely excluded from the best habitats, as assumed in the model in Section 3, possibly because extensive tracts of any "habitat" are typically mosaics of habitat patches varying in quality. More detailed observations on uniform patches of high-quality habitat have revealed complete dominance by a large species. For example, *S. isodon* occurs alone in high density in restricted areas of exceptionally favourable habitat (U. Skarén pers. comm.). Table 3 presents data on changes in the species composition of shrews at a site following clear-cutting, which increased the dominance of *S. araneus*. We suggest that clear-cutting reduces variation in habitat quality and thereby makes coexistence of many species more difficult.

The habitat productivity-interference competition hypothesis about coexistence of competitors is likely to apply to many other guilds apart from shrews. One good example is the coexistence of weasels and stoats in boreal regions (King & Moors 1979, Erlinge & Sandell 1988, King 1989).

We shall now turn to the geographical distribution of soricine shrews in Finland. Of the six factors mentioned in Section 2, and which could potentially explain the restricted distributions of *Sorex isodon*, *S. caecutiens* and *S. minutissimus* in Finland, some factors may be dismissed with certainty, some factors play at least some role, while the significance of the rest remains unknown.

All the species of shrew have spread to Finland probably from the east since the end of the last glaciation (Fig. 1). An idea of the potential rate of dispersal of soricine shrews is given by the introduction of *Sorex cinereus* to Newfoundland. Following the introduction, *S. cinereus* spread at the rate of 20 km per year to the still unoccupied regions (Warren 1970), suggesting that the dispersal rate as such can hardly explain the absence of the Siberian species in parts of Finland. Their absence from the Åland islands could be explained by isolation, but as the species do not occur in the most southwestern part of Finland there has probably always been little chance of colonization.

Climate is an unlikely explanation of the absence of the three Siberian species from southern Finland, even if these species have a generally more northern geographical distribution than the species that are present in all of Finland. There are no known bioenergetic differences between the European (*araneus* and *minutus*) and Siberian (*isodon*, *caecutiens* and *minutissimus*) species of *Sorex* (Hanski 1984) that would suggest any differences in their tolerances of high temperatures. Nor can interspecific competition as such be invoked as a feasible explanation, because all the six species occur together in most of Finland, and there are no other species of any kind in southern Finland that would compete with the Siberian *Sorex*.

There is, however, the possibility that interspecific competition plays a more subtle role, as assumed in the model of habitat selection in Section 3, in producing the observed patterns of geographical distribution. This model predicted a humped curve of species richness along a gradient of increasing productivity. Habitat productivity, whatever its exact meaning for soricine shrews, must increase from Lapland to South Finland. The observed initial increase but ultimate decrease of species richness with decreasing latitude is consistent with this model of habitat selection.

In accordance with this hypothesis, *S. caecutiens*, a relatively small species, is dominant in the most barren regions of Lapland, where *S. isodon*, the largest species, is entirely absent. Density of lumbricids (Terhivuo 1988), and probably also of other large invertebrates, is low in northern Lapland, probably making the habitats too unproductive for *S. isodon*.

A problem with the habitat selection hypothesis is the absence of *S. isodon*, the presumed superior competitor, in the best-quality habitat patches in southern Finland. We can suggest two testable explanations. First, perhaps the best-quality habitats for (large) shrews in general, and for *S. isodon* in particular, are more wide-spread in Central Finland than in the intensively cultivated areas in southern and northern Finland. Second, and related to the former, suitable habitat patches in the most southern and western parts of Finland may be so small or, which is more likely, so isolated that long-term persistence of *S. isodon* is unlikely. It would be illuminating to introduce *S. isodon* to suitable sites in southern and northern Finland and to follow up the dynamics of such introduced populations.

We conclude by suggesting that the geographical distribution of soricine shrews in Finland much depends on the same elements that determine their habitat selection: quality of habitat patches, and how the quality depends on the size of the species; asymmetric competition between the species, in which large body size is an advantage; and regional dynamics in more or less isolated patches of suitable habitat.

Acknowledgements. We are grateful to the following individuals for sending us their observations on the distribution of shrews: T. Ahola, P. Alaja, H. Henttonen, E. Korpimäki, E. Kuhlman, E. Lindgren, A. Nilsson, T. Nyman, J. Salonen, U. Skarén, R. Sulkava and S. Sulkava. Special thanks are due to the individuals working at the Department of Zoology in the University of Oulu for extensive records from northern Finland.

References

Abramsky, Z. & Rosenzweig, M. L. 1984: Tilman's predicted productivity-diversity relationship shown by desert rodents. — Nature 309:150–151.

Aitchison, C. W. 1984: A possible subnivean food chain. — Carnegie Mus. Nat. Hist. Spec. Publ. 10:363–372.

—"— 1987: Review of winter trophic relations of soricine shrews. — Mammal Rev. 17:1–24.

Barnard, C. J. & Brown, C. A. J. 1985: Risk-sensitive foraging in common shrews (Sorex araneus L.). — Behav. Ecol. Sociobiol. 16:161–164.

Barnard, C. J., Brown, C. A. J., Houston, A. I. & McNamara, J. M. 1985: Risk-sensitive foraging in common shrews: an interruption model and the effects of mean and variance in reward rate. — Behav. Ecol. Sociobiol. 18:139–146.

Brown, J. H. & Gibson, A. C. 1983: Biogeography. — C.V. Mosby Company, London, 643 pp.

Buckner, C. H. 1966: The role of vertebrate predators in the biological control of forest insects. — Ann. Rev. Entomol. 11:449–470.

Carter, R. N. & Prince, S. D. 1981: Epidemic models used to explain biogeographical distribution limits. — Nature 293:644–645.

Croin Michielsen, N. 1966: Intraspecific and interspecific competition in the shrews Sorex araneus L. and Sorex minutus L. — Arch. Néerl. Zool. 17:73–174.

Crowcroft, P. 1957: The life of the shrew. — London, Reinhardt.

Dickman, C. R. 1988: Body size, prey size, and community structure in insectivorous mammals. — Ecology 69:569–580.

Dokuchaev, N. E. 1989: Population ecology of Sorex shrews in North-East Siberia. — Ann. Zool. Fennici 26:371–379.

Erlinge, S. & Sandell, M. 1988: Co-existence of stoat (Mustela erminea) and weasel (Mustela nivalis): social dominance, scent communication and reciprocal distribution. — Oikos 53:242–246.

Fretwell, S. D. & Lucas, H. L. 1970: On territorial behaviour and other factors influencing habitat distribution in birds. — Acta Biotheor. 19:16–36.

Genoud, M. 1988: Energetic strategies of shrews: ecological constraints and evolutionary implications. — Mammal Rev. 4:173–193.

Halkka, L., Söderlund, V., Skarén, U. & Heikkilä, J. 1987: Chromosomal polymorphism and racial evolution of Sorex araneus L. in Finland. — Hereditas 106:257–275.

Hanski, I. 1984: Food consumption, assimilation and metabolic rate in six species of shrew (Sorex and Neomys). — Ann. Zool. Fennici 21:157–165.

—"— 1985: What does a shrew do in an energy crisis? — In: Sibly, R. M. & Smith, R. H. (eds.), Behavioural ecology: 247–252. Blackwell, Oxford.

—"— 1986: Population dynamics of shrews on small islands accord with the equilibrium model. — Biol. J. Linn. Soc. 28:23–36.

—"— 1989: Habitat selection in a patchy environment: individual differences in common shrews. — Anim. Behav. 38:414–422.

—"— 1990: Insectivorous mammals. — In: Crawley, M. J. (ed.), Natural enemies: the population biology of predators, parasites and diseases. Blackwell, Oxford (in press).

Hanski, I. & Pankakoski, E. 1989: Population biology of Eurasian shrews: Introduction. — Ann. Zool. Fennici 26: 335–338.

Haukisalmi, V. 1989: Intestinal helminth communities of Sorex shrews in Finland. — Ann. Zool. Fennici 26:401–409.

Hawes, M. L. 1977: Home range, territoriality and ecological separation in sympatric shrews Sorex vagrans and Sorex obscurus. — J. Mammal. 58:354–367.

Ivanter, E. V. (Ивантер, Э. В.) 1981: О биотопическом распределении землероекбуроэубок. — In: Ivanter, E. V. (ed.), Экология наземных поэвоночных северо-эапада СССР: 78–89. Karelian Branch of Academy of Sciences of USSR, Petrozavodsk.

Judin, B. S. 1962: Ecology of shrews (genus Sorex) of western Siberia. — Trudy Biol. Inst. Akad. Nauk SSSR, Sib. Otd., Novosibirsk.

Kaikusalo, A. & Hanski, I. 1985: Population dynamics of Sorex araneus and S. caecutiens in Finnish Lapland. — Acta Zool. Fennica 173:283–285.

King, C. 1989: The natural history of weasels & stoats. — 253 pp. Christopher Helm, London.

King, C. & Moors, P. J. 1979: On co-existence, foraging strategy and the biogeography of weasels and stoats (Mustela nivalis and M. erminea) in Britain. — Oecologia 39:129–150.

Korpimäki, E. & Norrdahl, K. 1989: Avian and mammalian predators of shrews in Europe: regional differences, between-year and seasonal variation, and mortality due to predation. — Ann. Zool. Fennici 26:389–400.

Lande, R. 1987: Extinction thresholds in demographic models of territorial populations. — Amer. Nat. 130:624–635.

Levins, R. 1969: Some demographic consequences of environmental heterogeneity for biological control. — Bull. Entomol. Soc. Amer. 15:237–240.

—"— 1970: Extinction. — In: Gerstenhaber, M. (ed.), Some mathematical problems in biology: 77–107. Amer. Math. Soc., Providence, R.I.

Malmquist, M. 1985: Interspecific competition in shrews (Soricidae): evolutionary and ecological consequences. — Ph.D. dissertation, Uppsala Univ., Sweden.

Merritt, J. F. 1986: Winter survival adaptations of the short-tailed shrew (Blarina brevicauda) in an Appalachian montane forest. — J. Mammal. 67:450–464.

Moraleva, N. V. 1983: Territoriality of shrews in the Yenisei taiga, based on mark-recapture studies. (In Russian.) — In: On the natural zonation of animals in the Yenesei taiga and forest tundra: 215–230. Nauka, Moscow.

Okhotina, M. V. 1974: Morpho-ecological features making possible joint habitation for shrews of the genus Sorex (Sorex, Insectivora). — In: Okhotina, M. V. (ed.), Fauna and Ecology of the terrestrial vertebrates of the southern part of the Soviet Far East. New Series Vol. 17 (120), Vladivostok.

Peltonen, A., Peltonen S., Vilpas, P. & Beloff, A. 1989: Distributional ecology of shrews in three archipelagoes in Finland. — Ann. Zool. Fennici 26:381–387.

Pernetta, J. C. 1976: Diets of the shrews Sorex araneus L. and Sorex minutus L. in Wytham grasslands. — J. Anim. Ecol. 45:899–912.

Pimm, S. L., Rosenzweig, M. L. & Mitchell, W. A. 1985: Competition and food selection: field tests of a theory. — Ecology 66:798–807.

Poitevin, F. 1984: Biogéographie et écologie des Crocidures Méditerranennées (Insectivores, Soricidés). — Mém. Trav. E.P.H.E., Inst. Montpellier 14. 100 p.

Repenning, C. A. 1967: Subfamilies and genera of the Soricidae. — U.S. Govern. Print. Off., Wash. Geol. Surv., Prof. Pap. 565.

Rosenzweig, M. L. 1981: A theory of habitat selection. — Ecology 62:327–335.

—"— 1985: Some theoretical aspects of habitat selection. — In: Cody, M. L. (ed.), Habitat selection in birds: 517–540. Academic Press, New York.

Rudge, M. R. 1968: The food of the common shrew Sorex araneus (Insectivora, Soricidae) in Britain. — J. Anim. Ecol. 37:565–581.

Saarikko, J. 1989: Foraging behaviour of shrews (Insectivora, Soricinae). — Ann. Zool. Fennici 26:411–423.

Sheftel, B. I. 1989: Long-term and seasonal dynamics of shrews in Central Siberia. — Ann. Zool. Fennici 26:357–369.

Skarén, U. 1980: Vesi Sorex-päästäisten leviämisesteenä. — Savon Luonto 12:44–47.

Tegelström, H. & Hansson, L. 1987: Evidence of long distance dispersal in the Common shrew (Sorex araneus). — Zeitschr. Säugetierk. 52:52–54.

Terhivuo, J. 1988: The Finnish Lumbricidae (Oligochaeta) fauna and its formation. — Ann. Zool. Fennici 25:229–247.

Vogel, P. 1976: Energy consumption of European and African shrews. — Acta Theriol. 21:195–206.

—"— 1980: Metabolic levels and biological strategies of shrews. — In: Schmidt-Nielsen, K., Bolis, L. & Taylor, C. R. (eds.), Comparative physiology: primitive mammals: 170–180. Cambridge University Press, Cambridge.

Warren, G. L. 1970: Introduction of the masked shrew to improve control of forest insects in Newfoundland. — Proc. Tall Timbers Conf., Tallahassee, Florida.

Zeveloff, S. I. & Boyce, M. S. 1988: Body size patterns in North American Mammal faunas. — In: Boyce, M. S. (ed.), Evolution of life histories of mammals: 123–148. Yale Univ. Press, New Haven and London.

Received 27.XI.1989
Printed 22.XII.1989