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Distributional ecology of shrews in three archipelagoes in Finland

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Three species of shrew were found on the Åland Islands: *Sorex araneus*, *S. minutus* and *Neomys fodiens*, whereas the mole *Talpa europaea* has not been able to disperse from the southwest of Finland to Åland. The distributions of insectivorous mammals on Åland and on other large Baltic islands and island groups do not indicate a dynamic balance between immigration and extinction, but the island faunas appear to be colonization limited. On small and less isolated islands in lakes, local shrew populations occur in a dynamic equilibrium between extinctions and colonizations. The dispersal rate of *Sorex araneus* was positively correlated with the density of the species on the mainland. The larger *Sorex araneus* and *S. caecutiens* had a better dispersal ability than the smaller *S. minutus*. *Sorex araneus* had the lowest minimum island size, presumably because of its low extinction rate on small islands.

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1. Introduction

The development of an insular community is affected by variation in the vagility of species (Adler & Wilson 1985, Lomolino 1984) by variation in their dispersal (Hanski 1986) and colonization abilities (Ebenhard 1987) and in their proneness to extinction, as well as by interactions between the species (Simberloff 1978, Haila & Järvinen 1982).

Some insular faunas of terrestrial mammals are colonizationlimited, in particular on oceanic islands, whereas the fragmentation of once contiguous continental habitats may lead to extinction-limited relictual populations, as on landbridge islands (Lawlor 1986). According to the equilibrium theory of MacArthur & Wilson (1963, 1967), the number of species is greatest on large islands situated close to the mainland, and lowest on small, isolated islands. Large islands have more available habitats than small ones (Williams 1964, Williamson 1981), and immigration to large islands is greater than to small ones (Connor & McCoy 1979). The extinction rate is highest on small islands because of small average population size, and because of the often more extreme environmental conditions on small islands than on large (McGuinness 1984). The equilibrium theory of island biogeography seems to be a good explanation for patterns in the occurrence of small mammals on relatively small islands which are not particularly isolated (Hanski 1986, Lomolino 1986).

Because of their small size and high metabolic rate (Vogel 1980) leading to a short starvation time, shrews have a limited capacity to colonize islands. However, shrews have been found on islands located 2–4 km from the mainland. Dispersal to islands may take place both in winter across the ice and in summer by swimming (Hanski 1986, A. Peltonen unpubl.). Absence of hibernating species of mammals from many islands (in North America) implies that crossing the ice is a common mode of dispersal (Crowell 1986, Lomolino 1986). Tegelström & Hansson (1987) found that one *Sorex araneus* had run 4.5 km on the ice and survived. Winter dispersal may be most common in early spring before the ice melts, when there are early insects on ice, which dispersing shrews may feed upon (Hanski 1986).

In this paper we examine the occurrence of shrews in three archipelagoes in Finland representing different scales for shrews. The Åland Islands in the Baltic are fairly isolated and mainland-like for shrews. We also review the occurrence of shrews on other large islands in the Baltic. Studies conducted in Lake

Sysmä in eastern Finland provide data on colonization and extinction events on small islands, while results from Lake Inari in Lapland provide comparative data on island occupancy from a region with only one species of shrew occurring on islands.

2. The three archipelagoes

The Åland Islands are located between Finland and Sweden in the northern Baltic (60°N, 20°E). They consist of the main island of Åland (956 km²) and several thousands of smaller islands, which form a fairly continuous belt as far as southwestern Finland. The longest open-sea distance between Åland and the Finnish mainland is about 2.5 km. Åland is separated from Sweden by 40 km of open sea to the west.

The study areas were Main Åland and four smaller islands: Sottunga, Kumlinge, Föglö and Kökar (27–132 km²). Isolation between these islands, or from other large islands, is 1–5 km, the only exception being Kökar, which is situated 20 km from the nearest large island. Habitat composition on these islands varies from lush deciduous woods to coniferous spruce and pine forests. Shrews were trapped by U-M. Liukko and S. Peltonen in June to September in 1984 and 1985 with snaptraps and pitfall traps (S. Peltonen 1988).

Lake Sysmä in eastern Finland (63°N, 32°E) has 17 islands (0.3 to 8.0 ha) and 25 small islets (<0.2 ha). Maximum isolation from the mainland is about 500 m for the islands and 800 m for the islets. The habitat on the islands is uniform, old mixed coniferous forest. Five mainland study sites represent the same forest type. Trapping was conducted from 1982 to 1986 mostly in May to August using snap-traps, pitfall traps and live-traps (for details see Hanski & Kuitunen 1986).

Forty-seven islands were surveyed by A. Beloff and P. Vilpas in Lake Inari (69°N, 28°E) in Finnish Lapland in 1988. Island area varied from 0.1 to 265 ha, and isolation from the mainland, or from the nearest large island (>20 ha), ranged from 100 to 2300 m. The main habitat on the islands and on the mainland is deciduous forest: birch *Betula pubescens* ssp. *tortuosa* and *B. nana*. Some of the islands and mainland sites on the eastern side of the lake have some coniferous forest. Trapping was carried out in June, July and August 1988, with snaptraps, pitfall traps and live-traps.

3. Results

3.1. Large NW European islands

Table 1 gives the distribution of small insectivorous mammals on some large islands and island groups in northwestern Europe. *Talpa europaea* is found only on Öland and, at least in the 1960s, on Jersey. *Sorex araneus*, *S. minutus* and *Neomys fodiens* are sympatric on Åland, Öland and Saaremaa. *Sorex minutus* is the only shrew on Gotland, Ireland, Outer Hebrides (excluding Lewis), Isle of Man and Orkney, while *S. araneus* is the only *Sorex* species on some smaller, less isolated islands (Malmquist 1985), and it coexists with *N. fodiens* on Hiiumaa.

Table 1. Occurrence of insectivorous mammals on islands and island groups in Northwestern Europe. ara = *Sorex araneus*, min = *Sorex minutus*, fod = *Neomys fodiens*, eur = *Talpa europaea*. + = species present, – = species absent. Data from The Handbook of British Mammals (1977), Siivonen (1977), Bishop and Delany (1963), Van den Brink (1967), Williamson (1981), Malmquist (1985) and Ernits (personal comm.).

Island/ Archipelago	Area (km²)	Isolation (km)	Presence eur	ara	min	fod
Main Åland	956	*	–	+	+	+
Gotland	3001	90	–	–	+	–?
Öland	1344	5	+	+	+	+
Bornholm	588	30	–	+	+	–
Hiiumaa	989	10	–	+	–	+
Saarémaa	2714	<10	–	+	+	+
Ireland	70283	25	–	+	+	–
Outer Hebrides	3500	30	–	Lewis	+	–
Isle of Man	572	30	–	–	+	–
Orkney Islands	881	10	–	–	+	–
Shetland	1426	170	–	–	–	–
The Channel Islands**	195	25–40	Jersey	Jersey	–	–

* See Sect. 2 for information on isolation.
**The Channel Islands have additionally *Crocidura russula* and *C. suaveolens*.

3.2. The Åland archipelago

The first mention of shrews on Åland is in Bergstrand's (1852) booklet, which includes the common shrew *Sorex vulgaris* (=*S. araneus*) and the water shrew *S. fodiens* (=*N. fodiens*). The pygmy shrew was not recorded from Åland before 1970 (Harberg & Harberg 1970). Three species of shrew were found in our survey (sample size 833 shrews): the common shrew *Sorex araneus*, the pygmy shrew *S. minutus* and the water shrew *Neomys fodiens* (for details see S. Peltonen 1988). Both the common shrew and the pygmy shrew were found on Main Åland, as well as on the four islands studied, while the water shrew was caught only on Main Åland. The faunal composition of insectivorous terrestrial small mammals on Main Åland is similar to that of the south-west coast of the Finnish mainland with the exception that the mole *Talpa europaea* is absent from the Åland.

Table 2. Numbers of islands surveyed, occupied by shrews, and the relative abundances of shrews on islands and on the mainland, in five years (individuals/100 trap-nights). We have excluded two islands (S4, S12) and one islet (I5) in 1982, and four islands (S3, S4, S5, S12) and one islet (I5) in 1983, because of very intensive trapping on these islands and islets with the intention of eliminating all small mammals.

	No. of islands	Island occupancy			Island abundance			Mainland abundance		
		ara	cae	min	ara	cae	min	ara	cae	min
1982	17	10	2	5	13.6	1.2	1.3	21.8	5.7	3.9
1983	16	7	4	1	8.6	2.1	0.5	4.1	0.9	1.5
1984	13	2	1	1	1.3	0.3	0.4	5.6	1.7	3.1
1985	3	3	1	1	14.3	1.1	4.6	10.9	3.8	4.4
1986	17	13	2	2	4.9	0.4	0.3	9.4	3.3	1.1

In the Åland archipelago, the islands increase in area and new islands emerge due to continuous postglacial land uplift (the present rate is 5.5 to 6.6 mm per year on the shores of Åland; Ohlson et al. 1984). The expanding land area has led to an increase in habitat diversity, and the distances between islands have shortened, facilitating inter-island dispersal and the establishment of populations of terrestrial mammals. According to Glückert (1978), the first islets in the northern parts of Åland emerged from the Yoldia Sea about 9000 years BP. The coast lines of that time are today 110–120 m above the present sea level. Human colonization began about 6000 years BP, when the climate was warmer than today (Dreijer 1983) and the islands were dominated by deciduous forests (Glückert 1978).

The limited dispersal abilities of shrews imply that their natural dispersal to Åland was not possible before the Bronze Age, about 3500–2500 years BP, when the shore line was still 12–23 m higher than it is today (Glückert 1978). This, however, assumes that the sea was frozen during some winters (during the warm Atlantic period freezing probably did not occur). Today, the sea between Åland and the Finnish mainland freezes in most winters (Anon. 1982).

3.3. Lake Sysmä in eastern Finland

Islands in Lake Sysmä in eastern Finland are small and not very isolated from the mainland. Populations of shrews on these islands are young and relatively unstable, though on the three largest islands (3.0–8.0 ha) populations of *Sorex araneus* have diverged in morphometrics from mainland populations and from each other (Hanski & Kuitunen 1986). At this spatial scale, processes affecting island occupancy depend on species ecology, not on insular history, and direct information about the colonization and extinction events of shrews on islands may be obtained.

Table 2 gives the relative abundances of the common species caught during five years in the study area. The species that were rare on the mainland were absent from the islands: *Sorex isodon*, *S. minutissimus* and *Neomys fodiens*. *Sorex araneus* dominated both on the mainland and on the islands. *Sorex caecutiens* and *S. minutus* had lower abundances on the mainland than *S. araneus*, and were absent from many islands.

The numbers of islands occupied varied from one year to another. *Sorex araneus* had the largest number of island populations in 1982 and in 1986 (Table 2), when its numbers on the mainland were also high. Changes in the numbers of island populations of the two smaller species followed the same pattern, except that *S. caecutiens* had a large number of island populations in 1983. The three species never occurred together on the same island in the same year.

All the shrews caught on small islets must have dispersed from the mainland or from islands, because the islets are too small for breeding and the establishment of local populations (I. Hanski and A. Peltonen, unpubl.). Dispersal to the islets occurred mainly in late summer, and nearly all individuals caught on the islets have been juveniles. The largest species *S. araneus* and *S. caecutiens* have been equally frequent on islets, in relation to their numbers on the mainland, but the smallest species, *S. minutus*, has been rarely caught on the islets. The rate of dispersal of *S. araneus* was highest in 1982 and in 1985, when the density of all small mammals on the mainland was high (I. Hanski and A. Peltonen, unpubl.).

Table 3. The number of possible versus realized colonizations and extinctions, of three species of shrew on 17 islands, and of the two smaller species when *S. araneus* was present on or absent from the island, and the pooled numbers of colonizations and extinctions on 10 small versus 7 large islands, and 9 far versus 8 near islands. Differences (χ^2) were significant in the numbers of extinctions between *S. araneus* and *S. caecutiens* (P=0.034) and between *S. araneus* and *S. minutus* (P=0.007). The extinction rate tended to be higher on small islands than on large islands (P=0.09).

	Colonizations		Extinctions	
	poss.	real.	poss.	real.
Sorex araneus	25	5	28	1
S. caecutiens	38	2	9	3
S. minutus	38	5	13	6
S. caecutiens				
S. araneus present	26	1	7	2
absent	12	1	2	1
S. minutus				
S. araneus present	25	2	11	4
absent	13	3	2	2
Large islands	35	2	34	4
Small islands	66	10	16	6
Far islands	51	6	29	3
Near islands	50	6	21	7

We have analyzed the effects of the size and isolation of islands on the rates of colonization and extinction. For this purpose, the 17 islands were divided into four classes: large islands, near versus far, and small islands, near versus far. The numbers of possible colonizations were counted for each of the three commonest species during five years by including islands where the species was absent in the previous year. The numbers of possible extinctions were counted by including islands in which the species was present in the previous year. Isolation did not significantly affect the rates of colonization and extinction (Table 3). The area of the island did not have a significant effect on colonizations, but populations on small islands tended to have higher extinction rates than populations on large islands (P=0.09). The three species of shrew did not differ in colonizations but the two smaller species had significantly higher extinction rates than *S. araneus*. There were no indications of negative interactions between observed colonizations and extinctions of the two small species and the presence of *S. araneus* on islands.

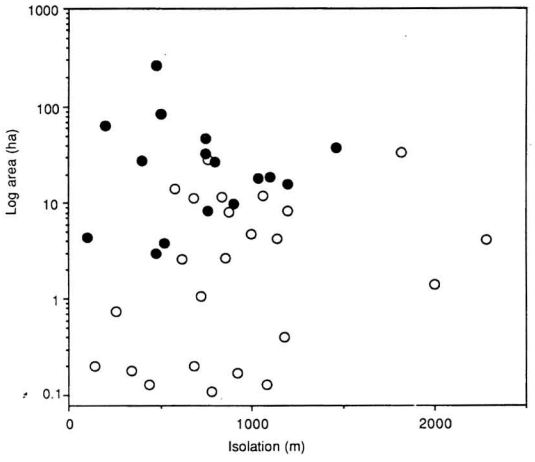

Fig. 1. Presence (●) and absence (○) of *Sorex caecutiens* on 40 islands in Lake Inari in Finnish Lapland in 1988.

3.4. Lake Inari in northern Finland

Sorex caecutiens and *Sorex araneus* were the only shrew species caught from the mainland surrounding Lake Inari in 1988, with 30 and 13 individuals caught, respectively. On the islands, *S. caecutiens* was clearly more dominant, being found on 15 islands (216 individuals), while *S. araneus* was caught only from one island (4 individuals).

The number of shrews caught per trap-night did not correlate with island area (r=–0.38, NS) nor with isolation (r=–0.15, NS), but it is apparent from Fig. 1 that shrews (*S. caecutiens*) were absent from the islands smaller than 3 ha and that they occurred regularly on islands greater than 15 ha. On the 14 islands of size between 3 and 15 ha, shrews tended to be present on the less isolated ones.

4. Discussion

Species number of non-volant mammals on oceanic islands tends to be low largely because colonization events via overwater dispersal are rare; large oceanic islands never attain the species number expected on the basis of their size (Lawlor 1986). Species richness of terrestrial mammals on oceanic islands is thus governed by history and exceedingly low invasion rates. Oceanic islands, as well as landbridge

islands, differ from mainlands in having fewer insectivores, small rodents and hibernators (Crowell 1986), presumably because these taxa have exeptionally low dispersal ability.

Distributions of insectivorous mammals on Åland and on other large islands and island groups in northwestern Europe do not indicate a dynamic balance between immigration and extinction; the island faunas appear to be colonization limited. In contrast, on small and less isolated (<2 km) islands in lakes, shrew populations occur in a dynamic equilibrium between extinctions and colonizations (Hanski 1986).

Surprisingly, although *S. araneus* has a better dispersal ability than *S. minutus* (Hanski 1986), the latter species is more frequent on the large NW European islands (Table 1). One possible explanation for the high frequency of *S. minutus* on these islands is that it may be more easily introduced than *araneus* to islands, for example in ships, which often have a sufficient insect fauna for small shrews to survive (Williamson 1981). However, we have no evidence for this explanation.

The situation in Ireland and on the Isle of Man, where only *S. minutus* is present, may be explained by a postglacial "filtering" landbridge between Scotland and Ireland (Yalden 1981). The land connection persisted about one thousand years (7000–8000 years BP), and it was a shallow and partially flooded peatland, where earthworms, the major prey of *S. araneus* (Pernetta 1976, Churchfield 1984), could not have lived. The landbridge may have been suitable for *S. minutus*, because this species feeds mainly on small beetles, spiders and opilionids, which are available throughout the year on peatlands (Butterfield et al. 1981, Yalden 1981).

The islands shown in Table 1 do not belong to the same category with respect to area and degree of isolation, but in view of the densities and dispersal abilities of shrews, the islands are all large and isolated. The distribution of shrew species on these islands appears to be due to historical contingency, and the variation in species number hardly implies any dynamic balance between immigration and extinction. The main factor determining island occupancy on this scale is probably dispersal, in some cases with human help. For example, there is no doubt that *S. araneus* could survive on Gotland, and by establishing a population there it would hardly increase the extinction probability of *S. minutus* or of any other small mammal.

Of the four species of insectivores and seven species of rodents that occur on the southwest coast of Finland, three insectivores and three rodents occur on Main Åland and two insectivores and two or three rodents on the smaller islands. The mole *Talpa europaea* is the only insectivore which has not been able to disperse from the southwest of Finland to Åland. Possible reasons for its absence from Åland include its subterranean way of life, and the rocky coastline in the archipelago to where the mole must travel long distances before and after dispersal over water. It is known to be a good swimmer but moving on ice must be very difficult if not impossible (Skarén & Kaikusalo 1966).

The present distributions of *S. araneus* and *S. minutus* in the archipelago may be due to island dispersal, though unintentional human introductions are also possible. The distributions of the chromosomal races of *S. araneus* indicate that this species arrived at Åland from the south-west of Finland (Halkka et al. 1987). Reasons for the absence of *N. fodiens* from the eastern, fairly large islands are unknown. The dispersal ability of this species must be at least as good as that of *S. minutus*. However, *N. fodiens* may require fresh water throughout the year, which is not available on these islands.

In contrast to the colonization limited assemblages of shrews on the large, isolated islands in northwestern Europe, shrew populations on small and less isolated islands in lakes appear to exist in an equilibrium between frequent colonizations and extinctions. The largest species *Sorex araneus* had the highest colonization rate and the lowest extinction rate, and consequently it occurred more regularly and on smaller islands than the two smaller species, *S. caecutiens* and *S. minutus*. As found in previous studies on small mammals (Lomolino 1984, Adler & Wilson 1985), species which were abundant on the mainland occurred frequently on islands.

The three common species never occurred together on the same island, which may at least partly be due to interspecific competition. Dickman (1988) has found that the larger *S. araneus* has an indirect influence on the diet of *S. minutus*. *Sorex araneus* excluded *S. minutus* from the more productive microhabitats, where prey items were larger (see also Croin Michielsen 1967, Ellenbroek 1980 and Malmquist 1985 for the relationship between *S. araneus* and *S. minutus*).

In Lake Sysmä, most of the dispersers were juveniles and the largest species, *S. araneus*, had the highest dispersal rate. Lomolino (1986) also found that for similar species of small mammals such as shrews, the smaller species had lower insular inci-

dence. The dispersal rate of *S. araneus* was positively correlated with its density on the mainland.

In Lake Inari, the occurrence of *S. caecutiens* on islands was similar to the occurence of *S. araneus* in Lake Koitere and Lake Sysmä in eastern Finland (Hanski 1986), but the latter species was present on every island greater than 1.6 ha, while *S. caecutiens* was absent on many islands smaller than 15 ha. The smaller *S. caecutiens* has a higher extinction rate than *S. araneus* (Table 3), which could explain the difference in their minimum requirements for island size. The islands in Lake Inari are relatively unproductive, which may contribute to the large minimum island size of *S. caecutiens* and may explain the absence of *S. araneus* from these islands.

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