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Distributional ecology in the shrews *Sorex araneus* L. and *Sorex minutus* L. in western Norway

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Relative abundance and distribution of Common and Pygmy Shrews in Hordaland county, western Norway, were studied at a number of sites along a coast-inland gradient by examining museum collections, and by trapping. Pygmy Shrews were found at all sites except one inland, while Common Shrews were lacking at two of the most western sites. A dramatic reduction in the percentage of Pygmy Shrews was found towards the interior, ranging from 80.9% on the outermost islands, 42.0% along the coast, and 2.2% inland. Pygmy Shrews were most abundant in poor habitat (habitat quality was subjectively evaluated from the diversity and richness of vegetation). A shift in body length between sympatry and allopatry was found in both species, increasing the difference between them in sympatry. At one site where they coexisted or were caught in about the same numbers, habitat segregation between the two was not very apparent. Habitat quality influenced the weight, but not size, of Common Shrews along an altitudinal gradient. Habitat type and quality probably control the distribution of the Common Shrew, but the abundance of Pygmy Shrews may be controlled by Common Shrews.

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INTRODUCTION

Common and Pygmy Shrews, *Sorex araneus* and *Sorex minutus,* are similar in morphology, diet, and behaviour (Michielsen 1966, Pernetta 1976, Malmquist 1985), yet their distribution is sympatric throughout most of Europe and Siberia (Butterfield et al. 1981, Sheftel 1989). Some differences exist, though: The Pygmy Shrew is smaller than the Common Shrew (Michielsen 1966), and earthworms (Lumbricidae) are not included in their diet (Pernetta 1976, Butterfield et al. 1981). The Common Shrew feeds extensively on earthworms (Pernetta 1976), and is believed to live more underground than the Pygmy Shrew (Michielsen 1966). The smaller species is more abundant in less productive and drier habitats; in other habitats the Common Shrew usually greatly outnumbers the Pygmy Shrew (Michielsen 1966, Hanski & Kaikusalo 1989). Both species are strictly territorial, and in experiments Pygmy Shrews left an area after the introduction of a Common Shrew (Dickman 1991). These observations indicates that Common Shrews are dominant to Pygmy Shrews.

Ellenbroek (1980) examined territory size, surface activity, population density, and body weight of Pygmy Shrews both in allopatry and in sympatry with the Common Shrew, and did not find any effect of sympatry. Malmquist (1986) suggested, however, that the low density of Pygmy Shrews on the mainland of northern Europe is a consequence of competition with the Common Shrew. He also found that the Pygmy Shrew had significantly smaller jaws in sympatry, and concluded that this resulted from competition with the Common Shrew (Malmquist 1985). No such effect was found in Common Shrews. The Common Shrew has a better dispersal ability and will more readily spread to islands along the coast (Peltonen et al. 1989). The peculiar absence of Common Shrews on some islands, e.g. Ireland, has been explained by a postglacial «filtering» land-bridge where earthworms may have been absent (Malmquist 1985, Peltonen et al. 1989).

In this study, the distribution of the two species of shrews along an inland, an altitudinal, and a habitat gradient in Hordaland

county, western Norway, is investigated. Four major questions are addressed:
1. What is the relative abundance of the two species along a gradient from coast to inland, and what kind of major habitats are associated with their distribution?
2. Is there any habitat segregation between the two species in sympatry?
3. Do the two species show any shift in size between sympatry and allopatry?
4. Does quality of the habitat influence size and weight of Common Shrews?

MATERIAL AND METHODS

The collection of shrews at the Museum of Zoology, University of Bergen, containing specimens from about 1940 to the present, was examined, and species and place of capture noted (Fig. 1). Most specimens had been taken in pit-fall traps during investigations of the invertebrate fauna in different years, but one sample (Eksingedalen) was caught in live traps during studies of microtines. Included were also three sites from outside Hordaland county; Kårstø in Rogaland county, Setesdalen in Telemark county and Tjøme in Vestfold county (Fig. 1). I examined the most recent collections myself (Øygarden, Radøy, Lindås, Stord, Os, Kårstø, Setesdalen, Tjøme). The rest of the samples at the Museum had recently been evaluated and species identification had been revised. In cases of overlapping morphological features, species were identified by measuring the angle of the posterior part of the lower mandible (Fredriksen, Langhelle & Frafjord in press). In some samples total length of shrews including tail was measured along the ventral side, and tail length was measured along the dorsal side (n = 210). Body length was calculated as total length minus tail length. All these specimens were stored in alcohol. No distinction was made between first and second year shrews, but the first probably greatly outnumbered the second.

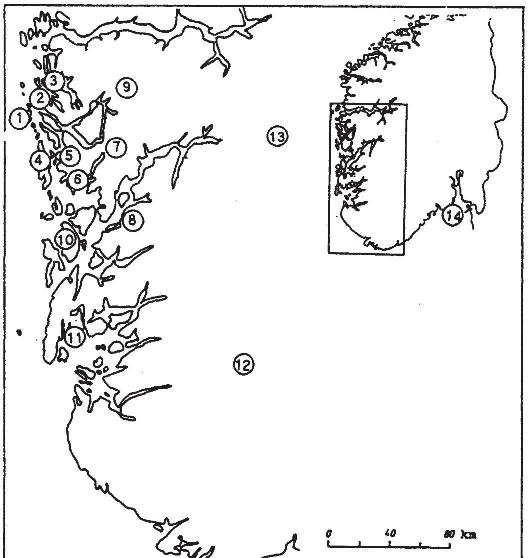

Fig. 1. Map showing the sites of trapping in South Norway. 1 = Øygarden (n = 27), 2 = Radøy, (19), 3 = Lindås (31), 4 = Sotra (26), 5 = Bergen (51), 6 = Os (85), 7 = Tysse (170), 8 = Rosendal (19), 9 = Eksingedalen (54), 10 = Stord (14), 11 = Kårstø (10), 12 = Setesdalen (33), 13 = Haugestøl (9), 14 = Tjøme (37).

During July and August 1991, I captured shrews in a valley at Tysse, Hordaland, on 5 sites in different habitats and at different altitudes. Pit-fall traps (3190 trap-days) and live traps (Ugglan special, 663.5 trap-days) baited with salted peanuts or dry dog chow were used. Traps were arranged on a line with distance 10 m between each. Live trapping was restricted to 2 periods of 1 1/2 day per month, and traps were emptied twice per period. Number of trap-days varied much between sites (live traps 54.0—262.5 trapdays) and at one site no pit-falls were used. Total length and tail length of fresh carcasses were measured, and their weights were recorded with a spring scale (±0.05 grams). A total of 170 individuals of the two species were caught, and 16 (9.4%) of these were caught in pit-fall traps.

Descriptions of the major habitats are available for most sites: Øygarden (Mortensen 1985, Pedersen 1986), Stord (Greve & Hauge 1989), Eksingedalen (Otto 1978), Kårstø (Pedersen 1982), Setesdalen (Simonsen 1981), Tjøme (Andersen & Søli 1988), Lindås (T. Fredriksen pers. comm. 1991), Sotra (T. Andersen pers. comm. 1991), Os (G. A. Halvorsen pers. comm. 1991), Tysse (own investigation). Quality of habitats was evaluated subjectively from the diversity and richness of the vegetation. Major habitats, arranged in order of generally decreasing quality, were deciduous forest, meadow, birch forest, heather, marsh, and coniferous forest.

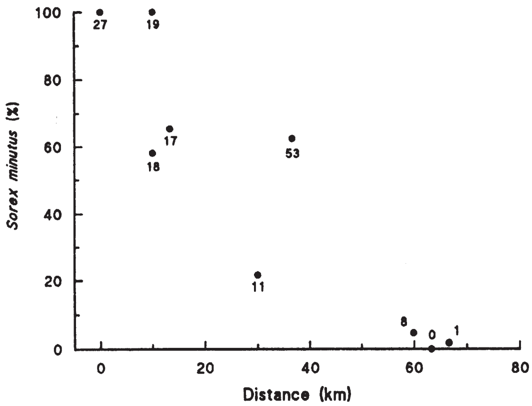

Fig. 2. Percentage of *Sorex minutus* caught in regions ranging from the outermost islands to about 67 km inland. Number of specimens caught at each site are given.

RESULTS

Relative abundance of the two shrews and major habitats

Trapping positions of samples containing at least 19 specimens were plotted on a map, transferred up or down until all lie on a straight line, and the air-line distance from the most western site calculated (Fig. 2). (19 was arbitrarily selected as minimum sample size.) A significant reduction in the percentage of Pygmy Shrews with increasing distance inland was found (Spearman rank r_s = 0.87, n = 9, p = 0.01). Pygmy Shrews were found at all sites except one. They were the only species on the outermost islands, but constituted only 2—5% of the catches inland. Thus, a sharp gradient in the relative abundance of the two species was found (Fig. 2). In Øygarden where only Pygmy Shrews were found, trapping was conducted in the richest and most diverse habitats. This implies that the Common Shrew seems to be absent from these islands altogether. The sites were grouped into coastal islands (0—20 km), coastal mainland (21—40 km), and inland areas (41—70 km). Mean proportions of Pygmy Shrews were 80.9%, 42.0%, and 2.2% respectively in these three areas.

The habitat at sites with more than 50% Pygmy Shrews were either barren country with vegetation mainly consisting of heather and marsh (Øygarden, Radøy, Lindås, Sotra), or coniferous forests (Os). In a smaller sample from the island Stord (Fig. 1), 78.6% Pygmy Shrews were caught in marsh habitats. In sites outside Hordaland county (Fig. 1) with a high percentage of Pygmy Shrews, the habitats were similar: Kårstø (90%), Setesdalen (54.6%), Tjøme (29.7%). A small sample from a high altitude birch forest east of the watershed (Haugastøl, 990 m.a.s.l.) contained 11.1% Pygmy Shrews.

Habitat segregation in sympatry

Habitat segregation between the two species of shrews was examined in the sample from Os. Both species occurred in high numbers here, and it was known which trap most individuals were caught in. Shrews were caught in 33 of the 50 pit-falls used, and in 12 (36.4%) of the 33 traps both species were caught. Of a total of 79 shrews, 40 (50.6%) were caught in a trap which caught at least one individual of each species.

The habitats at Os consisted mainly of pinewood, with some differences between trap sites in the amount of deciduous trees, grasses, heather or marsh. A comparison was made between the three trap sites which were used in two successive years (1990 and 1991, 10 pit-falls were used at each site). In the highest quality habitat 17 Common and 18 Pygmy Shrews were caught, in the most poor habitat (more marsh) the figures were 5 and 14, and in the habitat of intermediate quality 4 and 9. No association between species and habitats was found (χ^2 = 3.01, d.f. = 2, p = 0.22).

At Os most shrews were captured in the months June to August. The capture rate of Common Shrews was rather constant through these months (10, 7, and 8 respectively), but the number of Pygmy Shrews caught increased from 5 in June, 14 in July to 26 in August (χ^2 = 8.51, d.f. = 2, $p<0.05$).

Size of sympatric and allopatric shrews

Body length of Common Shrews increased slightly in sympatry, while body length of Pygmy Shrews decreased slightly (Table 1). Common Shrews in sympatry had a shorter tail than in allopatry (Table 1), representing 79.0 and 90.3% of the body length respectively. Thus, their total length (body + tail) was greatest in allopatry (105.9 v. 103.1 mm). Pygmy Shrews on the other hand, had a shorter tail in allopatry than in sympatry (Table 1), representing 85.8 and 98.4% of body

Table 1. Mean body and tail length (mm) of *Sorex araneus* and *Sorex minutus* in sympatry (Os + Stord), allopatry (Øygarden + Radøy, S.m.) and near allopatry (Tysse, S.a.).

	Sympatry		Allopatry		t-test	
	$\overline{X}$	SD	$\overline{X}$	SD	t	p
Sorex araneus						
Body length	57.6	4.1	55.6	4.9	2.17	0.03
Tail length	45.5	2.8	50.2	3.2	8.06	0.000
n	33		156			
Sorex minutus						
Body length	44.4	2.4	45.9	4.3	2.35	0.02
Tail length	43.7	3.1	39.4	4.3	6.48	0.000
n	64		63			

length respectively. Total length of Pygmy Shrews was greatest in sympatry (88.1 v. 85.2 mm). Thus, the shift in tail length was contrary to that of body length in both species, and in fact exceeded the shift in body length.

In the whole sample, mean body and tail length in the Common Shrew were 56.0 ± 4.7 and 48.6 ± 4.4 mm, respectively (n = 206). In the Pygmy Shrew, the means were 45.7 ± 4.8 and 41.6 ± 4.2 mm, respectively (n = 168). A significant negative correlation was found between body and tail length in both Common and Pygmy shrews (Pearson's r = -0.17, p<0.01 and r = -0.42, p<0.001, respectively). Thus, tail length decreased as body

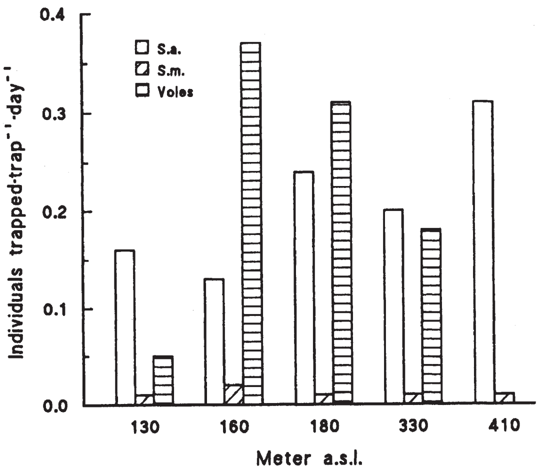

Fig. 3. Capture rate of the two shrews (n = 170) and of voles (n = 137) at different altitudes in the valley at Tysse, Hordaland.

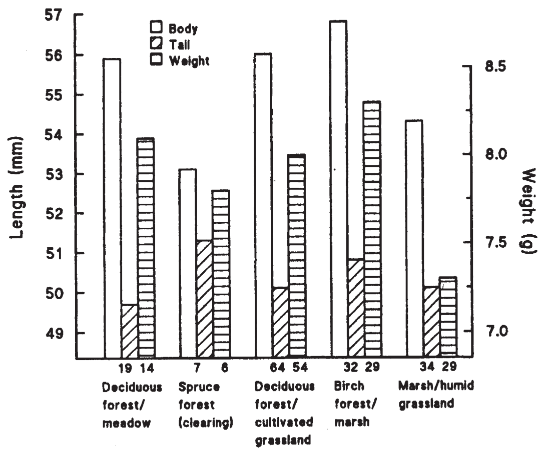

Fig. 4. Body and tail length, and weight of *Sorex araneus* caught in different habitats in the valley at Tysse, Hordaland. Number of specimens is given below each column (same in the two length measurements). (Abscissa is identical to Fig. 3).

length increased. A positive correlation between Common Shrew weight (mean 7.9 ± 0.9 g, Tysse sample) and body length was found (r = 0.48, p<0.01), but not between weight and tail length (r = 0.05, p>0.05).

Influence of habitat on body size

In the valley at Tysse, Pygmy Shrews were caught at all 5 sites, in about the same small number (Fig. 3). Common Shrews were more frequently caught at the three upper sites than at the two lower. Voles may have influenced on the trapping success, because they frequently occupied traps in the middle of the valley (Fig. 3). (Shrews were probably less likely to enter traps occupied by voles.)

Common Shrews weighed more at sites with higher quality habitats; deciduous forest/meadow, deciduous forest/cultivated grassland (traps were placed at the edge of the wood), and birch forest, and lowest in the poorest habitats, marsh/humid grassland, and spruce forest (ANOVA, F = 5.86, p<0.001) (Fig. 4). Shrews from the marsh/-humid grassland differed in weight from those at the birch forest/marsh, and from shrews in the deciduous forest/cultivated grassland (Scheffé multiple comparison test, p<0.05). No significant differences between shrews from different sites were found in body or tail lengths ($p>0.05$). When I mounted pit-fall traps earthworms were seen at three sites, but not in the marsh in the uppermost part of the valley (close to the tree-line). No pit-falls were used in the spruce forest, where live traps were placed in a narrow clearing with some grasses and heather. The low trapping success in the deciduous forest/-meadow at the lowest altitude was surprising, as was the high success at the marsh/humid grassland in the uppermost part of the valley (Fig. 3).

DISCUSSION

Absence of Common Shrews from the most western sites was probably due to absence of habitats suitable for this species, which has a more subterranean habit than the Pygmy Shrew and is more dependent upon earthworms (Michielsen 1966, Butterfield et al. 1981). A postglacial «filtering» land-bridge is not a likely explanation in this region, because the distance between the islands and between islands and mainland is short (recently, most islands have been interconnected by roads and bridges). The vegetation on these islands and peninsulas resemble mountainous areas, and includes many alpine plants, but patches of deciduous forest and cultivated land exist (Mortensen 1985). These patches may be too small to support a population of Common Shrews.

An effect of habitat quality on the weight of Common Shrews was found. This could be due to a direct effect of food availability, or indirectly as a higher proportion of Common Shrews caught in less suitable habitats may have been dispersing young. Such first year or immature shrews are smaller than mature second year shrews (Michielsen 1966), but body size did not differ significantly between habitats. Age and reproductive maturity were not examined, but at Tysse only 9.5% of the Common Shrews were heavier than 9 g. As indicated by Michielsen (1966) this weight may separate first and second year Common Shrews, but some shrews may grow in size and reproduce the year they were born (Pankakoski 1989).

The low numbers of Pygmy Shrews at several inland sites may have been due to competition with Common Shrews, i.e. the larger and dominant species excluding the smaller one from richer and more productive habitats. Competition between the two species was indicated by a shift in their body length in accordance with the hypotheses, i.e. that the larger species grows larger in sympatry and the smaller becomes even smaller (Dickman 1991). This would reduce competition and allow the two species to coexist. However, the shifts in body length were not large, and may have been influenced by a possible bias in the age distributions.

In the region where the two species coexisted in about the same numbers (or were caught in about equal frequency), segregation of the two species was small or absent. This result may have been due to an effect of trapping. In most habitats, parts of the area may be unsuitable for Common Shrews, but Pygmy Shrews may find a living there because they are smaller and have lower food requirements, and hence should be able to survive in lower quality habitats. As Common Shrews were removed, the territory was open to invasion by Pygmy Shrews, until another Common Shrew appeared on the scene. This effect will be greater if Common Shrews are less abundant.

Habitat type or quality seems to control the distribution of Common Shrews in western Norway, while Common Shrews may control the abundance of Pygmy Shrews. In habitats of intermediate quality (e.g. patchy habitats), both species may coexist.

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SAMMENDRAG

Utbredelse og tallrikhet av to spissmus-arter i Vest-Norge

Utbredelse og innbyrdes tallrikhet av vanlig spissmus *Sorex araneus* og dvergspissmus *Sorex minutus* ble undersøkt på ulike steder langs et kyst — innlands gradient i Hordaland v.hj.a. fellefangst og studie av museumssamlinger.

Dvergspissmus forekom overalt, mens vanlig spissmus manglet på de ytterste øyene. Prosent antallet av dvergspissmus avtok meget sterkt mot innlandet, fra ca. 80.9% på de ytre øyene til 42% ved kysten og 2,2% i innlandet. Dvergspissmus var mest vanlig i næringsfattige områder.

Størrelsesforskjellen mellom artene var større hvor begge forekom enn i allopatriske populasjoner, noe som peker i retning av konkurranse. Likevel ble det ikke funnet tegn til habitat oppdeling mellom de to artene i et område hvor begge spissmusartene var omtrent like vanlige. Vekten av vanlig spissmus var positivt korrelert med kvalitet av habitaten.

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