Study of a contact between two chromosomally monomorphic races of *Sorex araneus* L. (common shrew)

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One hundred and twelve specimens of the common shrew from 21 populations in NE Poland were studied from an area of contact between chromosomal race II (metacentric chromosomes: *hi*, *ko*, *gm*, *np*) and race VII (*ki*, *hn*, *gr*, *mp*). No direct contact was found between the races in the study area; there were no mixed or hybrid populations. The shortest distance between populations of the two races was 1.2–1.6 km. Possible explanations for this pattern of the races' disjunction are discussed.

Keywords: chromosomal races, hybrid zone, Robertsonian rearrangements, *Sorex araneus*.

Introduction

There is a great diversity of karyotypes in *Sorex araneus* as a result of Robertsonian rearrangements of a series of 12 autosomal arms (*g-r*; arms labelled according to Searle *et al.* (1991)). There are two aspects of this diversity: intrapopulational — Robertsonian polymorphism occurs over a large area of the species range — and interpopulational — the occurrence of separate races characterized by metacentrics with differing combinations of autosome arms in the *g-r* series (Fredga & Nawrin, 1977; Searle, 1988).

In NE Poland (Fig. 1b), seven basic chromosomal races of *S. araneus* have been reported so far (Fredga & Nawrin, 1977; Fedyk, 1980, 1986; Wójcik & Fedyk, 1985; Fedyk & Leniec, 1987) and labelled with Roman numerals I–VII (Fedyk, 1986). Studies of a hybrid zone between races II and IV have shown that shrews provisionally described as race III are in fact II/IV inter-racial recombinants and that they never occur as pure forms outside the hybrid zone (Fedyk *et al.*, 1991). Nevertheless, when local polymorphic and monomorphic variants are considered, as many as 10 specific combinations of metacentric chromosomes (Fedyk, 1987) can be distinguished in northern Poland (Table 1).

Contact zones among *S. araneus* have been studied in the U.K. (Searle, 1986; Mercer & Searle, 1991), Sweden (Fredga, 1987), Poland (Fedyk, 1986, unpublished data; Fedyk *et al.*, 1991), Switzerland (Hausser *et*

al., 1991) and Siberia (Aniskin & Lukianova, 1989). Most studies have been concerned with contacts between polymorphic races. In these contact zones post-hybridization modifications enhancing fertility in hybrid populations were observed. These modifications may include at least two known phenomena: (i) maximization of the frequency of acrocentric chromosomes in the contact zone (Searle, 1986); or (ii) maximization of frequency of interchromosomal recombinants in the centre of the hybridization zone (Fedyk *et al.*, 1991). The occurrence of maximum frequencies of acrocentric chromosomes, also known as an acrocentric buffer zone (Fedyk, 1986; Halkka *et al.*, 1987), is possible only in the case of a contact between two polymorphic races. Interchromosomal recombinants, however, may arise in the centre of a hybridization zone in which at least two independently segregating meiotic complexes are produced among the hybrids (for details see Fedyk *et al.*, 1991).

For the present study a sector of a II/VII inter-racial contact zone was chosen, where it was impossible for any of the known types of post-hybridization modification to arise. The absence of Robertsonian polymorphism prevents the occurrence of an acrocentric buffer zone. On the other hand, during meiosis potential hybrids of homozygotes of races II and VII should produce a single chain with a decavalent configuration (Fedyk, 1987) which rules out recombination between diagnostic metacentric chromosomes of the two races.

Table 1 Chromosomal races of *Sorex araneus*: races and variants found in NE Poland

Origin	Race	Variant§§	Diagnostic metacentrics				References
WEpg†	I	I a	hi,	ko¶	—	—	Wójcik & Fedyk, 1985; Fedyk, 1986
		I pol	hi,	ko¶,	gm¶	—	Fedyk, 1986
	II	II pol	hi,	ko,	gm¶,	np¶	Fedyk, 1986
		II mon	hi,	ko,	gm,	np	This paper
Hybrid origin‡	IV	IV pol	hk,	io¶,	gr¶,	mn¶	Fedyk, 1986; Wójcik, 1986
	V	V pol	hk,	—	gr¶,	mn¶	Fedyk, 1986
	VI	VI pol	ki¶,	hq¶	gr¶,	mn¶	Fedyk, 1986; Wójcik, 1986
EEPg§	VII	VII mon?	ki,	—	gr	—	Fedyk, 1987
		VII pol	ki,	hn¶,	gr¶,	mp¶	Fredga & Nawrin 1977; Fedyk, 1980
		VII mon	ki,	hn,	gr,	mp	This paper

†West European phylogenetic group, following Searle (1984b).

‡After Fedyk (1987).

§East European phylogenetic group, following Searle (1984b).

§§Polymorphic (pol) and monomorphic (mon) variants of races.

¶Polymorphic combinations of chromosome arms.

This study has parallels with the analysis carried out on a contact zone between the Oxford and Aberdeen homozygous races in Scotland (Mercer & Searle, 1991).

Materials and methods

Study area

The valleys of the lower reaches of the Bug and Narew Rivers converge in a lowland area of eastern Poland (Mazovian Lowland). This is a region characterized by slightly diversified relief (height varies between 60 m and 150 m above sea level). The humid habitats preferred by shrews directly adjoin rivers; these are the flood meadow terraces. In the valley of the Narew River the flood terrace is larger than that of the Bug valley. The flood terraces rapidly change to sand dune terraces, now covered with coniferous forest or arable land. The dune terraces are at least 2 m above the flood terrace and hence are protected from flooding. The flood terrace is a labile habitat: during periods of high water level it is flooded and in some meadows there are high groundwater levels all year round. This prevents permanent colonization of the area by small mammals.

Animal collection and characteristics of capture sites

The ranges of races II and VII were determined within a 50 km strip. Shrews were collected in 1986 and 1987 at 12 sites in the valleys of the Bug and Narew Rivers (Fig. 1c).

Detailed studies on the racial contact were conducted in 1991 at 12 sites situated along a 6 km strip of the Fiszor River (Fig. 1d). The collection sites were situated at reasonably regular intervals. The attempt was to locate them in habitats most suitable for *S. araneus*. In spite of this, these habitats varied substantially in their trappability coefficients for *S. araneus* and in the composition of the associated species group (Table 2). The animals were trapped in metal cones lined with moss, with food provided. The cones were checked every 2 h round the clock.

The Słopsk I and VII sites were located in a very narrow (about 50 m) strip of humid meadows. The groundwater level approaches 10 cm to 5 cm below ground surface. During periods of high groundwater level (especially in spring) this meadow is completely flooded. No animals were collected at either site. No doubt it is a habitat unsuitable for colonization by shrews. The Słopsk II site was in reeds in a very marshy old river meander. In such habitats *S. araneus* usually occurs in great numbers. In this case the absence of *S. araneus* in the animals collected might have been caused by improper arrangement of the traps in excessively humid places; this is supported by the fact that 150 m from this site, at Słopsk III situated in a narrow strip of alder forest, all three species of Insectivora and *C. glareolus* were collected. The Fiszor site was in a similar habitat (river bank alder forest); the composition of the species collected here was the same as at Słopsk III. Słopsk V was situated along a drainage ditch in a meadow used as pasture. Only *S. araneus* and *Micromys minutus* were collected here. The Dręszew, Słopsk VI and IV sites are far from the river bed and

Fig. 1 Distribution of chromosome races of the common shrew in NE Poland. (a) Outline of Poland. (b) Ranges of basic chromosomal races in NE Poland. The boundary between the West European and East European phylogenetic groups is marked by a solid line. The ranges of local chromosome races are marked by dotted lines. Shaded areas indicate monomorphic zones of races II and VII. (c) Distribution of race II (○) and race VII (●) in the valleys of the Bug and Narew; crosses denote populations containing *n/p* heterozygotes; numbers indicate sample sizes. (d) Contact zone of race II (○) and race VII (●). The sites at which no *S. araneus* were collected are marked by rectangles. Dotted areas are sand dune terraces. Population code: D, Dręszew; P, Powłoczki; N, Niegów; M, Młynarze; F, Fiszor; S_I–S_{VII}, Słopsk I–VII.

are therefore not susceptible to flooding. There are diversified habitats here (a mosaic of alder forest, meadow and scrubs). The greatest variety of species was collected at these three sites. The Niegów and Powłoczki sites are in isolated, more humid areas (alder forest with scrubs surrounded by coniferous woods) in

the area of a dune terrace. At these sites the number of individuals of *S. araneus* collected was low and the species compositions were similar (Table 2).

Viewing only the trappability coefficient for *S. araneus* (Table 2) it may be stated that in the contact zone of races II and VII there is a clear population density gradient connected with habitat conditions. Between Słopsk VI and Słopsk V there is about a 1 km strip of unfavourable habitats where the density of *S. araneus* is zero or minimal (Fig. 1d).

Karyological methods

Chromosome preparations from the spleen were made by standard methods and stained with Giemsa reagent after treatment with trypsin (Seabright, 1971).

Results

The studies in 1986 and 1987 demonstrated that the shrews from seven sites lying in the fork of the Narew and Bug Rivers belong to race II (Fig. 1c). At five sites only homozygous shrews with the diagnostic chromosomes *hi*, *ko*, *gm* and *np* were captured. One individual in each of the remaining two populations was a *n/p* heterozygote. Five other populations located eastward in the Bug River valley belong to race VII (Fig. 1c), with the diagnostic metacentrics *ik*, *hn*, *gr* and *mp*. In the latter populations Robertsonian polymorphism was not found.

The results of our detailed studies of the contact between races II and VII are presented in Table 3. In this case samples were collected along a 6 km strip (Fig. 1d). Along this transect, the Dręszew and Słopsk VI populations belong to race II. At the Dręszew site, 18 shrews homozygous for metacentrics (Fig. 2) and one shrew homozygous for the acrocentrics *n* and *p* were captured. In the Słopsk VI population one of the specimens was a *j/l* heterozygote. On the dune terrace, race II shrews were caught further to the east than on the main transect. These were the isolated populations of Powłoczki and Niegów (Fig. 1d). The remaining populations from the main transect (Słopsk V, IV, III, Młynarze and Fiszor) belong to race VII (Fig. 1d, Table 3). All the shrews of race VII were homozygotes (Fig. 3). At Słopsk I, VII and II, no specimens of *S. araneus* were collected. None of the nine sites under study yielded shrews of both races (Table 3). The shortest linear distances between sites where specimens of pure races II and VII were captured are: Słopsk VI–Słopsk V, 1.6 km; Powłoczki–Słopsk IV, 1.4 km; and Niegów–Słopsk III, 1.2 km (Fig. 1d).

Table 2 Numbers of small mammals collected in 1991 around the contact between races II and VII.

Population	Trap-nights	<i>S. ara</i>	<i>S. min</i>	<i>N. fod</i>	<i>M. sp</i>	<i>C. gla</i>	<i>M. min</i>	<i>S. bet</i>
Dęszew	172.5	22(0.13)	26(0.15)	1(0.01)	7(0.04)	10(0.06)	2(0.01)	—
Słopsk VI	190.5	16(0.08)	8(0.04)	—	6(0.03)	8(0.04)	1(0.005)	—
Słopsk I	20.3	—	—	—	—	—	—	—
Słopsk VII	58.9	—	—	—	—	—	—	—
Powłóczy	150.7	4(0.03)	6(0.04)	—	—	6(0.04)	—	—
Niegów	54.7	1(0.02)	2(0.04)	—	—	1(0.02)	—	—
Słopsk V	43.1	2(0.05)	—	—	—	—	2(0.05)	—
Słopsk IV	272.6	18(0.07)	7(0.03)	3(0.01)	1(0.004)	1(0.004)	1(0.004)	1(0.004)
Słopsk III	103.0	6(0.06)	2(0.02)	3(0.03)	—	1(0.01)	—	—
Słopsk II	48.4	—	1(0.02)	—	—	3(0.06)	—	—
Fiszor	178.3	14(0.08)	6(0.03)	3(0.02)	—	3(0.02)	—	—

[For each species the trappability coefficient (number of individual caught per trap-nights) is indicated in parentheses.]

S. ara, *Sorex araneus*; *S. min*, *Sorex minutus*; *N. fod*, *Neomys fodiens*; *M. sp*, *Microtus sp*; *C. gla*, *Clethrionomys glareolus*; *M. min*, *Micromys minutus*; *S. bet*, *Sicista betulina*.

Fig. 2 G-banded karyotype of a race II shrew. **Fig. 3** G-banded karyotype of a race VII shrew.

Discussion

This study suggests that in the area where races II and VII are monomorphic there is no direct contact between the races; no mixed populations were found. The pure populations were separated by 1–2 km of excessively wet habitats, unsuitable for permanent colonization by small mammals. On the other hand, the width of hybrid zone between the two polymorphic races Oxford and Hermitage is 10 km (Searle, 1986)

and that between II and IV races as much as 16 km (Fedyk *et al.*, 1991, unpublished data).

The presence of a 'demarcation zone' separating two races may be explained through a model of dispersal/selection balance. Theoretically, under considerable pressure of selection against hybrids contact zones should not move far as they are readily trapped by regions of low density or even slight natural barriers to dispersal (Hewitt & Barton, 1980). Probably the two races originally made contact further to the east of their

Table 3 Frequencies of variable chromosomes at sites from the contact zone between races II and VII

Site	Code	Frequency of metacentrics									N
		hi	ko	gm	np	ki	hn	gr	mp	jl	
Dręszew	D	1.00	1.00	1.00	0.95	—	—	—	—	1.00	19
Słópsk VI	S _{VI}	1.00	1.00	1.00	1.00	—	—	—	—	0.96	12
Powłóczyk	P	1.00	1.00	1.00	1.00	—	—	—	—	1.00	3
Niegów	N	1.00	1.00	1.00	1.00	—	—	—	—	1.00	1
Słópsk V	S _V	—	—	—	—	1.00	1.00	1.00	1.00	1.00	2
Słópsk IV	S _{IV}	—	—	—	—	1.00	1.00	1.00	1.00	1.00	12
Słópsk III	S _{III}	—	—	—	—	1.00	1.00	1.00	1.00	1.00	4
Młynarze†	M	—	—	—	—	1.00	1.00	1.00	1.00	1.00	6
Fiszor	F	—	—	—	—	1.00	1.00	1.00	1.00	1.00	10

†1986 sample (S. Fedyk & H. Leniec, unpublished data), all others collected in 1991.

present position, as suggested by the presence of race II shrews in the Powłóczyk and Niegów populations (Fig. 1d). At meiosis I, hybrids should produce chains of 10 chromosomes: *o/ok/ki/ih/hn/np/pm/mg/gr/r*. Hybrids with large meiotic complexes have been obtained in *S. araneus* in breeding conditions (Searle, 1984a; Mercer *et al.*, 1992) and they also occur under natural conditions (Aniskin & Lukianova, 1989). Studies of heterozygous mice suggest that the probability of producing chromosomally balanced gametes is inversely proportional to the number of chromosomes within a meiotic complex (Capanna, 1975; Capanna *et al.*, 1977; Gropp & Winking, 1981; Gropp *et al.*, 1982). This dependence has also been supported by studies of *S. araneus* hybrid zones: shrews characterized by short meiotic chains are much commoner than those with long chains (Searle, 1986, 1990; Fedyk *et al.*, 1991). It may be supposed that as a result of significant hybrid unfitness the tension zone became trapped in an environmental sharp gradient at the present position in the Słópsk area.

Obviously a 1 km strip of unfavourable habitat is not a complete isolation barrier for a shrew. In Scandinavia, *S. araneus* has been shown to disperse 4 km (Tegelström & Hansen, 1987). Also, an excessively humid habitat, although unsuitable for permanent colonization, may not constitute an obstacle to the exchange of individuals between races as it is known that shrews regularly colonize islands in lakes (Hanski, 1986; Hanski & Kuitunen, 1986; Hanski *et al.*, 1991). That shrews can swim long distances in quiet water has been demonstrated experimentally (Skarén, 1980) and it has also been shown that *S. araneus* is often the prey of carnivorous fish (Teplov, 1943).

Thus, it may be suggested that very wet habitats are not a complete barrier and that along with selection against hybrids they only serve to stabilize allopatric ranges. In this context the suggestion by Mercer & Searle (1991) that a small river may constitute a boundary for the Oxford and Aberdeen races seems quite plausible.

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