

Zeitschrift: Mémoires de la Société Vaudoise des Sciences Naturelles
Herausgeber: Société Vaudoise des Sciences Naturelles
Band: 19 (1991-1999)
Heft: 1: The cytogenetics of the Sorex araneus group and related topics

Artikel: Chromosomal polymorphism in the common shrew Sorex araneus and its adaptive significance
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DOI: <https://doi.org/10.5169/seals-260077>

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Chromosomal polymorphism in the common shrew *Sorex araneus* and its adaptive significance

BY

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Summary.—WÓJCIK J.M., 1991. Chromosomal polymorphism in the common shrew *Sorex araneus* and its adaptive significance. In: J. HAUSSE, ed. The cytogenetics of the *Sorex araneus* group and related topics. Proceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat.* 19.1: 51-62.

A chromosomal polymorphism in the common shrew from Białowieża, north-eastern Poland, first described by FEDYK (1980) was re-examined. In 1989 and 1990, a total of 166 shrews from five sites, of three different habitats were studied. Eight karyomorphs of three polymorphic chromosome arm combinations *jl*, *gr*, and *mp* were found. The observed frequencies for each polymorphic arm combination at each site were a close fit to the Hardy-Weinberg expectation. The frequency of the twin-acrocentric morphs of polymorphic arm combinations in the population was stable during the following years: 0.030 in 1983 (S. FEDYK and J.M. WÓJCIK, unpubl.), 0.033 in 1989, and 0.031 in 1990. The results suggest that a balanced polymorphism exists. In general, the frequency of the heterozygous arm combinations was higher in wet sedge bogs with shrubs (25.5%) than in open sedge bogs (18.0%) and dry abandoned meadows (8.6%). A statistically significant difference in frequency was found between samples collected from wet sedge bogs with shrubs and those from abandoned meadows, for arm combination *mp* and for the three polymorphic arm combinations taken together. The hypothesis is presented that the chromosomal polymorphism in the common shrew has an adaptive significance.

Résumé.—WÓJCIK J.M., 1991. Le polymorphisme chromosomique de la musaraigne carlelet *Sorex araneus* et son rôle adaptatif. In: J. HAUSSE, dir. The cytogenetics of the *Sorex araneus* group and related topics. Proceedings of the ISACC's Second International Meeting. *Mém. Soc. vaud. Sc. nat.* 19.1: 51-62.

Le polymorphisme chromosomique de la musaraigne carlelet à Białowieża, nord-est de la Pologne, décrit une première fois par FEDYK (1980) est réexaminé. En 1989 et 1990 un total de 166 musaraignes de 5 localités représentatives de 3 habitats ont été analysées. Huit caryomorphes ont été relevés pour les métacentriques polymorphes *jl*, *gr* et *mp*. Les fréquences observées pour chaque combinaison dans chaque localité ne

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s'écarter pas significativement des fréquences prédites par la loi de Hardy-Weinberg. La fréquence des morphes à doubles acrocentriques est restée stable au cours des années suivantes: 0.030 en 1983 (S. FEDYK et J.M. WÓJCIK, non publié), 0.033 en 1989 et 0.031 en 1990. Ces résultats suggèrent l'existence d'un polymorphisme équilibré. En général, la fréquence des hétérozygotes est supérieure dans les marais embuissonnés (25.5%) à celle trouvée dans les marais ouverts (18.0%) et les prairies abandonnées (8.6%). La différence est statistiquement significative entre les échantillons collectés dans les marais embuissonnés et ceux des prairies abandonnées, tant pour la combinaison *mp* que pour les trois combinaisons de bras chromosomiques prises ensemble. Il est suggéré que le polymorphisme de la musaraigne carrelé joue un rôle adaptatif.

INTRODUCTION

A chromosomal polymorphism involving Robertsonian rearrangements in the common shrew *Sorex araneus* L. was first described in England by SHARMAN (1956). The common shrew is an exceptionally variable species with respect to its chromosomes. Numerous karyotypic races have been described all over the extensive range of this species (see e.g. FREDGA and NAWRIN 1977, KRAL *et al.* 1981, SEARLE 1984a, WÓJCIK and FEDYK 1985, ZIMA and KRAL 1985, HAUSSE *et al.* 1986, WÓJCIK 1986, FEDYK and LENIEC 1987, HALKKA *et al.* 1987, SEARLE 1988, ZIMA *et al.* 1988, ANISKIN and LUKIANOVA 1989).

A detailed study of chromosomal polymorphism in common shrews has been conducted in the Oxford area, initially by FORD *et al.* (1957). FORD and HAMERTON (1970) assumed that this polymorphism is maintained by heterozygote advantage. Heterozygote advantage has traditionally been proposed as the mechanism for maintenance of chromosomal polymorphism (WHITE 1973). More recent studies by SEARLE (1986a) suggest that the polymorphism in the Oxford area is associated with the presence of a hybrid zone between two karyotypic races. These karyotypic races are characterized by different metacentric chromosomes (formed by Robertsonian fusion) while within the hybrid zone (the ancestral-type) acrocentric chromosomes are selected for and exist at a high frequency. High heterozygosity occurs where the acrocentric and metacentric dominated regions meet.

The chromosomal polymorphism in the common shrew at Białowieża, north-eastern Poland, was studied by FEDYK (1980, 1982). The polymorphism involves three arm combinations *jl*, *gr*, and *mp*, with low frequency of twin acrocentric morphs. On the basis of changes of frequency over a seven-year period, FEDYK (1980) suggested that the chromosomal polymorphism in this population of shrews is transient, but the data he presented later (FEDYK 1982) did not support this hypothesis. Thus, the factors responsible for this polymorphism were not clear. SEARLE (1986a) suggested that a significant proportion of karyotypic polymorphisms are associated with hybrid zones. However, the chromosome polymorphism in shrews at Białowieża is not obviously associated with a hybrid zone. We need more information on how this polymorphism originated and how it is maintained.

The detailed studies of Dobzhansky and co-workers on the inversion polymorphism in *Drosophila* showed that a chromosomal polymorphism may have significance for adaptation and evolutionary change within species (see DOBZHANSKY 1970). Can it be suggested that the chromosomal polymorphism in the common shrew also has an adaptive significance? There is, however, no experimental evidence supporting this hypothesis (see BENGTTSSON and FRYKMAN 1990).

The specific aims of the present study were:

1.—To determine if there have been any changes in the chromosomal polymorphism in the Białowieża shrew population since the last published findings.

2.—To conduct between-biotope frequency studies. These may give some information about factors involved in the maintenance of the polymorphism.

MATERIAL AND METHODS

Samples were collected during 1989 and 1990 from five areas of less than 1 ha of non-forest biotopes (Fig. 1). Site No 1 was situated in sedge bogs near floodplain forest, a very wet heterogeneous biotope with willow shrubs and places with permanent water. Sites N° 2 and N° 3 were in wet and open sedge bogs, a homogeneous biotope along the Narewka river. Sites N° 4 and N° 5 were located in abandoned meadows, a homogeneous dry grassland biotope on higher ground.

Table 1.—Samples of common shrews collected from five sites at Białowieża.

Site	Biotope	Date of collection	males		females		total
			ad	juv	ad	juv	
No 1	SS	12.4. - 29.6.1989*	5	13	2	4	24
		19.3. - 26.4.1990	13		10		23
No 2	OS	11.4. - 27.6.1989	10	8	5	5	28
No 3	OS	24.8. - 29.8.1990		15		18	33
No 4	AM	29.3. - 10.4.1989#	15		3		18
		30.3. - 06.4.1990	11		9		20
No 5	AM	23.4. - 26.4.1990	8		12		20
Total			62	36	41	27	166

SS: Sedge bogs with shrubs. OS: open sedge bogs. AM: Abandoned meadows. * : two individuals collected on 29.09.1989; # : one individual collected on 15.10.1988.

Shrews were trapped mainly during spring (March and April), with only one sample collected in August (Table 1). A total of 166 shrews, 103 adults and 63 young, were used for the chromosome study. Mitotic preparations were made from spleen according to a standard method after injection with colcemid. G-banded karyotypes were prepared by the method of SEABRIGHT (1971). Chromosome arms were labelled according to the nomenclature proposed by SEARLE *et al.* (1991).

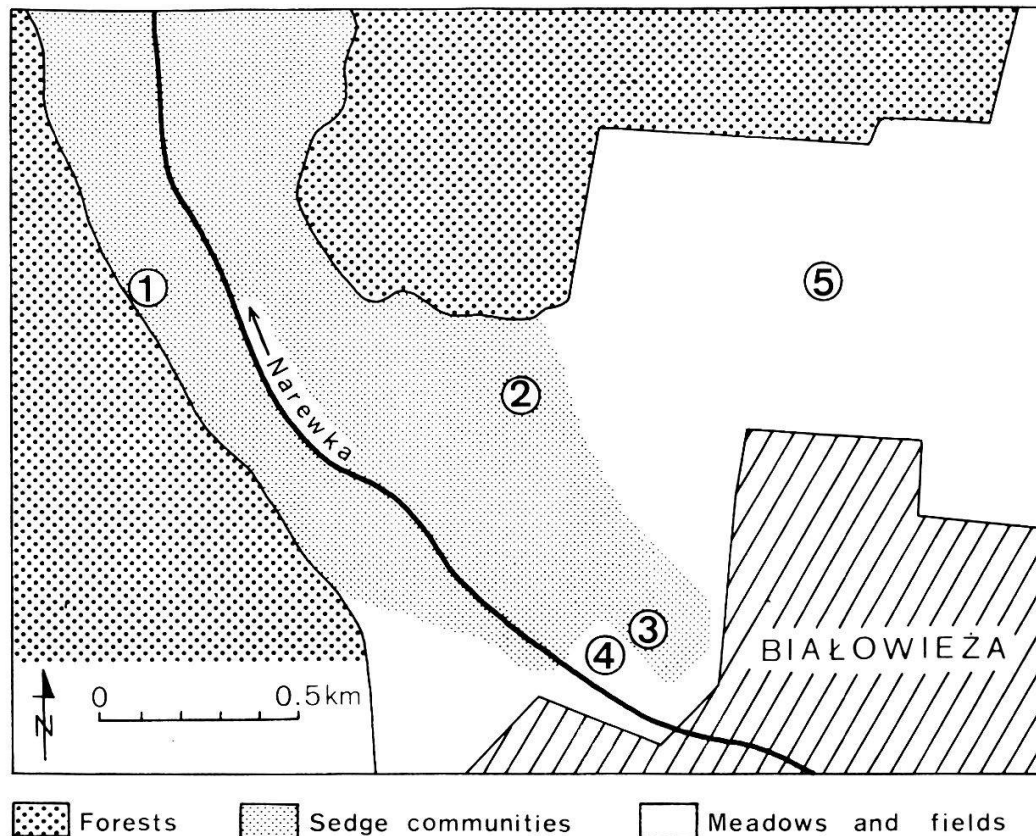


Figure 1.—Study area in different habitats at Białowieża.

RESULTS AND DISCUSSION

Eight karyomorphs of three polymorphic arm combinations *jl*, *gr*, and *mp* were present (Table 2 and Fig. 2). The highest number of different karyomorphs was found in sedge bogs with shrubs.

Within-site frequency analysis showed that the observed frequencies for each polymorphic arm combination at each site were, in general, a close fit to the Hardy-Weinberg expectation (Table 3). These data were compatible with random mating and an absence of selective differential between karyotypes.

Table 2.–Frequencies of different karyomorphs of common shrews from five sites of different biotopes at Białowieża.

Karyotype*	2Na	Site and biotope#					Total
		No 1 SS	No 2 OS	No 3 OS	No 4 AM	No 5 AM	
<i>jl, gr, mp</i>	20	36	23	27	35	17	138
<i>j/l, gr, mp</i>	21	-	2	2	1	1	6
<i>jl, g/r, mp</i>	21	5	2	2	1	2	12
<i>jl, gr, m/p</i>	21	3	1	2	-	-	6
<i>j/l, g/r, mp</i>	22	1	-	-	-	-	1
<i>j/l, gr, m/p</i>	22	1	-	-	-	-	1
<i>jl, g,r, mp</i>	22	-	-	-	1	-	1
<i>jl, gr, m,p</i>	22	1	-	-	-	-	1
Total		47	28	33	38	20	166

* Partial karyotype (invariant chromosomes not included), format *xy* for metacentric homozygotes, format *x/y* for heterozygotes of one metacentric and two acrocentrics, format *x,y* for twin-acrocentric homozygotes. 2Na: diploid autosomic number.

See table 1 and Figure 1

Table 3.–Karyotype frequencies in comparison with the Hardy-Weinberg expectation for individual polymorphic arm combinations.

Site	<i>jl</i>			<i>gr</i>			<i>mp</i>		
	2*	1*	0*	2	1	0	2	1	0
No 1									
Observed:	45	2	0	41	6	0	42	4	1
Expected:	45.0	2.0	0.0	41.2	5.6	0.2	41.2	5.6	0.2
No 2									
Observed:	26	2	0	26	2	0	27	1	0
Expected:	26.0	1.9	0.0	26.0	1.9	0.0	27.0	1.0	0
No 3									
Observed:	31	2	0	31	2	0	31	2	0
Expected:	31.0	1.9	0.0	31.0	1.9	0.0	31.0	1.9	0.0
No 4									
Observed:	37	1	0	36	1	1	38	0	0
Expected:	37.0	1.0	0.0	35.1	2.9	0.1	38.0	0.0	0.0
No 5									
Observed:	19	1	0	18	2	0	20	0	0
Expected:	19.0	1.0	0.0	18.1	2.0	0.1	20.0	0.0	0.0

* Number of copies of metacentrics

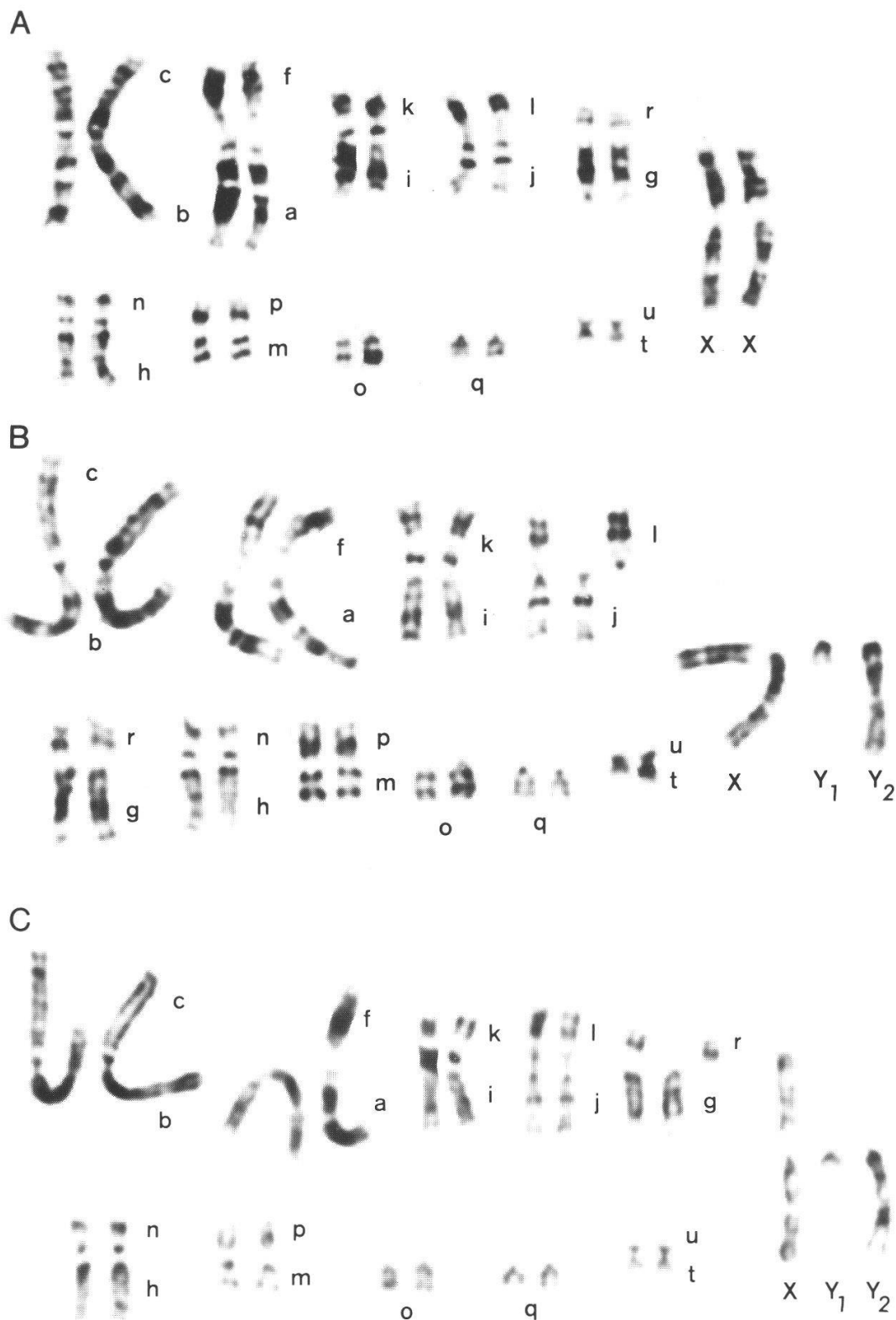


Figure 2.—Eight karyomorphs of three polymorphic arm combinations.
 A.—homozygous metacentric for *jl*, *gr* and *mp*,
 B.—heterozygote for *jl*.
 C.—heterozygote for *gr*.

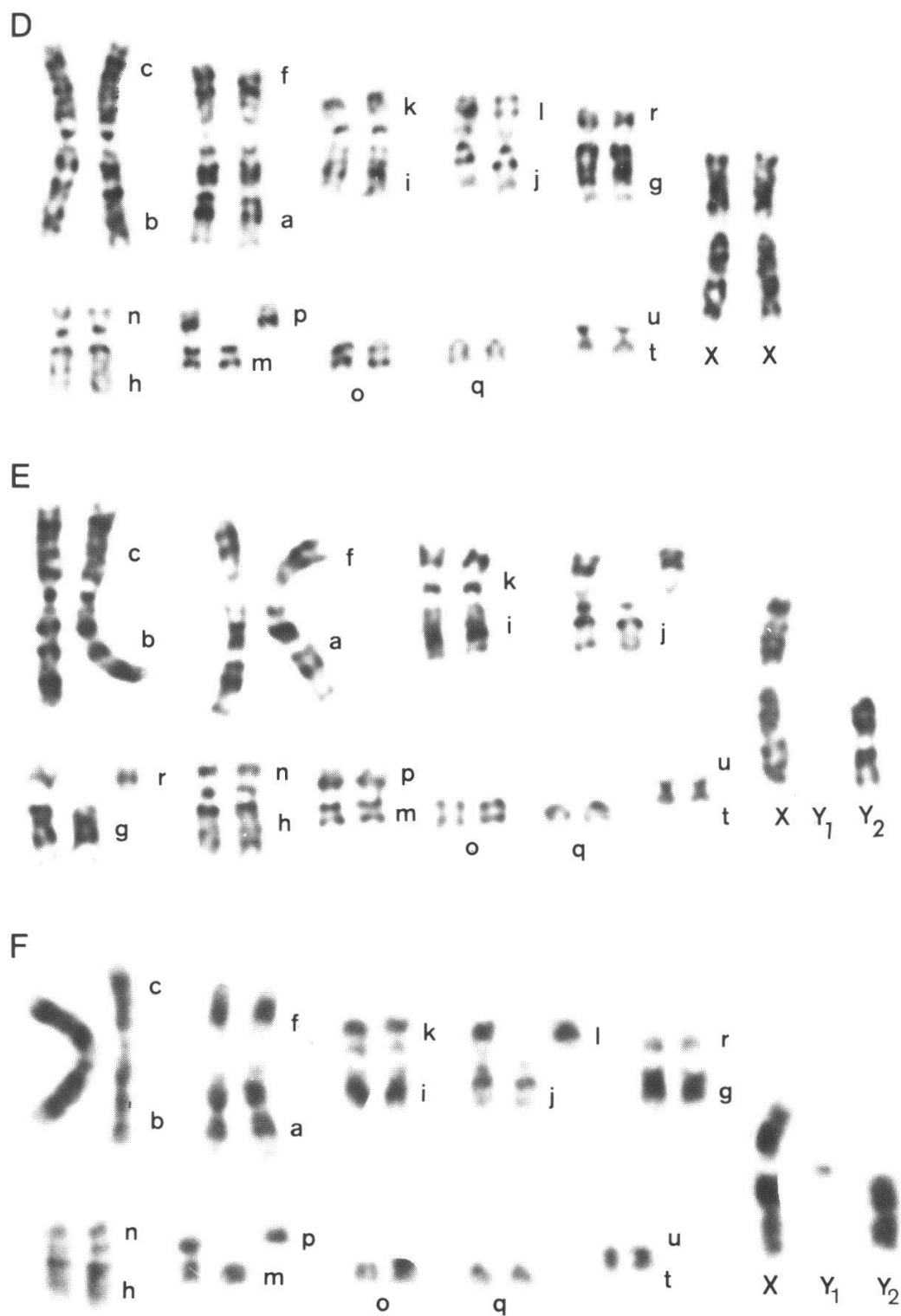


Figure 2. (continuation).
D.—heterozygote for *mp*,
E.—heterozygote for *jl* and *gr*,
F.—heterozygote for *jl* and *mp*.

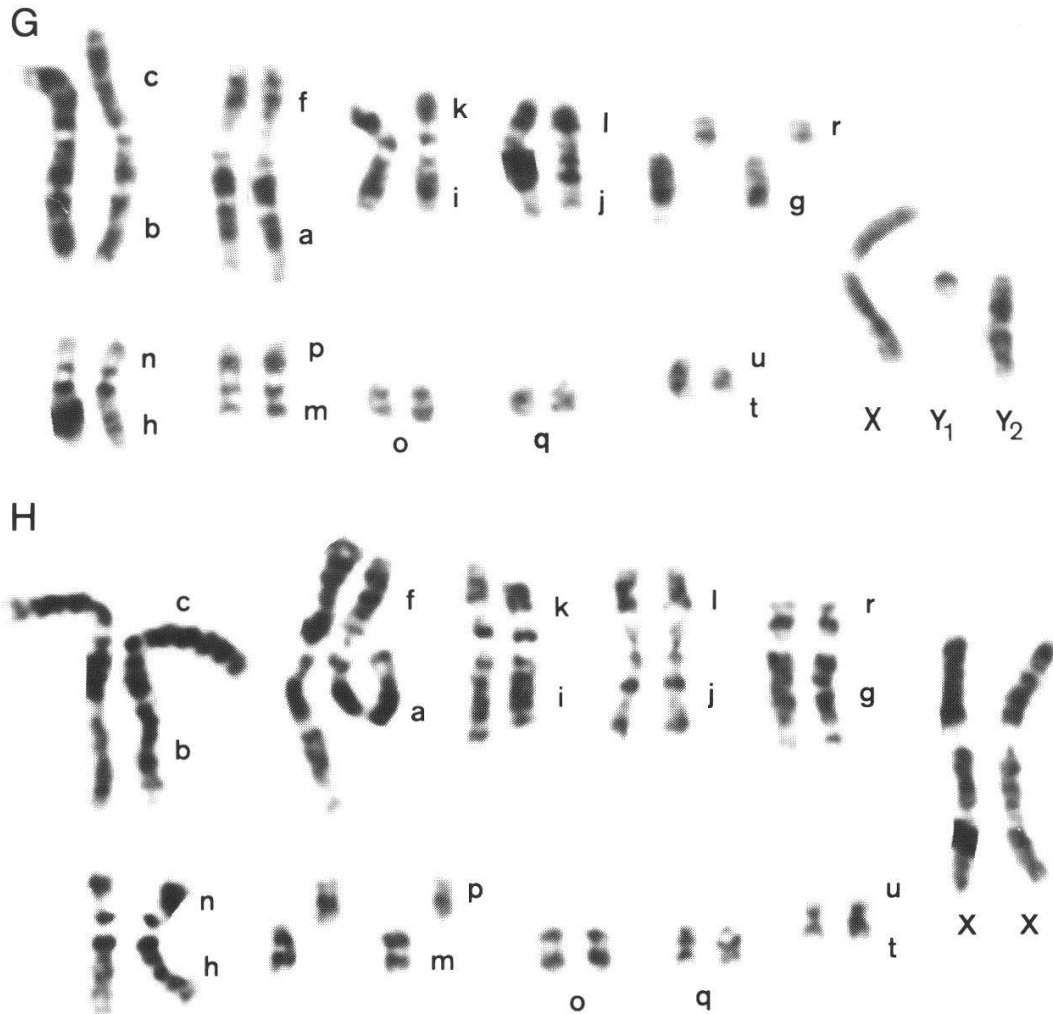


Figure 2. (continuation).

G.—homozygous twin-acrocentric for *g* and *r*,

H.—homozygous twin-acrocentric for *m* and *p*.

No significant differences between samples collected in a particular site or between sites within one biotope were found.

FEDYK (1980) suggested that the polymorphism in this population is transient because the frequency of twin-acrocentric morphs has gradually decreased from 1968 to 1974. But present results suggest that there is a balanced polymorphism. The total frequency of the twin-acrocentric morphs for three polymorphic arm combinations was stable over the following years: 0.036 in 1977 (FEDYK 1982), 0.030 in 1983 (S. FEDYK and J.M. WÓJCIK, unpubl.), 0.033 in 1989, and 0.031 in 1990 (Fig. 3). It is difficult to understand why the frequency was decreasing from 1968 to 1974. Two possibilities may be considered:

- (i) it was a natural decrease due to some unknown population processes, or
- (ii) it was an artificial decrease caused by collecting methods; e.g. samples in following years might have included different proportions of shrews from heterogeneous habitats, thus with different frequencies of twin-acrocentric morphs.

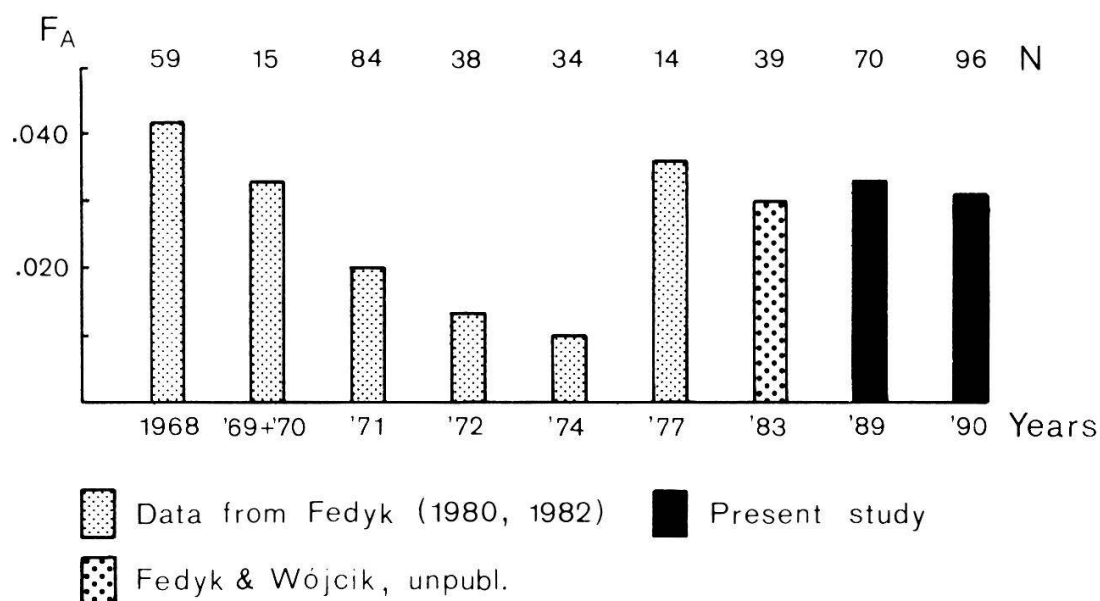


Figure 3.—Frequency of twin-acrocentric morphs of three polymorphic arm combinations in different years. Sample sizes are given above each bar.

Between-habitat frequency analysis may give some information on the factors involved in the maintenance of this polymorphism. The frequency of heterozygous arm combinations was, in general, higher in the very wet sedge bogs with shrubs (25.5%) than in the less damp open sedge bogs (18.0%) and dry abandoned meadows (8.6%). Thus there is a clear tendency for heterozygosity to increase with dampness of habitat. There is a similar pattern of variation for the frequency of the twin-acrocentric morphs (sedge bogs with shrubs: 14.8%, open sedge bogs: 9.0%, abandoned meadows: 6.0%). The frequency of twin-acrocentric morphs of particular polymorphic arm combinations varied between biotopes. However, the frequency of the acrocentrics *j* and *l* was low in all habitats, and no significant differences were found (Fig. 4). There were clear differences in the frequency of the twin-acrocentric morphs of arm combinations *gr* and *mp*, particularly between the wettest and driest habitats (sedge bogs with shrubs and abandoned meadows, respectively) with highest frequencies in the former. In the case of arm combination *mp*, no twin-acrocentric morphs were found in dry abandoned meadows (Fig. 4). Statistically significant differences were detected between samples from sedge bogs with shrubs and those from abandoned meadows for *mp* ($\chi^2 = 5.496$, d.f. = 1, $p < 0.02$; value calculated with Yates's correction) and for all combined polymorphic arm combinations ($\chi^2 = 4.216$, d.f. = 1, $p < 0.05$).

This study shows that a chromosomal polymorphism still exists in common shrews at Białowieża. It can be suggested that a balanced polymorphism occurs there and that environmental heterogeneity is an important factor in maintaining this polymorphism, particularly in relation to arm combination *mp*. FEDYK (1980) also suggested that the polymorphism for arm combination *gr* could be related to the environment. Despite the relatively low frequency of twin-acrocentric morphs in this population, the

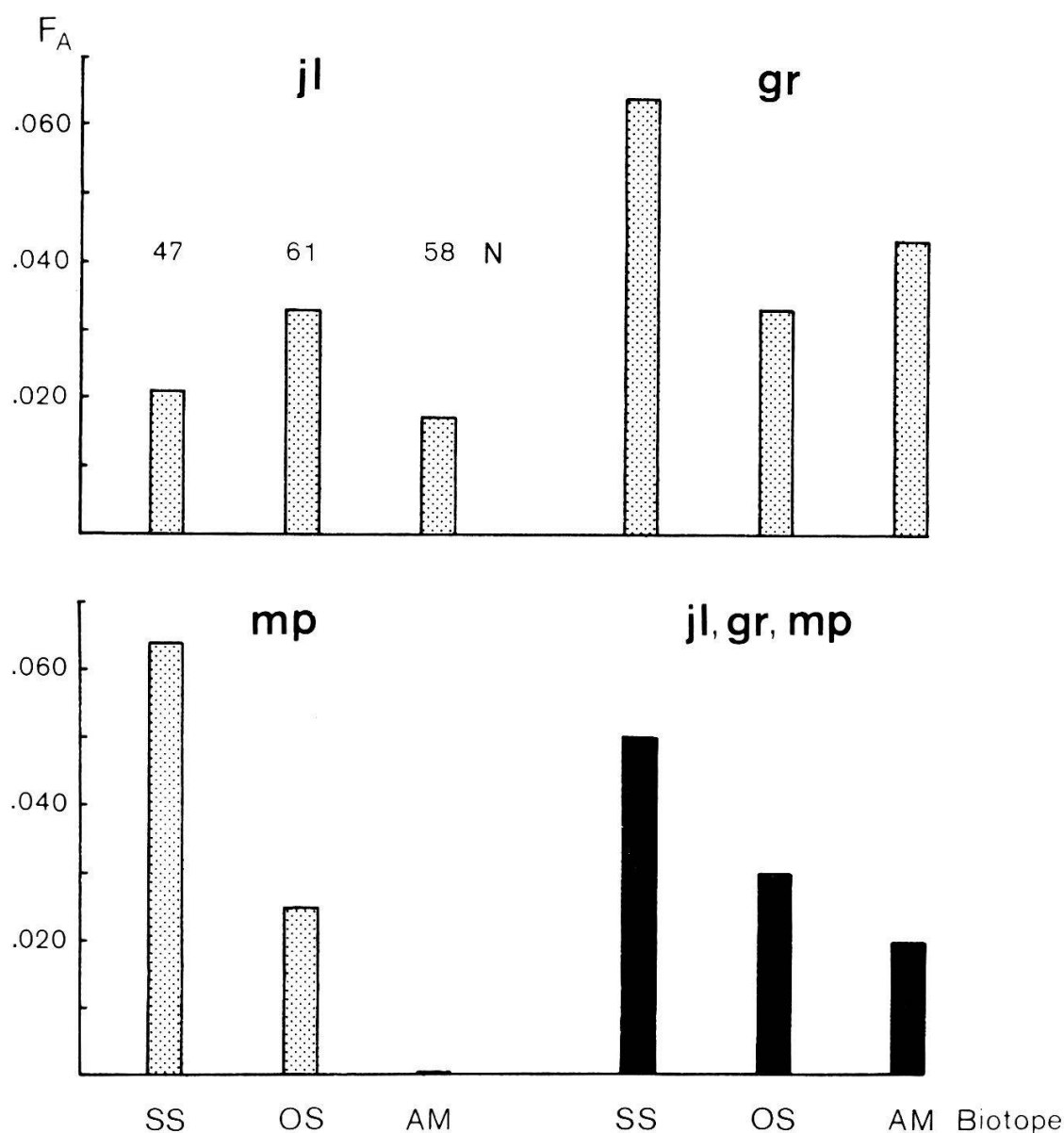


Figure 4.—Frequency of twin-acrocentric morphs of each polymorphic arm combination in different biotopes (see Table 1 and Fig. 1). Sample sizes are given above bars.

clear differences observed between biotopes suggest the action of selection rather than of random processes. However, further data will be collected to provide a stringent test of the hypothesis presented here.

The most detailed studies of karyotypic polymorphism in common shrews have been conducted in the Oxford area. SEARLE (1986a) explained that the polymorphism is associated with a hybrid zone between two karyotypic races occurring there. But it was also suggested that other factors are involved in the maintenance of the cline of polymorphism for one of the arm combination (*pr*). The possibility that the polymorphism is due to environmental changes was considered.

This study gives indirect evidence supporting the hypothesis that chromosomal polymorphism in common shrews is related to environmental heterogeneity. Chromosomal polymorphism could have significance for adaptation and evolutionary change within this species.

In chromosomally heterozygous common shrews there is a low frequency of anaphase I non-disjunction (for males 0.8% and for females 1.0-2.5%): (SEARLE 1984b, 1986b, 1988). It is hard to judge whether Robertsonian heterozygotes are at a fitness disadvantage in nature in comparison with homozygotes. BENGTTSSON and FRYKMAN (1990) assumed that chromosomal heterozygotes are always at a fitness disadvantage and that chromosome evolution in shrews may be mainly affected by cytological factors and have little or nothing to do with the animals' relation to their environment. The present results argue against BENGTTSSON and FRYKMAN's suggestions. HALKKA *et al.* (1987) also suggested that chromosomal polymorphism in common shrews acts as a source of adaptive variation relating to different environmental conditions. It can thus be argued that chromosomal polymorphism in the common shrew has an adaptive significance.

ACKNOWLEDGEMENTS

I would like to thank Prof. K. Fredga, Dr J.B. Searle and Dr M. Wolsan for their helpful comments on an earlier drafts of this paper. I thank Dr M.D. Sikorski and Dr A.M. Wójcik for their help in collecting the study material and Mrs J. Lipińska for her technical help in laboratory.

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