Heredity **59** (1987) 345–351

Received 20 December 1986

Karyotypic variation in the common shrew (*Sorex araneus*) in Britain – a "Celtic Fringe"

J. B. Searle* and
P. J. Wilkinson†

Department of Agricultural Science, University of Oxford, Parks Road, Oxford OX1 3PF, U.K.

Eight samples comprising 73 common shrews were collected from sites close to the coast in the south and west of England and Wales and analysed for karyotype. These samples included individuals of all three known British karyotypic races (Oxford, Aberdeen, Hermitage). Two new karyotypes were recorded: (a) individuals homozygous metacentric for arm combinations *ko* and *np* and homozygous acrocentric for chromosome arms *q* and *r* (classified as Aberdeen race) and (b) individuals homozygous metacentric for arm combinations *ko* and *pr* and homozygous acrocentric for chromosome arms *n* and *q* (classified as Hermitage race). The Aberdeen race occurs in the northern and western periphery of Britain (a "Celtic fringe"), the Oxford race is more central and eastern and the Hermitage race has an intermediate range (at least in England and Wales). This distribution is consistent with the hypothesis that the races spread into Britain at the end of the last glaciation in successive waves, the Oxford race partially displacing the Hermitage race which had, in turn, displaced the Aberdeen race. However, allele frequencies at the *Mpi*-1 locus may be more consistent with an independent origin of the separated northern and western subdivisions of the Aberdeen race.

INTRODUCTION

The karyotype of the common shrew (*Sorex araneus*) is exceptionally variable throughout its northern Palaearctic range, with many recorded examples of both polymorphism and polytypy (reviewed in Searle, 1984, 1986). This variation is of a Robertsonian type, so that the karyotypes of all individuals consist of the same basic set of chromosome arms but they may differ firstly in the number of chromosome arms which are fused together as metacentrics (as opposed to being separate as acrocentrics) and secondly in the combinations of chromosome arms that make up these metacentrics. In Britain, three distinct karyotypic races ("Aberdeen", "Hermitage" and "Oxford") have been described (Searle, 1984). The karyotypes of these races differ with respect to the set of metacentrics composed of chromosome arms *k*, *n*, *o*, *p*, *q* and *r*. The sex chromosomes XX/XY_1Y_2 and the autosomal metacentrics *af*, *bc*, *hi*, *gm*, *jl* and *tu* are universally present (although acrocentrics *j* and *l* may be present in place of the metacentric *jl* at low frequency).

The karyotype of the Aberdeen race is characterised by metacentrics *ko*, *np* and *qr*, that of the Oxford race has metacentrics *kq*, *no* and *pr*, while that of the Hermitage race includes metacentric *ko* with chromosome arms *n*, *p*, *q* and *r* in the acrocentric state. Around the hybrid zone between the Oxford and Hermitage races near Oxford, there are a variety of karyotypes which include chromosomes characteristic of both races and also the acrocentrics *k* and *o* (Searle, 1986).

The three karyotypic races of common shrew in Britain have been characterised on the basis of restricted geographical sampling, largely within 50 km of Aberdeen and Oxford (Searle, 1984). However, results from a study by J. L. Hamerton in the1950s (reviewed in C. E. Ford and Hamerton, 1970) suggest that shrews from the south and west of England and Wales may not readily be categorised as Aberdeen, Oxford or Hermitage race individuals. However, interpretation of these data is difficult as banding methods for accurate chromosome identification were not available at that time. This paper reports on a new investigation of the karyotypic variation along the south and

Present addresses: * School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, U.K., and † Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

west coasts of England and Wales. Altogether the karyotypes of 73 individuals from 8 sites were obtained. Furthermore, it has been possible to re-analyse almost completely the data of Ford and Hamerton (1970) on 102 individuals from 20 sites around Britain.

To assist in the interpretation of the karyotypic variation revealed in the present study, animals were typed at two isoenzyme loci: a mannose phosphate isomerase (E.C. 5.3.1.8) locus (*Mpi*-1) and a phosphoglucomutase (E.C. 2.7.5.1) locus (*Pgm*-3). In a previous study, allele frequency differences were identified between Oxford and Hermitage race and Aberdeen race samples at these loci (Searle, 1985).

MATERIALS AND METHODS

All samples were collected during 1984 from grass-dominated habitats. Animals from Wirral, Merseyside (Ordnance Survey grid reference: SJ 24/83) were collected by M. Dodds-Smith at various times during the Spring and maintained for several weeks in captivity. All other animals were captured during the latter half of the year, with each sample collected over a 2-day period, and all individuals killed for karyotypic analysis within a week of capture. These samples consisted of immatures only or a mixture of immatures and adults, including animals of both sexes. Because of the small sample sizes no attempt was made to separate these categories; there is no clear indication of an effect of age or sex. The sample sites were Abbeytown, Cumbria (NY 19/49); Ty'n-y-rhôs, Anglesey (SH 37/88); Dale, Dyfed (SM 80/04), Chysauster, Cornwall (SW 47/34); Rewe, Devon (SS 94/00); Arreton, Isle of Wight (SZ 53/86); and Ashurst, West Sussex (TQ 17/16). All sample site locations are indicated in fig. 1.

For karyotypic analysis, bone marrow chromosome preparations were made as described previously (Searle, 1984). Preparations from most individuals, including animals from all sites, were scored for karyotype after G-banding. The karyotypes of other individuals were deduced from conventional preparations.

The methods used for electrophoretic analysis of *Mpi*-1 and *Pgm*-3 follow Searle (1985). In some cases the animals used for isoenzyme studies were not the same as those karyotyped and *vice versa*.

RESULTS

Table 1 presents details of the karyotypes of the animals collected. As with all individuals from Britain previously examined, the sex chromosomes XX/XY_1Y_2 and the autosomes *bc*, *af*, *hi*, *gm* and *tu* were invariant (*e.g.*, see figs 2 and 3). Also, as found elsewhere in Britain and throughout the range of the species (Searle and Fredga, in preparation), arm combination *jl* displayed low-level polymorphism at Wirral, Ashurst and Chysauster, with the metacentric morph predominating. Thus, as expected, the major karyotypic variation detected in the present study involved chromosome arms *k*, *n*, *o*, *p*, *q* and *r*. Furthermore, the karyotypes of all individuals sampled had similarities with either the Oxford, Hermitage or Aberdeen race karyotypes, although with some important deviations from the standard.

All individuals from Abbeytown had the standard Oxford race karyotype with arm combinations *kq*, *no* and *pr* in the homozygous metacentric state (as illustrated in Searle, 1984). The Oxford race has been detected previously in southern Scotland and north-eastern and central-southern England (fig. 1). Its presence in north-western

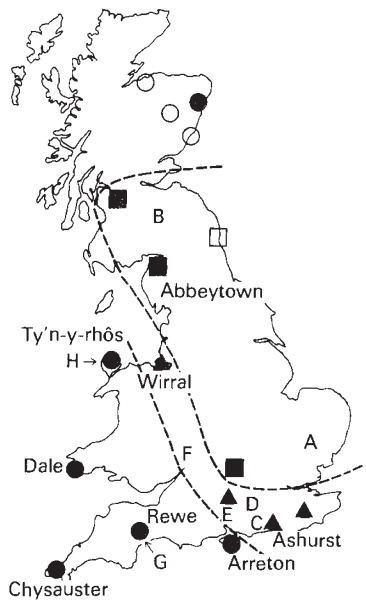

Figure 1 The sites sampled in the present study (named) and the location of previous samples or groups of samples collected by Searle (1984). The karyotypic characteristics are represented as follows: Oxford race (squares), Hermitage race (triangles), Aberdeen race (circles). "A"–"H" indicate the location of major samples reported by Ford and Hamerton (1970), see table 3. Dashed lines are drawn as a guide to indicate that the Oxford race has a central distribution, the Aberdeen race has a peripheral distribution to the north and west and the Hermitage race has an intermediate distribution. Solid symbols indicate samples subjected to analysis of isoenzymes.

Table 1 The karyotypes of all individuals from all samples collected

Sample	*N*	Arm combinations*			
Oxford Race		*jl*	*kq*	*no*	*pr*
Abbeytown	6	M	M	M	M
Hermitage Race		*jl*	*ko*	*pr*	
Wirral	4 (3)†	M	M	M	
	1	H	M	M	
Ashurst	4 (2)	M	M	A	
	2 (2)	H	M	A	
	1	M	M	M	
Aberdeen Race		*jl*	*ko*	*np*	*qr*
Ty'n-y-rhôs	12 (2)	M	M	M	A
Dale	9	M	M	M	M
	4	M	M	M	H
	1	M	M	M	A
Chysauster	7	M	M	M	A
	2	H	M	M	A
Rewe	5	M	M	M	M
	5	M	M	M	H
Arreton	10	M	M	M	A

* M = homozygous metacentric; H = heterozygous; A = homozygous acrocentric. Only arm combination *jl* and those arm combinations which characterise each race are considered.
† Number of individuals where karyotype deduced from conventional preparations, rather than G-banded preparations.

England is further evidence of the widespread occurrence of this race in central Britain.

Six of the individuals in the Ashurst sample had the standard Hermitage race karyotype with arm combination *ko* in homozygous metacentric state and chromosome arms *n*, *p*, *q* and *r* in an acrocentric state (as illustrated in Searle, 1984). This is to be expected as other individuals from the extreme south-east of England have had this karyotype. However, one individual from the Ashurst sample was homozygous metacentric for both arm combinations *ko* and *pr*. The same karyotype was also recorded in all individuals from Wirral. This karyotype has previously not been reported and is illustrated in fig. 2.

Around the hybrid zone between the Oxford and Hermitage races in the Oxford area, where there is Robertsonian polymorphism for arm combinations *kq*, *no*, *pr* and *ko*, previous samples have indicated that the metacentric *pr* occurs at high frequencies to the north where there are high frequencies of metacentrics *kq* and *no*; but at low frequencies to the south where there are high frequencies of metacentric *ko* (Searle, 1986). Therefore, *pr* has been considered to be an Oxford

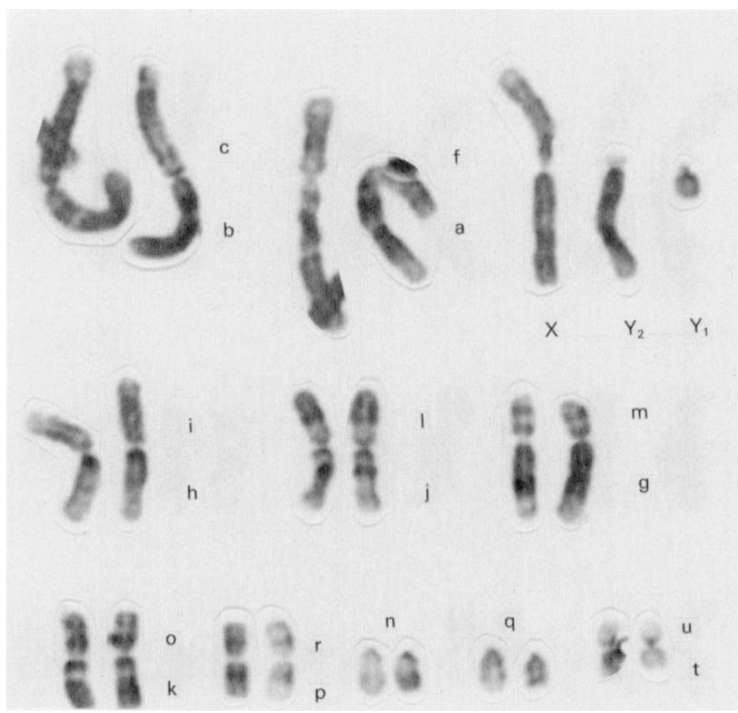

Figure 2 A new "Hermitage race" karyotype: homozygous metacentric for arm combinations *ko* and *pr* and homozygous acrocentric for chromosome arms *n* and *q*. (This individual is also homozygous metacentric for arm combination *jl*.) Karyotype obtained from a male common shrew from Wirral.

race-specific metacentric (along with *kq* and *no*; see Introduction). This was supported by the occurrence together of *kq*, *no* and *pr* in other earlier samples from central Britain and the absence of *pr* from other such samples consisting of Hermitage race individuals from south-eastern England (Searle, 1984). However, given that (a) metacentric *pr* occurred (albeit at low frequencies) in all five samples collected from the Oxford area that would otherwise have been catagorised as pure Hermitage race (Searle, 1986) and (b) metacentrics *ko* and *pr* occurred together in the Ashurst and Wirral samples, it is considered that *both* those animals whose karyotype includes metacentrics *ko* and *pr and* those that are homozygous acrocentric for chromosome arms *p* and *r*, should be assigned to the Hermitage race. Thus the samples from Wirral and Ashurst are considered to belong to the Hermitage race.

A further karyotype that has not been previously recorded was found in all individuals from Ty'n-y-rhôs, Chysauster, Arreton and in one individual from Dale (table 1). In this case, arm combinations *ko* and *np* were present in the homozygous metacentric state, as in the standard Aberdeen race karyotype, but chromosome arms *q* and *r* were present in the homozygous acrocentric state with the Aberdeen race metacentric *qr* absent (fig. 3). The samples from Rewe and Dale differed from the animals above only in that the Aberdeen race metacentric *qr* was present at a high frequency, in a homozygous or heterozygous state. Clearly, all individuals from Ty'n-y-rhôs, Dale, Chysauster, Rewe and Arreton had karyotypes closely related to the standard Aberdeen race karyotype and are thus considered to belong to the Aberdeen race.

Table 2 presents the allele frequencies and mean heterozygosities at the *Mpi*-1 and *Pgm*-3 loci for each sample. While the values for the new Oxford race site of Abbeytown and the new Hermitage race sites of Wirral and Ashurst were often outside the upper and lower values of previous Oxford and Hermitage race samples respectively, such discrepancies can be attributed to sampling error given the small sample sizes in this study. The same may be said for the allele frequencies and mean heterozygosities at the *Pgm*-3 locus for T'yn-y-rhôs, Dale, Chysauster, Rewe and Arreton in comparison with previous Aberdeen race samples. However, there were marked differences in allele frequencies and mean heterozygosities at the *Mpi*-1 locus between the new Aberdeen race samples and the three Aberdeen area samples given

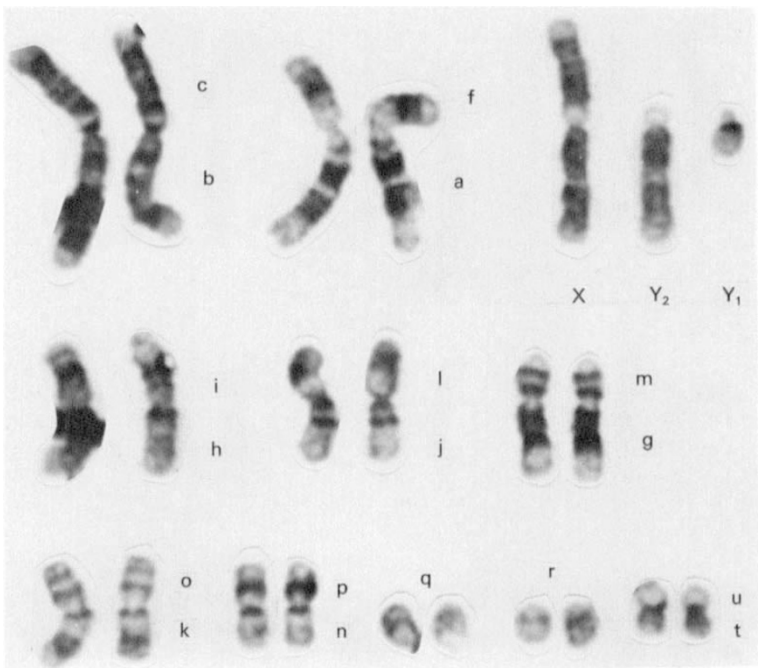

Figure 3 A new "Aberdeen race" karyotype: homozygous metacentric for arm combinations *ko* and *np* and homozygous acrocentric for chromosome arms *q* and *r*. (This individual is also homozygous metacentric for arm combination *jl*.) Karyotype obtained from a male common shrew from Chysauster.

Table 2 Isoenzyme allele frequencies and mean heterozygosities for each sample in comparison with previous data (Searle, 1985).

Sample		*N*	*Mpi*-1 Frequency a	b	c	d	e	f	Mean heterozygosity	*Pgm*-3 Frequency a	b	c	d	e	Mean heterozygosity
	upper		0·67	0·47	0·10	0·11	0·11	0·02	0·67	0·80	0·47	0·18	0·02	0·03	0·63
Oxford race		99													
(4 samples)	lower		0·48	0·11	0	0	0	0	0·44	0·48	0·17	0·02	0	0	0·37
Abbeytown		4	0·75	0·13	0·13	0	0	0	0·50	0·88	0·13	0	0	0	0·25
	upper		0·67	0·43	0·07	0	0	0	0·71	0·71	0·25	0·14	0·03	0	0·53
Hermitage race		37													
(2 samples)	lower		0·50	0·30	0·03	0	0	0	0·40	0·70	0·14	0·02	0	0	0·43
Wirral		7	0·57	0·21	0·21	0	0	0	0·43	1·00	0	0	0	0	0
Ashurst		7	0·79	0·21	0	0	0	0	0·43	0·50	0·36	0	0·14	0	0·86
	upper		0·97	0·05	0·02	0	0	0	0·10	0·88	0·18	0	0	0	0·23
Aberdeen race		90													
(3 samples)	lower		0·95	0·02	0	0	0	0	0·07	0·82	0·12	0	0	0	0·17
T'yn-y-rhôs		11	0·27	0·36	0·36	0	0	0	0·73	0·82	0·18	0	0	0	0·36
Dale		13	0·23	0·50	0·23	0	0	0·04	0·69	1·00	0	0	0	0	0
Chysauster		8	0·13	0·56	0·31	0	0	0	0·75	0·94	0·06	0	0	0	0·13
Rewe		11	0·59	0·41	0	0	0	0	0·45	0·68	0·32	0	0	0	0·45
Arreton		13	0·46	0·54	0	0	0	0	0·62	0·88	0·08	0·04	0	0	0·23

in Searle (1985). In the samples from the Aberdeen area the mean heterozygosity at the *Mpi*-1 locus was low (0·07–0·10), with the samples practically monomorphic for the *Mpi*-1^a allele (frequency 0·95–0·97). In the new samples mean heterozygosities were high (0·45–0·75) and in four of the five samples *Mpi*-1^a was not the commonest allele. Of the new samples there were striking similarities in allele frequencies and mean heterozygosities at the *Mpi*-1 locus between the three westernmost samples of T'yn-y-rhôs, Dale and Chysauster. In each case heterozygosities were very high (0·69–0·75), with alleles *a*, *b* and *c* all common and in the order of frequency $b \geqq c \geqq a$. No other sample had similar characteristics. The two Aberdeen race samples from the south coast of England, Rewe and Arreton, also had similar characteristics to each other with respect to *Mpi*-1, with high heterozygosities and only two alleles (*Mpi*-1^a and *Mpi*-1^b) both at a frequency of about 0·5. Similar *Mpi*-1 characteristics have been recorded for some of the Oxford and Hermitage race samples from south-eastern England (Searle, 1985).

DISCUSSION

Previous to this study, three karyotypic races of common shrew had been identified in Britain: the "Oxford", "Aberdeen" and "Hermitage" races (Searle, 1984). While new karyotypes have been found in the area sampled here, it is not considered justified to define further karyotypic races as the new karyotypes are clearly related to the "standard" Aberdeen and Hermitage race karyotypes, respectively. The new data provide much interesting information on the distribution of the Aberdeen,Hermitage and Oxford races. From this new information it is possible (a) to reinterpret the data of Ford and Hamerton (1970) and (b) to consider, in general terms, the origin and mode of spread of the races.

Table 3 presents a reinterpretation of the geographical survey of Ford and Hamerton (1970) and the locations of their main samples are marked on fig. 1. Clearly, the present study has been most useful in the interpretation of the data of Ford and Hamerton from the south and west of England and Wales; Searle (1984) provides an analysis of the data for south-eastern England. It is proposed that element 4 of Ford and Hamerton is arm combination *jl*, element 5 can be either arm combination *ko* or *kq*, element 6 can be arm combination *no*, *np* or *pr* and element 7 can be arm combination *pr* or *qr*. Considering the apparently Hermitage race samples of Ford and Hamerton, those from south-eastern England appear to have consisted primarily of animals with the "standard" Hermitage race karyotype (homozygous metacentric for *ko* and homozygous acrocentric for chromosome arms *n*, *p*, *q* and *r*). However, in common with the samples from the Oxford area (Searle,

Table 3 A reinterpretation of the karyotypes reported in Ford and Hamerton (1970; table 1)

Code for fig. 1	Sample	*N*	Arm combinations			
	Oxford race		*jl*	*kq*	*no*	*pr*
A	Bradfield Combust, Suffolk	21	0·98	1·00	1·00	0·29
	Epping Forest, Essex	1	1·00	0·50	0·50	1·00
B	Peebles, Scotland	7	1·00	1·00	1·00	1·00
	Hermitage race		*jl*	*ko*	*pr*	
	Addington Park, Kent	2	1·00	1·00	0	
	Fetcham, Surrey	2	1·00	1·00	0	
	Beddington, Surrey	1	1·00	0·50	0	
C	Kirdford, Sussex	10	1·00	1·00	0	
	Alice Holt Forest, Hants	2	1·00	1·00	0	
D	Bentley Station, Hants	8	1·00	0·94	0	
E	Andover, Hants	20	1·00	1·00	0	
F	Tewkesbury, Gloucs	6	0·92	0·75	0·83	
	Aberdeen race		*jl*	*ko*	*np*	*qr*
G	Exeter,* Devon	10	1·00	1·00	1·00	0·90
	Holsworthy,† Devon	2	0·50	1·00	1·00	0
	Cape Cornwall, Cornwall	1	1·00	1·00	1·00	0
H	Anglesey, Wales	6	0·92	1·00	1·00	0

* Includes nearby Mutter's Moor, Harpford Wood, Windy Cross and Ladrum Bay.
† 'Molesworthy' in Ford and Hamerton (1970).

1986) and Ashurst and Wirral (present study), the sample from Tewkesbury appears to have included Hermitage race individuals homozygous or heterozygous for the metacentric *pr*. (This interpretation is supported by recent samples collected close to Tewkesbury: J. B. Searle and A. J. Reilly, unpublished data.) Considering the apparently Aberdeen race samples of Ford and Hamerton, the data on shrews collected from Exeter, Cape Cornwall and Anglesey are as expected on the basis of samples from Rewe, Chysauster and T'yn-y-rhôs, which are the respective nearby sites sampled in the present study. Holsworthy is intermediate in location between Rewe and Chysauster. Due to a lack of recent data on shrews from western Scotland it is, as yet, difficult to interpret the data reported by C. E. Ford and Hamerton (1970) on shrews from the Kyle of Lochalsh and those described by P. J. Ford and Graham (1964) on shrews from Kintyre, Islay, Jura and Gigha.

As indicated in fig. 1, the available information suggests that the Oxford, Hermitage and Aberdeen races are widespread forms with the Oxford race occurring in central Britain, the Aberdeen race present in the western and northern periphery and the Hermitage race apparently occupying an intermediate range. Given that we have this general picture of the distribution of karyotypic races in Britain, how may this distribution be explained? In particular, there is a need to account for the subdivision of the Aberdeen race into two geographically separate ranges (in western England and Wales and in northern Scotland).

There is substantial evidence that at the last glacial maximum Britain was climatically inhospitable to the common shrew (Yalden, 1982). Thus, any model for the origin and spread of the British karyotypic races must take into account that the common shrew invaded Britain while there was still a land bridge at the end of the glaciation (Searle, 1984). The distribution of the British karyotypic races suggests that these races originated outside Britain and invaded in successive waves with partial displacement of earlier invading races. Therefore it is suggested that the Aberdeen race represents a "Celtic fringe". In a roughly analogous way to the Celtic peoples, the Aberdeen race shrews are envisaged as representing a once continuous race that invaded Britain from continental Europe, but that with partial displacement by the Oxford race this race is now limited to the northern and western periphery. The occurrence of the Hermitage race at Wirral suggests that the Hermitage race may form an intermediate ring between the Oxford and Aberdeen races and thus could represent an intermediate wave of invasion between the Aberdeen and Oxford races. The projected boundaries between the races (fig. 1), which must be considered highly approximate, are consistent with the preposed waves of invasion coming across at the position of the North Sea, which on the basis of present day sea level data is the site

of the major land bridge between Britain and continental Europe at the end of the last glaciation (Yalden, 1982).

The model of invasion and displacement by karyotypic races outlined above requires that in each case the boundary between successive races (presumably a hybrid zone) should move. The conditions under which racial boundaries, specifically hybrid zones, may move are fully discussed in Barton and Hewitt (1985); we shall not speculate further here.

It is of significance that the common shrews on Anglesey and the Isle of Wight have an Aberdeen race karyotype. Both of these islands were separated from the mainland at approximately the time of separation of Britain from the continent of Europe, *i.e.*, 9000 years b.p. (Yalden, 1982; Trueman, 1971; Melville and Freshney, 1982). Because of their physical attributes (they are not particularly agile and have poor vision) and feeding habits (they need to feed at least every 2 hours largely on an invertebrate diet), common shrews are not easily transported by man on boats. Therefore, it is likely that they crossed to Anglesey and the Isle of Wight while there was still a land bridge to the mainland. If, in future studies, it is demonstrated that samples of common shrew from the mainland close to the islands are of Hermitage or Oxford race it will further support the contention that these latter races displaced the Aberdeen race.

Previous studies in Britain (Searle, 1985) and Sweden (Frykman *et al.*, 1983) have indicated that allele frequencies at the *Mpi*-1 locus may differ between karyotypic races of common shrew. The present study shows that in Britain there is, in fact, not a simple relationship between *Mpi*-1 allele frequencies and karyotypic race. The allele frequencies at this locus differ markedly between the two main subdivisions of the Aberdeen race, in north-eastern and south-western Britain. This suggests an independent origin of the Aberdeen karotypic race in these two parts of Britain, rather than a common origin with subsequent partial displacement by other races. However, there is some indication that *Mpi*-1 allele frequencies in samples from the south of Britain may be more related to geographical location of the sample than to their karyotypic race. Samples from the extreme west (Anglesey, south-western Wales, Cornwall) of the south-western subdivision of the Aberdeen race differ in *Mpi*-1 allele frequencies from samples from more central localities, which are more similar to some Oxford and Hermitage race samples from south-eastern England. The further survey of Britain will help establish the relative importance of geographic location and karyotypic race as determinants of *Mpi*-1 allele frequency and hence the usefulness of this locus as a marker of karyotypic race.

Acknowledgements This work was supported in part by the Mammal Society of Great Britain. We thank Dr J. R. Clarke (Department of Agricultural Science, University of Oxford) and Dr W. A. F. Watson (Department of Genetics, University of Aberdeen) for laboratory facilities, Mr M. Dodds-Smith for shrews, Mrs J. Gorton and Ms A. J. Reilly (School of Biological Sciences, University of East Anglia) for help with preparation of the manuscript and Drs G. M. Hewitt and A. E. Douglas (School of Biological Sciences, University of East Anglia) for comments on the paper. The manuscript was prepared while J.B.S. was supported by N.E.R.C. grant GR3/5413 to Dr G. M. Hewitt.

REFERENCES

BARTON, N. H. AND HEWITT, G. M. 1985. Analysis of hybrid zones. *Ann. Rev. Ecol. Syst.*, *16*, 113–148.

FORD, C. E. AND HAMERTON, J. L. 1970. Chromosome polymorphism in the common shrew, *Sorex araneus*. *Symp. zool. Soc. Lond.*, *26*, 223–236.

FORD, P. J. AND GRAHAM, C. F. 1964. The chromosome number in the common shrew, *Sorex araneus* L. *Bull. Mammal Soc. Br. Isl.*, *22*, 10–11.

FRYKMAN, I. SIMONSEN, V. AND BENGTSSON, B. O. 1983. Genetic differentiation in *Sorex*. I. Electrophoretic analysis of the karyotypic races of *Sorex araneus* in Sweden. *Hereditas*, *99*, 279–292.

MELVILLE, R. V. AND FRESHNEY, E. C. 1982. *Hampshire Basin and Adjoining Areas*. Geological Sciences Institute, London.

SEARLE, J. B. 1984. Three new karyotypic races of the common shrew *Sorex araneus* (Mammalian: Insectivora) and a phylogeny, *Syst. Zool.*, *33*, 184–194.

SEARLE, J. B. 1985. Isoenzyme variation in the common shrew (*Sorex araneus*) in Britain, in relation to karyotype. *Heredity*, *55*, 175–180.

SEARLE, J. B. 1986. Factors responsible for a karyotypic polymorphism in the common shrew, *Sorex araneus*, *Proc. R. Soc. Lond. B*, *229*, 272–298.

TRUEMAN, A. E. 1971. *Geology and Scenery in England and Wales*. Penguin, London.

YALDEN, D. W. 1982. When did the mammal fauna of the British Isles arrive? *Mammal Rev.*, *12*, 1–57.