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Geographical variation in house-fly (*Musca domestica* L.) sex determinants within the British Isles

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Summary

Genetic and cytological analyses of house-flies collected from 12 pig-breeding farms throughout the British Isles demonstrated that the non-standard sex determination mechanism prevailing in South-East England, involving a dominant female determinant (F) and virtual homozygosity for a male determinant on the *X* chromosome (X^m, both males and females morphologically *XX*), was not typical of the country as a whole. Instead there was a gradual decrease in the frequency of F, X^m and a rarer male determinant *M* III, and a concomitant increase in the standard male determining *Y* chromosome, on moving north, east and west of this region. Only the Scottish and probably the Irish populations were fully standard (*XX* females *XY* males), although one from the East Anglian coast in which non-standard determinants were rare was predominantly of this type. Populations from intermediate areas possessed complex multifactorial mechanisms in which *Y*, F X^m and *M* III coexisted. It is hypothesized that this radial cline in sex determinants, like the latitudinal cline known from mainland Europe, represents a transient polymorphism caused by the recent and continuing invasion of non-standard determinants into originally standard populations. The cause(s) of this apparently rapid evolutionary change, however, remain unclear.

1. Introduction

In recent years there has been a reshaping of views regarding the sex determination mechanism in natural populations of house-flies. Originally the 'standard' heterogametic mechanism involving a male determining *Y* chromosome was thought to prevail; isolated reports of linkage between sex determinants and autosomal genes (Milani & Franco, 1959; Kerr, 1961; Sullivan, 1961; Hiroyoshi, 1964; Milani, Rubini & Franco, 1967; Wagoner, 1969) were generally considered atypical of the species as a whole. However, discoveries in several parts of the world of 'non-standard' mechanisms involving dominant autosomal or *X*-linked male determinants (*M* factors) and sometimes a female determinant (F* factor) (e.g. McDonald *et al.* 1975; Hiroyoshi & Fukumori, 1977; Rubini, Van Heermart & Franco, 1977; Hiroyoshi & Inoue, 1979; Tsukamoto, Sono & Horio, 1980; Franco, Rubini & Vecchi, 1982; Denholm *et al.* 1983) demonstrate that this is no longer so, and that sex may often be independent of the *XY* genotype.

These findings have prompted suggestions (Hiroyoshi, 1980; Franco *et al.* 1982) that *M* and F factors may be recent invaders that are competitively supplanting the ancestral *XY* mechanism. The most substantive evidence for this comes from fly populations in Continental Europe, which show a clinal transition from wholly non-standard populations (*XX* ♀♀ and ♂♂) at low altitudes in the south to standard ones *XX* ♀♀, *XY* ♂♂) in the north (Franco *et al.* 1982). Populations near Rome now possess *M* factors on autosomes 2 and 3 (*M* II and *M* III) but were almost certainly standard as recently as 30 years ago (Milani, 1956; 1964). Moreover, populations in the transition zone in Northern Italy, where *M* factors and *Y* coexist, showed a significant decrease in the frequency of *Y* between 1975 and 1982 (Rubini, Vecchi & Franco, 1983).

A previous paper (Denholm *et al.* 1983) demonstrated that house-fly populations on animals farms in South-East England are non-standard and possess an unlocated F factor, and *M* factors on autosome 3 (*M* III) and the *X* chromosome (X^m). Most flies of both sexes were *XX* and homozygous for X^m. However, preliminary data suggested that X^m was less frequent, and *Y* more frequent, in the north of Britain than in the south. We report here on geographical variation in sex determinants within the country as a whole, and consider whether an evolutionary change

* F is not italicized because its nature and location have not been satisfactorily resolved.

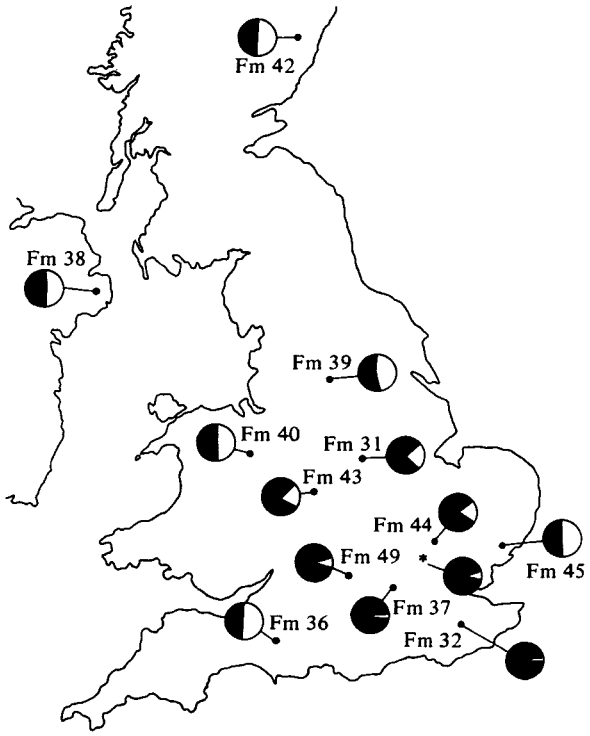

Fig. 1. Geographical origin of the 12 field strains referred to in the text. The asterisk denotes the approximate origin of eight field strains collected in 1980–81 within 15 km of Harpenden. Black areas of circles indicate the proportion of males in F_1 progeny of the mass cross (standard ♀ × field strain ♂).

similar to that apparent for mainland Europe is also presently occurring within the British Isles.

2. Materials and Methods

(i) *House-fly strains*

(*a*) *Field strains.* 12 field strains collected between March 1981 and July 1983 from pig-breeding farms throughout the British Isles (Fig. 1) are identified by code numbers of the farms (Fm31, Fm32, Fm36, Fm37, Fm38, Fm39, Fm40, Fm42, Fm43, Fm44, Fm45, Fm49). Eight field strains collected within 15 km of Harpenden (35 km N.W. of London) and analysed previously (Denholm *et al.* 1983) are also considered here. These strains, reared in the laboratory for at least one generation before analysis, varied greatly in resistance to many insecticides (Farnham *et al.* 1984).

(*b*) *Laboratory strains.* Cooper, SRS (WHO Standard Reference Strain) – 2 wild-type strains, susceptible to insecticides, with a long history of laboratory culture. *ac*; *ar*; *bwb*; *ocra* – marked with recessive visible mutations on autosomes 1 (ali-curvae, *ac*), 2 (aristapedia, *ar*), 3 (brown-body, *bwb*) and 5 (ocra-eyes, *ocra*); insecticide susceptible. *bwb* SRS – containing the autosome 3 *bwb* marker in the susceptible SRS genome. All four laboratory strains have the standard *XY* sex determination mechanism.

(ii) *Rearing methods*

Mass crosses and single-pair crosses were established as described by Denholm *et al.* (1983).

(iii) *Cytogenetic studies*

Karyotypes of some strains were examined, usually in the first two generations of laboratory culture, in squashes of gonads stained with acetolactic-orcein (cf. Rubini, Vecchi & Franco, 1980). The parental karyotypes of some single-pair crosses were also investigated.

(iv) *Genetic analyses*

Mass crosses between field strain males and standard females gave preliminary information on the frequency and homozygosity of male determinants in field strains. Reciprocal single-pair crosses between field and standard strains disclosed the frequency of flies responsible for sex-ratios departing from 1♀:1♂ in F_1 progeny, and the presence of F in field strain females.

The linkage relationships of male determinants in two strains (Fm44 and Fm45) were investigated by test-crossing F_1 (marked ♀ × field ♂) males to marked females in single-pairs, using either the *ac*; *ar*; *bwb*; *ocra* (which tests autosomes 1, 2, 3 and 5) or *bwb* SRS (which tests only for *M* III) strains. Test-cross progeny were scored for sex and phenotype as described by Denholm *et al.* (1983).

3. Theoretical considerations

Expected segregations and sex-ratios from crosses performed to resolve the sex determining mechanism of non-standard populations were detailed by Denholm *et al.* (1983). This section expands on the most pertinent of these and introduces some approaches not used earlier. Field strains may contain, singly or in combination, male determinants on *Y*, $X(X^m*)$ or one or more of the autosomes (e.g. *M* III). Females may also be heterozygous for the F factor. Sex-ratios expected from single-pair crosses between standard *XX* females and field strain males homozygous or heterozygous for 1 or 2 male determinants (*Y*, X^m or *M* III) are:

Cross	Genotype of male parent	Sex-ratio
1	X/X^m or X/Y or *M* III/+	1♀:1♂
2	X/X^m; *M* III/+ or X/Y; *M* III/+	1♀:3♂
3	X^m/X^m or *M* III/*M* III or X^m/Y	All male

Homozygosity for one *M* factor, or the presence of both X^m and *Y* in Cross 3 masks the effect of any other male determinants present. Cross 3 families occasionally contain small numbers of females, resulting from

* X^m is used here to denote both the *X*-linked male determinant and an *X* chromosome that bears it. *X* denotes a standard *X* chromosome lacking X^m.

meiotic non-disjunction of male determining chromosomes in the male parent. Since all such females examined have proved to be aneuploid *XO*, and non-disjunction of autosomes is unknown in this species, these occurrences are probably diagnostic of at least one X^m chromosome in the paternal genome. Sex-ratios from mass crosses in this direction depend on the number, frequency and extent of homozygosity for *M* factor(s) in the field population.

The reciprocal cross (field ♀ × standard *XY* ♂) is less informative, but sex-ratios from single-pair crosses can disclose the presence of F, with or without 1 or 2 *M* factors in heterozygous form:

Cross	Genotype of female parent	Sex-ratio
4	*X*/*X*, no F or X^m/Y; F/+ or X^m/X^m; F/+	1♀:1♂
5	*X*/*X*; F/+	3♀:1♂
6	*X*/*Y*; F/+ or X/X^m; F/+ or *M* III/+; F/+	5♀:3♂
7	*X*/*Y*; *M* III+; F/+ or X/X^m; M III/+; F/+	9♀:7♂

Since most departures from 1 ♀:1 ♂ are less extreme than for Crosses 1–3, sex ratios from mass crosses in this direction may approach, and often be indistinguishable from 1 ♀:1 ♂.

The presence of autosomal *M* factors is established from single-pair test-crosses to standard *XX* females marked with visible recessive mutations on the required autosomes (Denholm *et al.* 1983). The presence of X^m is deduced from the lack of sex-limited expression of markers in test-cross progeny, and the absence of a *Y* chromosome in the parental male karyotype.

Single-pair crosses between field strain females and standard *XY* males can provide more conclusive evidence for X^m. The scheme is as follows: female parents are scored for karyotype once eggs are laid, and F_1 families having *XX* mothers and showing a sex-ratio of 5 ♀:3 ♂ kept for further analysis. These mothers probably possessed F and a non-standard male determinant, possibly X^m, in heterozygous form (cf. Cross 6). If so, the F_1 males have three possible genotypes as shown below:

$$\text{Parental cross} \quad \frac{X^m}{X};\frac{F}{+}\text{♀} \times \frac{X}{Y};\ \frac{+}{+}\text{♂}$$

$$\downarrow$$

$$F_1\ \frac{X^m}{X};\frac{F}{+}\text{♀} : \frac{X^m}{Y};\frac{F}{+}\text{♀} : \frac{X^m}{X};\frac{+}{+}\text{♂} : \frac{X^m}{Y};\frac{+}{+}\text{♂}$$

$$\frac{X}{X};\frac{F}{+}\text{♀} : \frac{X}{Y};\frac{F}{+}\text{♀} : \frac{X}{X};\frac{+}{+}\text{♀} : \frac{X}{Y};\frac{+}{+}\text{♂}$$

The F_1 males (XX^m, $X^m Y$ and *XY*) are mated in single-pairs to standard *XX* females. Expected sex-ratios in F_2 progeny depend on the genotype of the male parent thus:

Cross	Genotype of male parent	Sex-ratio
8	XX^m	1♀:1♂
9	$X^m Y$	All male
10	*XY*	1♀:1♂

When the original field strain female parent has an autosomal *M* factor instead of X^m, one quarter of gametes produced by F_1 males used in Cross 9 lacks male determinants, yielding an F_2 sex-ratio of 1 ♀:3 ♂ (cf. Cross 2). Hence the occurrence of some all male families at F_2 confirms X^m in the original field strain parent.

4. Results

(i) *Karyotypes of field strains*

The typical male-determining *Y* chromosome, extremely rare in most strains collected in the south of England where both sexes were *XX* (Fm44 and Harpenden), increased steadily in frequency on moving north (Fm31 and Fm39) and was present in all males of the Scottish Fm42 strain (Table 1). This was accompanied by a change in *Y* chromosome morphology; those in south-east England being small and those in Scotland the longest so far observed in Britain (Fig. 2). However, these changes were not solely latitudinal since Fm45, collected in East Suffolk at a similar latitude to Fm44, contained a high frequency of *Y* chromosomes of intermediate length. Aneuploidy of the *X* chromosome, probably reflecting meiotic non-disjunction in one or both sexes, occurred in most strains, but was generally rare.

(ii) *Crosses with standard strains*

F_1 sex-ratios of mass crosses between standard females and field strain males were also dependent on latitude (Table 2, Fig. 1). The large excess of males produced by most southern strains decreased northward to the extent that sex-ratios from the Scottish (Fm42) and Northern Irish (Fm38) strains were approximately normal (1 ♀:1 ♂). There were, however, two important exceptions to this latitudinal trend; males from the East Suffolk (Fm45) and Dorset (Fm36) strains gave an approximately normal sex-ratio despite their southern origin (Fig. 1). The few reciprocal crosses gave either a normal sex-ratio or a slight excess of females, the latter perhaps reflecting the presence of F in some female parents (i.e. a combination of Crosses 4–7 above). The crosses also produced varied numbers of intersexes (Milani, 1967) not ascribable to either sex.

The apparent latitudinal cline in sex-ratios and the concomitant change in the frequency of *Y* (Table 1) demonstrate a transition from predominantly standard populations in the north of Britain to wholly non-standard populations in much of the south-east. Furthermore, earlier findings (Denholm *et al.* 1983) suggest that the magnitude of variation in sex-ratios signifies not merely a change from standard to non-standard sex determinants but an increase in the frequency of homozygosity for X^m. Five strains were analysed further to test this interpretation.

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Table 1. *Sex chromosome karyotypes observed in field strains*

	Strain					
	Fm42	Fm39	Fm31	Fm44	Fm45	Harpenden[a]
(*a*) Females						
No. examined	42	34	34	51	36	175
XXX	0	0	0	5	1	0
XX	40	30	25	44	32	161
XO	2	1	5	0	3	5
XY	0	3	4	2	0	9
(*b*) Males						
No. examined	51	33	28	47	48	223
XXY	4	0	0	0	1	0
XXX	0	0	0	1	0	1
XX	0	13	22	46	9	207
XO	0	1	0	0	0	4
XY	45	19	6	0	36	11
OY	2	0	0	0	2	0
Proportion of ♂♂ with *Y*	1·0	0·58	0·21	0·0	0·81	0·05

[a] Pooled results for eight field strains collected near Harpenden. Strains are listed in order of decreasing latitude of farms of origin.

Table 2. *Sex-ratio of* F_1 *progeny of mass crosses between field and standard* [a] *strains*

Field parent	No. scored	♀	♂	?[b]	Sex ratio[c]
F_1 (standard ♀ × field ♂)					
Fm42	625	303	322	0	0·515
Fm38	965	489	476	0	0·493
Fm39	892	392	500	0	0·561
Fm40	1008	508	500	0	0·496
Fm31	990	255	733	2	0·740
Fm43	639	110	502	27	0·786
Fm44	1086	180	880	26	0·810
Fm45	948	465	483	0	0·510
Harpenden[d]	3302	161	3000	141	0·909
Fm49	347	18	318	11	0·916
Fm37	1213	47	1166	0	0·961
Fm32	1050	2	1048	0	0·998
Fm36	868	435	433	0	0·499
F_1 (field ♀ × standard ♂)					
Fm42	608	299	309	0	0·508
Fm44	1427	742	669	16	0·469
Fm45	763	398	365	0	0·478
Harpenden[d]	5557	2750	2749	58	0·494

[a] Cooper, SRS or *ac*; *ar*; *bwb*; *ocra* strains.
[b] ? = intersexes.
[c] No. ♂/total no. progeny, i.e. including intersexes.
[d] Pooled results for six field strains collected near Harpenden. Strains are listed in order of decreasing latitude of farms of origin.

(iii) *Analyses of individual strains*

(*a*) *Fm31 and Fm39.* Nearly 50% of single-pair crosses between Fm31 males, collected 170 km north of Harpenden (Fig. 1), and SRS females gave all male progenies (Table 3*b*), demonstrating a significant frequency of males homozygous for a male determinant (most likely X^m) or with the genotype X^m *Y* (Cross 3, Section 3). However, the latter genotype was probably of little importance in this respect since *ca.* 80% of Fm31 males lacked *Y* (Table 1). The presence of a single *XO* female in two otherwise all male families

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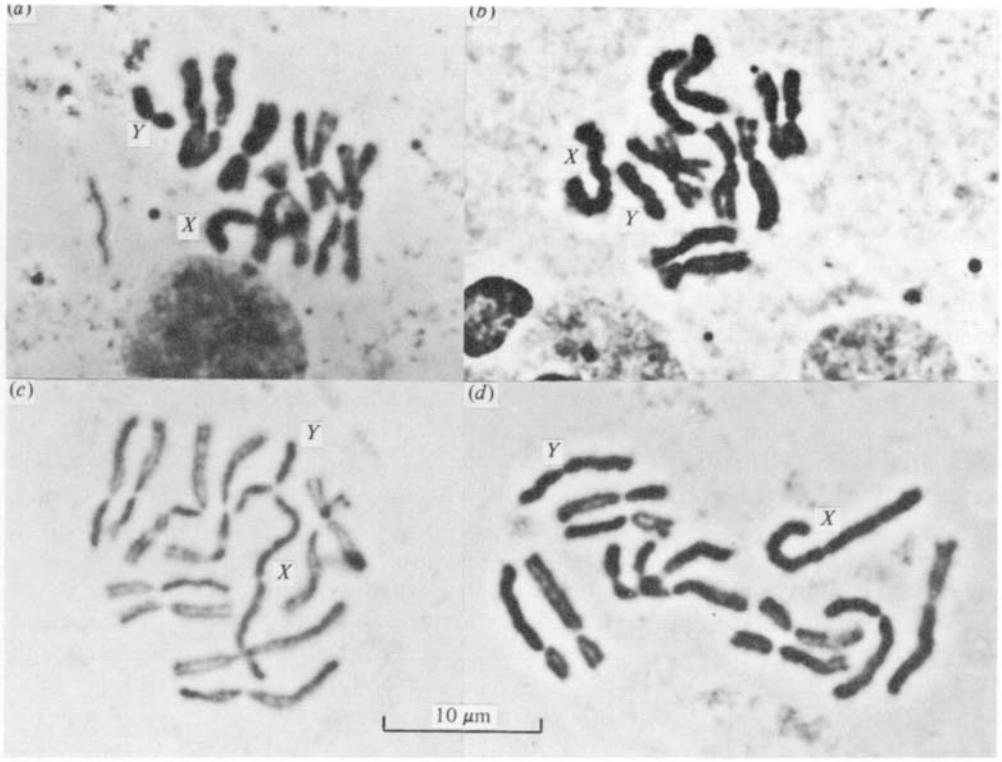

Fig. 2. Variants of the *Y* chromosome observed in four field strains of house-flies (photographed at mitotic metaphase from squashes of gonads). (*a*) one of the Harpenden strains, *Y* chromosome small; (*b*) Fm39 and (*c*) Fm45, *Y* of intermediate size; (*d*) Fm42, *Y* large.

Table 3. *Sex-ratio of* F_1 *progeny of single-pair crosses between field strain males and standard females*

Origin of father	Origin of mother	F_1 progeny: No. scored	♀	♂	?[a]	Sex-ratio[b]
		(*a*) Pooled data for all pairs				
Fm42	SRS	2014	1041	973	0	0·483
Fm39	SRS	1487	687	800	0	0·538
Fm31	SRS	1539	375	1164	0	0·756
Fm45	SRS	1936	946	990	0	0·511
Fm44(a)	SRS	2016	352	1606	58	0·797
Fm44(b)	Cooper	2250	566	1648	36	0·733
Harpenden[c]	SRS	12021	770	11061	190	0·920

Origin of father	Total no. of pairs	No. of pairs producing: < 2% females	2–12%	20–35%	*ca.* 50%	> 50%
	(*b*) Analysis of progeny of individual pairs					
Fm42	18	0	0	1	16	1
Fm39	18	0	0	3	14	1
Fm31	18	8	0	0	10	0
Fm45	20	0	0	1	18	1
Fm44(a)	19	10	0	4	5	0
Fm44(b)	25	9	2	5	9	0
Harpenden[c]	100	84	3	1	12	0

[a] ? = intersexes.
[b] No. ♂/total no. of progeny.
[c] Pooled results for four field strains collected near Harpenden.

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identified X^m in each of the male parents (see Section 3). Hence there was good evidence that in populations as far north as central England males, at least, show substantial homozygosity for X^m

In contrast, progenies of similar crosses with Fm39 males collected 100 km further north than Fm31 were mostly 1♀:1♂ and none were all male (Table 3*b*). Nonetheless, the occurrence of *XX* males implicated non-standard male determinants in this strain (Table 1), and the production of 1♀:3♂ families by *XX* fathers demonstrated that at least two such factors were present (Cross 2, Section 3). A test-cross to *ac*; *ar*; *bwb*; *ocra* females showed sex-linkage of *bwb* and identified one of these factors as *M* III. The other showing no autosomal linkage was almost certainly X^m which in Fm39 occurred only in heterozygous form.

Although the occurrence of *XY* females demonstrated that the F factor was present in both Fm31 and Fm39, its frequency in these strains was not investigated further.

(*b*) *Fm42*. The approximately normal pooled F_1 sex-ratio of single-pair crosses between SRS females and Scottish Fm42 males (Table 3*a*), and of all but two individual single-pair progenies (Table 3*b*), showed that male parents were heterozygous for a single male determinant previously identified as *Y* (Table 1). These results thus confirmed that this strain possessed the standard *XY* mechanism. The two single pair progenies that deviated significantly, but in opposite directions, from a normal sex-ratio were not examined further.

(*c*) *Fm45*. Although the great majority of single-pair crosses between SRS females and Fm45 males gave a normal sex-ratio (Table 3*b*), this could not be attributed solely to *Y* since *ca.* 20% of Fm45 males lacked this chromosome (Table 1). Test-crosses involving two Fm45 males, subsequently identified as *XX*, and *ac*; *ar*; *bwb*; *ocra* females identified *M* III in parental males. Two other test-crosses using *XX* males showed no abnormal segregation of markers and provided indirect evidence for X^m. Thus, although

Table 4. *Sex-ratio of* F_1 *progeny of single-pair crosses between field strain females and standard males*

Origin of mother	Origin of father	F_1 progeny: No. scored	♀	♂	?[a]	Sex-ratio[b]
(*a*) Pooled data for all pairs						
Fm45	SRS	2721	1402	1319	0	0·483
Fm44(*a*)	SRS	5106	2795	2311	0	0·453
Fm44(*b*)	Cooper	1427	742	669	16	0·469

Origin of mother	Total no. of pairs	No. of pairs[c] producing: 1♀:1♂	9♀:7♂	5♀:3♂
(*b*) Analysis of progeny of individual pairs				
Fm45	20	18	0	2
Fm44(*a*)	29	14	3	12
Fm44(*b*)	18	12	2	4

[a] ? = intersexes.
[b] No. ♂/total no. of progeny.
[c] Determined by χ^2 test.

Table 5. *Distribution and nature of family types in Fm44 test-cross progeny*

Family type	Sex-ratio	Segregation of *bwb*	No. of pairs	Probable interpretation
A	1♀:1♂	Independent of sex	34	X^m (or ?) only
B	1♀:3♂	One-third ♂ and all ♀ *bwb*	8	$X^m + M$ III
C	1♀:1♂	All ♂ wildtype All ♀ *bwb*	4	*M* III only
D	1♀:3♂	Independent of sex	5	X^m + ?

? = unlocated male determinant.

Fm45 from East Anglia apparently did not conform to the latitudinal trends described above, both non-standard male determinants present in populations near Harpenden also occurred in this strain. However, X^m in particular was much less frequent and found only in heterozygous form.

Two of 20 single-pair crosses between Fm45 females and standard *XY* males gave an F_1 sex-ratio conforming to 5♀:3♂ (Table 4*b*), a result expected when female parents possess F and a single male determinant (Cross 6 above). However, the normal sex-ratio in progeny of other pairs showed that F, like X^m and *M* III, was uncommon in this strain.

(*d*) *Fm44*. Single-pair crosses to standard females indicated that 35–52% of Fm44 males were homozygous for a male determinant, most likely X^m (Table 3*b*). This result was intermediate to those for Harpenden strains collected *ca.* 30 km south-west of Fm44 (84% of males homozygous) and Fm45 collected at a similar latitude to Fm44 but 90 km further east (where none were homozygous). Since none of the male parents examined possessed *Y*, other Fm44 males contained either one or two non-standard male determinants in heterozygous form (Crosses 1 and 2 in Section 3 respectively).

Progenies of reciprocal single-pair crosses conformed to three different sex-ratios (Table 4*b*). Fm44 females producing 5♀:3♂ and 9♀:7♂ probably possessed F in combination with one (Cross 6) and two (Cross 7) heterozygous male determinants respectively, whilst, in view of results for Fm44 males, those yielding a normal sex-ratio were most likely X^m/X^m; F (cf. Cross 4). The preponderance of F coupled with only partial homozygosity for X^m accounted for the excess of females produced by mass crosses in this direction (bottom of Table 2); this contrasted with results for Harpenden strains in which homozygosity for X^m is nearly complete. Hence results for both sexes were consistent in showing that Fm44 contained at least two independent male determinants in addition to *Y*, which was very rare in this strain (Table 1).

Test-crosses to *bwb* SRS females gave four types of family differing in phenotypic segregation of *bwb* and overall sex-ratio (Table 5). Family types A, B and C corresponded with those described for Harpenden strains (Denholm *et al.* 1983) and identified *M* III and a second more frequent male determinant, again assumed to be X^m. Type D families implicated a third unidentified and less frequent male determinant, perhaps located on an autosome other than no. 3.

Conclusive evidence of X^m in Fm44 was obtained from crosses outlined in Section 3. F_1 male progeny of two single-pair crosses (nos. 746 and 748) between standard *XY* males and *XX* Fm44 females that gave a 5♀:3♂ sex ratio (Table 6*a*) were mated to SRS females in single-pairs. Males from both pairs produced both all-male and 1♀:1♂ progenies, confirming that the original Fm44 female parent was X^m/X^m; F (Crosses 8–10, Section 3). Cytogenetic data supported the hypothesis of segregation of X^m, *Y* and F in these crosses (Table 7); F_1 progeny contained *XX* and *XY* flies of both sexes, and all-male F_2 progeny were both *XX* and *XY*. These results verified assumptions regarding the importance of X^m in Fm44.

Table 6. *Confirmation of* X^m *in Fm44 females*

Pair no.	F_1 progeny: No. scored	♀	♂	$\chi^2_{(1)}$ [a]
(*a*) F_1 progeny of single-pairs (Fm44♀ × SRS XY♂)				
746	237	148	89	0·00
748	189	120	69	0·08

Origin of father	Total no. of pairs	No. of pairs producing: All males	1♀:1♂
(*b*) F_2 progeny of single-pairs (SRS♀ × F_1 746♂ or F_1 748♂)			
746	14	9	5
748	12	5	7

[a] Expected sex-ratio of 5♀:3♂.

Table 7. *Karyotypes of progeny summarized in Table 6*

Pair no.	F_1 karyotypes: ♀ *XX*	♀ *XY*	♂ *XX*	♂ *XY*
(*a*) F_1 progeny of single-pairs (Fm44♀ × SRS XY♂)				
746	7	4	4	7
748	5	1	5	3

Origin of father	Sex-ratio of progeny	Karyotypes of progeny: ♀ *XX*	♂ *XX*	♂ *XY*
(*b*) Progeny of individual single-pairs (SRS♀ × F_1 746♂ or F_1 748♂)				
746	All-male	—	11	8
746	All-male	—	4	7
746	All-male	—	4	6
746	1♀:1♂	9	8	0
748	All-male	—	3	7

5. Discussion and Conclusions

The mechanism of female heterogamety based on F (with X^m homozygous) that prevails in South-East England (Denholm *et al.* 1983) is clearly not typical of the British Isles as a whole. Instead there is an almost complete clinal transition from this mechanism to one of standard *XY* male heterogamety in the north. Populations within this cline possess complex inter-

mediate mechanisms in which X^m, *M* III, F and *Y* may coexist. Limited data from populations in the south-west (Fm36) and extreme east (Fm45) of England show that this cline differs from that in mainland Europe (Franco, Rubini & Vecchi, 1982) in being radial rather than latitudinal or altitudinal, and hence independent of obvious climatic gradients.

There are, however, sufficient similarities between patterns of variation in sex determinants and *Y* chromosome morphology in Britain and Europe to suggest a common underlying cause. It now appears certain that the polymorphism in Europe is transient, reflecting a rapid northward spread of non-standard sex determinants into originally standard populations. Genetic data collected 25–30 years ago in Central Italy (Milani, 1956; 1964 and pers. comm. 1985) provide no evidence of the autosomal *M* factors that now predominate in the region, and the frequency of *Y* has decreased markedly in populations further north during the last ten years (Rubini, Vecchi & Franco, 1983). Although there are no comparable data for British strains collected before 1980, and no single locality has been studied sufficiently to disclose a directional trend, the present results are consistent with a hypothesis that British populations are currently undergoing a similar evolutionary change.

If this is so, the non-standard factors presently radiating outward from South-East England may have originated independently in this area, since populations closest to Britain in mainland Europe retain the standard mechanism (Franco *et al.* 1982 and unpublished data). Furthermore, although it is very frequent in South-East England, X^m is rare in mainland Europe has only been detected since 1980 in strains from Sardinia, mainland Italy and Yugoslavia (Rubini *et al.* 1984).

Theoretical models (Bull & Charnov, 1977; Bull, 1983) predict two stages by which the transition from *XY* male heterogamety to a system based on *F* might occur. Firstly an invading strong male determinant (X^m in this case) creates new, competitively-superior genotypes that spread and supplant *Y* in the population. Secondly this new system of male heterogamety is invaded by a strong epistatic *F* factor that enables a further increase of X^m genotypes and eventual fixation of X^m. Data for strains such as Fm45, with *XX* males but X^m (and *M* III) still rare, and the Harpenden strains, with *ca.* 85% homozygosity for X^m and a high frequency of F, appear broadly consistent with these predictions. However, the likely presence of F in Fm45 (Table 4*b*) is earlier than anticipated by the models. The actual occurrence of such a transition over this restricted geographical area would provide an ideal opportunity to test models of heterogametic systems with empirical data.

The reason why non-standard genotypes are apparently being favoured by selection is still obscure. Suggestions that the appearance of *M* and F factors is causally related to the evolution of insecticide resistance in house-flies (Hiroyoshi, 1980) or a consequence of tight linkage to resistance genes (Franco *et al.* 1982; Bull, 1983) remain highly speculative, particularly since these factors are not obviously correlated with the distribution of known resistance genes. Linkage to resistance genes is very unlikely to account for the spread of X^m as there is no evidence that the typical house-fly *X* chromosome contains structural genes (Milani, 1967; Rubini & Palenzona, 1967; Tsukamoto *et al.* 1980) and it has not been implicated in insecticide resistance.

Further monitoring of British populations is obviously needed to test the invasion hypothesis, and very detailed laboratory work will be required to discern the cause(s) of such a rapid and recent evolutionary change.

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