# The population cytogenetics of *Crepis* capillaris IV. The distribution of B-chromosomes in British populations

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Populations of *Crepis capillaris* to the south of latitude 53° 30′N in Britain are often polymorphic for the presence of B-chromosomes. Individual plants may have 0B, 1B or rarely 2B. Eleven out of 24 southern populations carried B-chromosomes with an overall average of 14 per cent B-containing plants in polymorphic populations. The maximum frequency of B-containing plants observed in a population was 25 per cent. In a detailed survey of Bredon Hill, Hereford and Worcester, B-chromosomes reached maximum frequencies at mid-altitudes in large populations, declining both towards the summit and in the small, isolated lowland populations. It is suggested that Bs in *Crepis* are excluded from populations growing under sub-optimal conditions. B-frequency in a population at East Wretham Heath, Norfolk, remained constant over three generations despite a very strong accumulation mechanism operating in *C. capillaris*. Selection must operate against individuals with one or more B-chromosomes to maintain this constancy.

**Keywords:** B-chromosomes, *Crepis capillaris*, geographical distribution, population structure, selection.

#### Introduction

B-chromosomes have been known in *Crepis capillaris* for many years and have been found in populations from as far apart as Switzerland (Rutishauser, 1960) and Britain (Whitehouse *et al.*, 1981). The Bs from both these sources are small metacentric elements about one-third the length of chromosome C, the smallest member of the standard complement, suggesting that these Bs have a common origin.

The structural similarity of these two B-accessions has recently been reinforced. C-banding studies show that repetitive DNA sequences occur on each side of the centromere in both accessions. Maluszynska & Schweizer (1989 and personal communication) have recently demonstrated ribosomal cistrons symmetrically placed in both arms of the B from both Swissderived and British material by silver staining and by in situ hybridization of an rDNA probe. This indicates that the B has an isochromosomal organization. This conclusion has been reported by Jones et al. (1989) for British-derived B-chromosomes demonstrating symmetrical hair-pin loops in surface-spread preparations of synaptonemal complexes from pollen mother cells.

As well as structural similarity, the Bs from these two widely separated sources show common behavioural characteristics. They undergo directed somatic non-disjunction so that the floral parts usually contain a higher number of Bs than the roots or leaves (Rutishauser & Röthlisberger, 1966; Parker *et al.*, 1989). Bs also affect the chiasma-forming properties of the A-chromosomes, although the details of the B-effect differ between the Swiss accession (Brown & Jones, 1976) and all the British accessions (Parker *et al.*, 1990).

The B-chromosome's polymorphism is thus wide spread and presumably ancient in *C. capillaris* across a large proportion of the species range (Western and Central Europe; Babcock, 1947). Very little information exists on the geographical distribution of the Bs, and the structure and behaviour of B-containing populations is unknown. In view of this deficiency, and coupled with the highly effective transmission behaviour, which should lead to a strong drive in populations, it is of great interest to investigate natural populations containing B-chromosomes.

In this paper the status of B-chromosomes in British populations of *Crepis capillaris* is recorded. A general

survey of Britain has been carried out as well as detailed observations of B-frequency within populations from a single small area in lowland England. In addition, a population has been followed over 3 years to assess whether changes in B-frequency occur.

### Materials and methods

#### Materials

- 1 Ripe achenes were collected from between 10 and 17 individuals in populations across the southern half of Britain in 1976 (10 populations) and 1977 (8 populations). Two offspring were grown to maturity from each parent plant, and B-constitution assessed in PMCs of between 20 and 34 individuals per population. Further collections of achenes were made in 1978, from 22 populations mainly in northern England and Scotland. Two offspring per parent were again screened for B-number, giving between 20 and 28 individuals per population. Scoring was carried out on root-tips of young plants.
- 2 Bulk achene samples were taken from 15 plants per population in 20 populations on and around Bredon Hill, Hereford and Worcester, in August 1979. Sixty achenes per population were germinated and between 31 and 60 individuals scored for B-number by root-tip analysis.
- 3 Mature plants were collected at East Wretham Heath in 1978 and scored by root-tip analysis. In 1979, a leaf collection was made in May and a capitulum (bud) collection in June.

#### Methods

Root-tips and young leaves were treated with 0.05 per cent colchicine solution for 2 h, fixed in 1:3 acetic alcohol, and stained by the Feulgen-orcein method. Capitula (buds) were fixed in 6:3:1 alcohol:chloroform:glacial acetic acid, and squashed in 2 per cent lactopropionic orcein to study meiosis.

# Results

## B-chromosome distribution in Britain

In the general survey, 40 populations from a wide variety of habitats were sampled from England, Wales and Scotland. A minimum of 20 plants was examined from each population to give a total of 1021 plants. B-chromosomes have been found in 11 of these populations (Table 1).

There is a very clear geographical pattern associated with the Bs which appears to reflect a North/South

divide (Fig. 1). Bs were not found in the 16 populations sampled from north of latitude 53° 30'N, corresponding to a line through the south of Yorkshire and Lancashire. South of this line a patchwork of populations with and without Bs was found. The B-containing populations showed no further geographical partitioning, occurring both in the Western (Highland) zone in Cornwall (Boscastle) and North Wales (Porthmadog), and across the Lowland zone to East Anglia (East Wretham Heath). The Bs were found in a wide variety of habitats including both permanent and temporarysand dunes, roadside verges, permanent pasture and grassy heathland. Characteristically, populations with and without Bs are often in close proximity (e.g. Santon Downham and East Wretham Heath, Norfolk, separated by only 5 km). This pattern clearly cuts across many of the obvious climatic divisions of Britain, such as those based on rainfall and both summer and winter temperatures.

The pattern established from our data, however, may not be as rigid as it appears. The B-chromosomes examined by Abraham *et al.* (1968), in their studies of chromosome replication patterns in *Crepis*, were obtained by R. A. Finch from a population at Ardgartan, Strathclyde, Scotland. In our survey, the nearest sampling site to this was at Shandon, Strathclyde, about 19 km to the north-west. Thus pockets of Bs may well exist to the north of latitude 53° 30′N, even though none were found in the 448 plants analysed by us from northern England and Scotland.

Estimates of the frequency of B-chromosomes in natural populations of *Crepis capillaris* will vary depending on the stage of the life-history which is studied. Thus estimates based on B-numbers in meiocytes will exceed those derived from somatic tissues such as roots or leaves as a result of accumulation due to directed non-disjunction during floral initiation (Parker *et al.*, 1989). In this study, 18 of the populations were examined solely at meiosis and the other 22 by analysis of root-tip cells. However, if we consider only the proportion of plants with B-chromosomes all 40 populations can be compared.

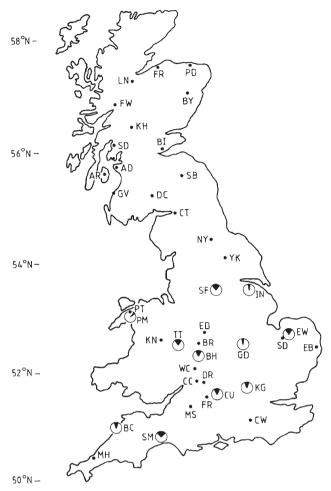
Of the 1021 plants examined, only 37 (3.6 per cent) carried B-chromosomes (Table 1). The 11 B-containing populations comprised 264 individuals; in these populations the overall proportion of plants with Bs was 14 per cent. The maximum B-frequency was observed in a field-margin population from Sidmouth, Devon, in which 25 per cent of the plants carried Bs.

The B-number per plant cannot be directly assessed except in the four B-containing populations scored from root-tips. In these, 11 1B and a single 2B plant were found. In the plants scored at meiosis in PMCs, 24 had two B-chromosomes per PMC while a single

Table 1 B-chromosome constitutions of populations of Crepis capillaris in Britain. In populations marked with an asterisk the somatic B-number was inferred from the number of Bs present in PMCs

Population name and code		C=:d	Come Vinc	B-number			Diames mists Da	N I D	7D 4 1
		Grid reference	Sampling year	0	1	2	Plants with Bs (%)	Number Bs per plant	Total plants
Ardrossan, Strathclyde	AD	NS 22441	1978	28	0	_	0	_	28
Arran, Strathclyde	AR	NS 020329	1978	28	0	_	0	_	28
Boscastle, Cornwall	BC*	SX 095911	1977	18	2	_	10.0	0.10	20
Bredon Hill, Worcestershire	BH*	SO 973405	1976	22	4		25.4	0.15	26
Burntisland, Fife	BI	NT 257864	1978	28	0		0	_	28
Bromsgrove, Worcestershire	BR*	SO 961701	1976	30	0	_	0	_	30
Banchory, Grampian	BY	NO 692953	1978	28	0	_	0	_	28
Cirencester, Gloucestershire	CC*	SP 015015	1977	20	0	_	0	_	20
Carleton, Cumbria	CT	NY 427527	1978	28	0	_	0		28
Cumnor, Oxfordshire	CU	SP 475043	1977	17	3		15.0	0.15	20
Coldwaltham, Sussex	CW*	TQ 018164	1977	20	0	_	0	_	20
Dunscore, Galloway	DC	NX 805544	1978	28	0	_	0	_	28
Driffield, Gloucestershire	DR*	SU 074997	1976	24	0	_	0	_	24
East Bridge, Suffolk	EB*	TM 452662	1976	28	0	_	0	_	28
Edgbaston, West Midlands	ED*	SP 045837	1976	30	0		0	_	30
East Wretham Heath, Norfolk	EW*	TL 910885	1976	24	6	_	20.0	0.20	30
Farringdon, Oxfordshire	FA	SU 288961	1977	20	Ŏ		0	_	20
Forres, Grampian	FR	NJ 025582	1978	28	0	_	0	_	28
Fort William, Highland	FW	NN 122728	1978	28	0	_	0	_	28
Grendon, Northants	GD	SP 934923	1979	19	1	_	5.0	0.05	20
Girvan, Strathclyde	GV	NX 183964	1978	28	0	_	0	_	28
Ingham, Lincolnshire	IN*	SK 963833	1976	23	1	_	4.1	0.04	24
Knotty Green, Bucks	KG	SU 934923	1979	18	2	_	10.0	0.10	20
Kingshouse, Central	KH	NN 563202	1978	28	0	_	0	_	28
Knighton, Powys	KN*	SO 280720	1976	34	0	_	0	_	34
Loch Ness, Highland	LN	NH 515233	1978	28	0	_	0	_	28
Mount Hawke, Cornwall	MH*	SW 716477	1977	20	0		0	<u></u>	20
Melksham, Wiltshire	MS*	ST 900640	1977	20	0	_	0	_	20
Masham, North Yorkshire	NY	SE 208826	1978	28	0	_	0	-	28
Plaidy, Grampian	PD	NJ 727553	1978	28	0	_	0	_	28
Portmadog, Gwynedd	PM*	SH 562371	1976	27	1	_	3.6	0.04	28
Prenteg, Gwynedd	PT*	SH 585414	1977	20	0	_	0	<del>-</del>	20
Santon Downham, Norfolk	SA	TL 821880	1977	23	0	_	0	_	23
•	SB	NT 588309	1978	28	0	_	0	_	28
St Boswell's, Borders	SD	NS 255868	1978	28	0		0		28
Shandon, Strathclyde	_			22	5	1	21.4	0.25	28
Sheffield, South Yorkshire	SF SM*	SK 312826 SY 112871	1978	15	5	1	25.0	0.25	20
Sidmouth, Devon	SM* TT*		1977		5				28
Titton, Worcestershire		SO 828697	1976	22	0	1	21.4	0.25	20
Winchcombe, Gloucestershire	WC*	SP 025285	1977	20		_	0	_	28
Poppleton, North Yorkshire	YK	SE 554575	1978	28	0		0		
Totals				984	35	. 2	3.6	0.04	1021

plant had 4B. If we assume regular doubling during floral initiation these would correspond to 1B and 2B somatic constitutions, respectively, but this cannot necessarily be assumed (Parker et al., 1989). Thus summing these observed and inferred figures gives a provisional total of 35 1B plants and only two 2B plants, giving an average of 0.15 Bs per plant in the polymorphic populations. Thus the B-polymorphism of Crepis capillaris in Britain is very widespread geographically, but Bs reach only low frequencies in any population, and most B-containing plants have only a single B-chromosome. This pattern may be repeated in other parts of the range of the species. In 150 plants from six French populations only one plant



**Fig. 1** Location of the 40 populations of *Crepis capillaris* in Britain scored for B-frequency. The proportion of B-chromosome containing plants in polymorphic populations is shown by the size of the black segment.

containing Bs was found: a plant with 2B PMCs from St Jean Trolimon in Finistère.

### B-chromosome distribution on Bredon Hill

The extensive survey of natural populations for the presence of B-chromosomes thus indicates that Bs are limited to southern Britain, but even in this region their distribution is markedly patchy. A more intensive study of an area where Bs are relatively frequent has, therefore, been carried out in an attempt to identify any factors contributing to this patchwork distribution.

The area chosen was Bredon Hill (Hereford & Worcester), an isolated outlier of the Cotswold Hills rising from the valley of the River Avon and roughly  $6 \times 5$  km in extent. The hill rises from a plain of about 50 m above sea level to about 300 m at the summit.

Samples were taken along four transects up the hill, a total of 20 populations in all (Fig. 2). The transects had different aspects: Elmley Castle (EC) north-facing, Ashton under Hill (AH) east, Kemerton (KE) south, and Bredon's Norton (BN) south-west. Four samples were also taken from near the summit (SU) and one from the plain near Beckford (BE) to the south-east (Fig. 2). The minimum sample size was 31 individuals (Beckford) and the mean number of individuals sampled per population was 54.1. A total of 1082 plants from this area were scored for B-number by root-tip analysis of seedlings (Table 2).

B-chromosomes were found in 16 of the 20 populations on and around Bredon Hill (Fig. 2). The overall average proportion of plants with Bs in these populations, however, was only 8.2 per cent, rising to 10.4 per cent if populations without B-chromosomes are excluded (cf. 3.6 per cent and 14 per cent in the national survey). In addition, the great majority of B-containing plants carry a single B (82/89) in somatic tissues, with the remaining seven having 2Bs. The average B-frequency over this area is then only 0.089 per plant. There is great heterogeneity in B-frequency between the 20 samples. The proportion of plants with Bs ranges from 0 to 38.2 per cent (EC 2) while the mean B-number per plant ranges from 0.0 to 0.4.

The total altitudinal range studied was 46–298 m. If the mean B-number per plant is plotted against altitude then a clear pattern emerges. In each of the four transects, the peak B-frequency lies in a relatively narrow band at mid-altitude, between 120 (BN) and 197 m (KE), with lower B-frequencies both above and below this band (Fig. 3). This altitudinal band also encompasses all six populations with mean frequencies greater than 0.10 per plant, while all seven populations growing above 215 m had B-frequencies lower than 0.055 per plant.

A direct correlation of B-frequency with altitude, however, must be treated with some caution since the populations sampled also differ in size. They may be roughly categorized as Small (0-25 individuals; 5 populations), Medium (26-50; 6 populations), and Large (51–100; 9 populations) (Table 2). B-frequencies for these three classes are 0.028, 0.049 and 0.148, respectively. Thus B-frequency may be partly dependent on population size although population size itself may be a reflection of the suitability of the habitat for C. capillaris. Under the environmental conditions prevailing on and around Bredon Hill, the low altitude populations are small and isolated in predominantly arable areas, while at higher altitudes large populations flourish in permanent sheep-grazed pastures. Within the high frequency zone, two aberrant populations are found: KE2 without Bs and AH3 with only 0.019 Bs

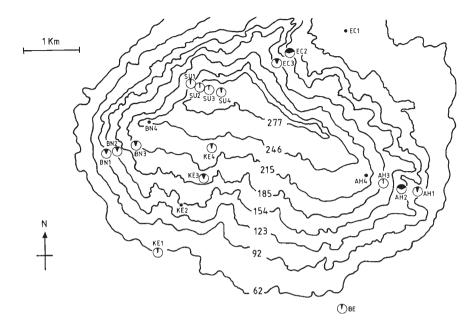


Fig. 2 Contour map of Bredon Hill showing the C. capillaris collection sites and the proportion of B-containing plants (black sectors). (•) Populations with no B-chromosomes.

per plant. The former is a very small, isolated, population while the latter is of medium size.

Despite the variability introduced by population size, it seems possible that B-frequency is indeed correlated with altitude. The highest B-frequencies occur in the large populations at the lower altitudinal levels of the sheep-pastures; towards the summit the equally large populations, also in permanent pasture, have much lower B-frequencies. The coincidence of this pattern in the four transects with their distinctive aspects reinforces this conjecture.

# B-chromosomes stability over years

The proportion of B-containing individuals in the population at East Wretham Heath was estimated on four separate occasions between 1976 and 1979 (Table 3). The first study was made of achenes collected in 1976, while one study in 1978 and two in 1979 were made on plants in situ. Since C. capillaris is an annual with one generation per year, this sampling scheme represents three consecutive generations, although in different phases of the life cycle.

In the 1976 seed collection there were 20 per cent B-containing individuals all with a single B (6/30). In 1978, a collection of mature individuals, which had initiated flower buds, gave a value of 17.9 per cent plants with 1B (5/28). The first collection made in May 1979, however, was distinctive. It was very large (105 individuals) including all plants growing within the sampling area, from which leaves were removed in situ. In this collection, 26.6 per cent of plants had Bs (28/ 105) and four 2B plants were detected. The fourth collection was made in June 1979 when capitula from 41 plants were sampled. In this collection 17 per cent of plants contained Bs (7/41), and in all the PMCs scored 2Bs were found. Assuming that a high frequency of accumulation operates in nature as in the experimental glasshouse, we may infer that these plants all contained 1B in somatic tissues. The difference between the May and June samples, however, is not significant ( $\chi^2$ = 1.46; P > 0.05).

Over these three generations, B-chromosome frequency remains roughly constant at about 20 per cent. The high B-frequency obtained from leaf samples perhaps indicates that plants with 2Bs die before flowering, fail to flower, or are delayed in flowering relative to 0B and 1B individuals. Although B-number may be partly controlled in this manner, this is unsufficient to balance the effects of B-accumulation due to directed non-disjunction into the flowers. Strong selection against both 2B and 1B individuals must occur at some stage in the life cycle.

# **Discussion**

B-chromosomes are a widespread component of the genetic system of Crepis capillaris. They have been reported from Germany (Barthelmiss & Bauchinger, 1962), Switzerland (Rutishauser, 1960), France and Britain (Parker et al., 1989; this paper). Crepis capillaris has also spread widely around the world as an adventive, and Bs have also been dispersed: Bs occur in plants collected in north India (Kaushal & Mehra, 1976). On the basis of morphology, DNA composition, and pre-meiotic and meiotic behaviour it is

**Table 2** B-chromosome constitutions of populations of C. capillaris from Bredon Hill, Worcestershire. Population sizes are given as Small (S, 0-25 plants), Medium (M, 26-50 plants) and Large (L, 51 + plants)

Population	Population size	Altitude (m)	Numbe	er of Bs		Total plants	B-frequency per plant	Plants with Bs (%)
			0	1	2			
Ashton under Hill								
AH1	S	90	49	4	0	53	0.075	7.6
AH2	L	125	34	16	2	52	0.385	34.6
AH3	M	185	52	1	0	53	0.019	1.9
AH4	M	220	57	0	0	57	0	0
Elmley Castle								
EC1	S	70	53	0	0	53	0	0
EC2	L	150	34	20	1	55	0.400	38.2
EC3	L	170	49	7	1	57	0.158	14.0
Bredon's Norton								
BN1	M	120	46	6	1	53	0.151	13.2
BN2	L	140	53	5	2	60	0.150	11.7
BN3	M	205	52	5	0	57	0.088	8.8
BN4	L	250	59	0	0	59	0	0
Kemerton								
KE1	S	60	58	2	0	60	0.033	3.3
KE2	S	155	59	0	0	59	0	0
KE3	L	195	50	7	0	57	0.123	12.3
KE4	L	235	40	2	0	42	0.048	4.8
Beckford								
BE	S	45	30	1	0	31	0.032	3.2
Summit								
SU1	M	250	53	1	0	54	0.019	1.9
SU2	M	175	56	1	0	57	0.018	1.8
SU3	L	285	55	1	0	56	0.018	1.8
WU4	L	298	54	3	0	57	0.053	5.3
Totals			993	82	7	1082	0.089	8.2

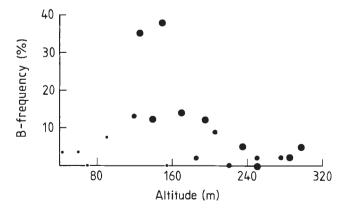


Fig. 3 The relationship between altitude and proportion of plants containing B-chromosomes on Bredon Hill. Small, medium and large populations are indicated by the size of the circle.

clear that the Swiss and British Bs are very similar and may have a common and presumably ancient origin (Rutishauser & Röthlisberger, 1966; Jones et al., 1989; Maluszynska & Schweizer, 1989; Parker et al., 1989). Despite numerous experimental studies of the B-chromosomes of this species, little is known of the basic population parameters of the B-polymorphism.

The survey of B-chromosome distribution in Britain indicates that Bs are found only in populations in the southern half of the range. No populations with Bs were found to the north of Yorkshire. However, the Bs studied by Abraham *et al.* (1968) were derived from a population collected in the Scottish lowlands. If not entirely absent from northern Britain then, Bs must be present at a much lower frequency than in the south since none was found in the 448 plants of northern origin in the present study.

**Table 3** B-chromosome constitution of samples taken from a population at East Wretham Heath, Norfolk, on four separate occasions spanning three generations. In the June 1979 samples somatic B numbers are inferred from the numbers present in **PMCs** 

		Nun	iber of	Bs	m	
Sample date	Material sampled	0	1	2	Total plants	Plants with Bs (%)
August 1976	Achenes	24	6	0	30	20.0
May 1978	Mature plants	23	5	0	28	17.9
May 1979	Leaves in population	77	24	4	105	26.7
June 1979	Capitula in population	34	7	0	41	17.1

It is remarkable that closely similar patterns of B-distribution in Britain have been recorded in two other species with nationwide distribution. In the plant Rananculus ficaria, B-chromosomes reach their highest frequencies in diploid populations from the south-west of England and are scattered through the south-east of England (Gill et al., 1972). No B-chromosomes have been recorded from populations growing to the north of Manchester (53° 30'N). Similarly, B-chromosomes are a common feature of southern populations of the mottled grasshopper Myrmeleotettix maculatus, but Bs have not been located in populations to the north of the Humber (Hewitt, 1973) (53° 45′N). Is the coincidence of the cut-off point for B-chromosomes in populations of these three dissimilar organisms purely fortuitous, or does it represent some feature of the environment jointly affecting all three, or perhaps the post-glacial history of colonization of Britain?

In M. maculatus, B-chromosomes are found in populations in the south and east of Britain which are climatically more optimal for grasshoppers (Hewitt, 1973). Correlations of B-frequencies with temperature gradients have been demonstrated in East Anglia (Hewitt & Brown, 1970) and, on a small scale, with microclimate on a disused lead mine in Wales (Hewitt & Ruscoe, 1971). Perhaps Bs are tolerated only in populations which are not under severe selective stress.

In C. capillaris, B-distribution on Bredon Hill suggests that altitude, or some associated environmental variable, is influential in determining frequency. Maximal B-frequencies are attained at mid-altitudes, with a decline towards the summit and into the lowlands. It is possible that the effects of population size and associated factors are confounding here. Small populations have low B-frequencies, or are without Bs entirely. Such populations are likely to be relatively inbred, and a notable feature of B-systems is that they are found only in outbreeders (Jones & Rees, 1982). The small populations of C. capillaris at low altitudes

also exist in transient habitats, such as road verges, field margins and waste land, in less than optimal conditions for the species, and are probably subject to a regular cycle of extinction and recolonization with low numbers of founders. The likelihood of B-loss by sampling is high under such a regime. These stochastic processes may play a large part in maintaining the patchwork of 0B/+B populations in the polymorphic part of the range. In the large pasture populations, which stretch continuously to the summit, and where there is relative environmental stability, B-frequency declines with increasing altitude on all four transects. In terms of average temperature, 100 m of altitude corresponds roughly to a decline of 1.5°C. The average temperature also declines with increasing latitude, and thus latitudinal and altitudinal clines in B-frequency may both reflect temperature-dependence.

The B-polymorphism of C. capillaris consists essentially of two morphs -0B and 1B. Plants with 2Bs have been found in seed samples and in mature plants at East Wretham Heath but are rare. The Crepis B, however, has a very powerful accumulation mechanism into meiocytes, and transmission through both pollen and eggs is about 0.8 per B, rather than the expected 0.5 (Parker et al., 1989). The expectation is that Bs should increase in frequency in the population over generations, giving both more plants with B-chromosomes and higher numbers of Bs in any one individual. This is not the case; B-frequency seems to remain fairly constant over generations, at least in the EWH population. The limited data from this population suggests that 2B plants fail to flower, which will reduce overall B-number. The selection pressure is insufficient to maintain the equilibrium in the face of enhanced transmission, and selection must operate against 1B individuals at some phase of the life-cycle. Robinson & Hewitt (1976) have shown that stability of B-frequency between generations of Myrmeleotettix maculatus is maintained by a combination of drive into functional

eggs and subsequent drag by selective death of B-containing embryos. Observations of B-behaviour throughout the life cycle of *C. capillaris* in populations on Bredon Hill and East Wretham Heath will be presented in a subsequent paper.

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