Original article

Selection in sympatric populations of *Cepaea*

L.I. Mazon[1], M.A. Martinez de Pancorbo[2], A. Vicario[1],
A.I. Aguirre[1], A. Estomba[1] and C.M. Lostao[1]

[1] *Universidad del Pais Vasco, faculdad de ciencias, departamento de biologia y genetica, APDO, 644, 48080*
[2] *Universidad del Pais Vasco, faculdad de medicina, departamento de histologia y biologia, 48080, Spain*

Summary – Interspecific competition is often thought to produce evolutionary changes. This competition has been studied mainly, using subjects whose heritability is not well known. Hence it is preferable to study polymorphic characters whose inheritance is known. Land snails of the genus *Cepaea* have several advantages for such studies.

Ninety-five samples of allopatric and sympatric populations of *Cepaea nemoralis* and *Cepaea hortensis* were collected near the southern limit of the aera occupied by *Cepaea hortensis*. In the area studied, *Cepaea nemoralis* and *Cepaea hortensis* populations are divided into two zones corresponding to the north and south-facing slopes of the Iberian Mountains.

Changes in phenotype frequencies were observed passing from allopatry to sympatry in both species. In the North, a decrease in the frequencies of yellow, yellow-banded and effectively banded yellow snails was detected in sympatric populations of *Cepaea nemoralis* and, at the same time, the frequencies of the banded, five-banded, and effectively banded phenotypes in *Cepaea hortensis* increased. These changes in phenotype frequencies between allopatric and sympatric populations in one species may depend upon the phenotype frequency of the other. Such frequency dependent selection may interact with other selective forces and with competitive selection.

We believe that, in southern populations, these changes are due to climatic selection in both species.

Cepaea – **polymorphism** – **climatic selection** – **allopatry** – **sympatry**

Résumé – **Sélection dans les populations sympatriques de *Cepaea*.** *La compétition interspécifique produit des modifications évolutives. Cette compétition a été étudiée surtout sur des caractères dont l'hérédité était mal connue. Comme il est préférable d'utiliser des caractères dont l'hérédité est établie, les escargots du genre* Cepaea *constituent un bon modèle pour ces recherches. On a prélevé 95 échantillons de populations allopatriques et sympatriques de* Cepaea nemoralis *et de* Cepaea hortensis *à proximité de l'extrémité méridionale de l'aire d'extension de* Cepaea hortensis. *Dans l'aire de la présente étude, les populations de* Cepaea nemoralis *et de* Cepaea hortensis *sont séparées en deux zones correspondant aux versants méridionaux et septentrionaux des montagnes ibériques. On a observé des variations de fréquences phénotypiques, en passant de l'allopatrie à la sympatrie, dans les deux espèces. Au nord, dans les populations sympatriques de* Cepaea nemoralis, *on a observé une décroissance des fréquences d'escargots jaune, jaune-bandé,*

et jaune effectivement bandé, et simultanément, chez Cepaea hortensis, *un accroissement des fréquences des phénotypes bandé, cinq-bandé, et effectivement bandé. Ces variations de fréquences phénotypiques observées dans une espèce entre des populations allopatriques et sympatriques peuvent dépendre des fréquences phénotypiques dans l'autre espèce. Cette sélection dépendant de la fréquence peut interagir avec d'autres forces sélectives et avec la sélection compétitive. Les variations observées ici dans les populations méridionales semblent dues à la sélection climatique dans les deux espèces.*

Cepaea *– polymorphisme – sélection climatique – allopatrie – sympatrie*

INTRODUCTION

Cepaea nemoralis and *Cepaea hortensis* are two closely related and morphologically similar species (Lamotte, 1951). Each presents a very similar polymorphism with the same patterns of colour and banding of shell, and they frequently form mixed populations.

The range of these two species overlaps. In Northern Europe, *Cepaea hortensis* reaches higher latitudes, while *Cepaea nemoralis* reaches more southerly latitudes. This may indicate that *Cepaea hortensis* is more resistant to cold climates than *Cepaea nemoralis*, which in turn, is better adapted to milder climates (Cameron, 1970a, b, Jones *et. al.*, 1977).

In mixed populations, different morph frequencies are often found for each species, and some local correlations have also been found between morphs of the two. This could be due to several factors: to visual selection on shell pattern or size (Clarke, 1960, 1962a, b; Carter, 1967; Bantock & Bayley, 1973; Bantock *et al.*, 1976); to interspecific competition (Arthur, 1978, 1980); to climatic selection (Arthur, 1982a) or to interspecific competition and intra and interspecific effects of population density (Cameron & Carter, 1979).

Various modes of evolutionary change resulting from interspecific competition have been proposed: character displacement (unilateral or bilateral), convergence of characters and alteration of the variance of morphological characters, evolution of competitive capacity and "genetic feedback" (Arthur, 1982b).

Here, we study populations of *Cepaea nemoralis* and *Cepaea hortensis* in allopatry and sympatry, to analyse whether climatic selection or interspecific competition cause any differences between allopatric and sympatric populations. We study them in a zone where *Cepaea hortensis* is at the edge of its range. Marginal populations are interesting since they may be found in limiting environmental or competitive conditions (Bantock & Price, 1975).

MATERIAL AND METHODS

Sampling was carried out in the western part of the Iberian Mountains (Fig. 1). This zone has high peaks (San Lorenzo 2,262 meters, Picos de Urbion 2,228 meters, etc.) and deep valleys. It is very cold in winter and hot in summer. Each sample was taken in an area of approximately 400 m^2.
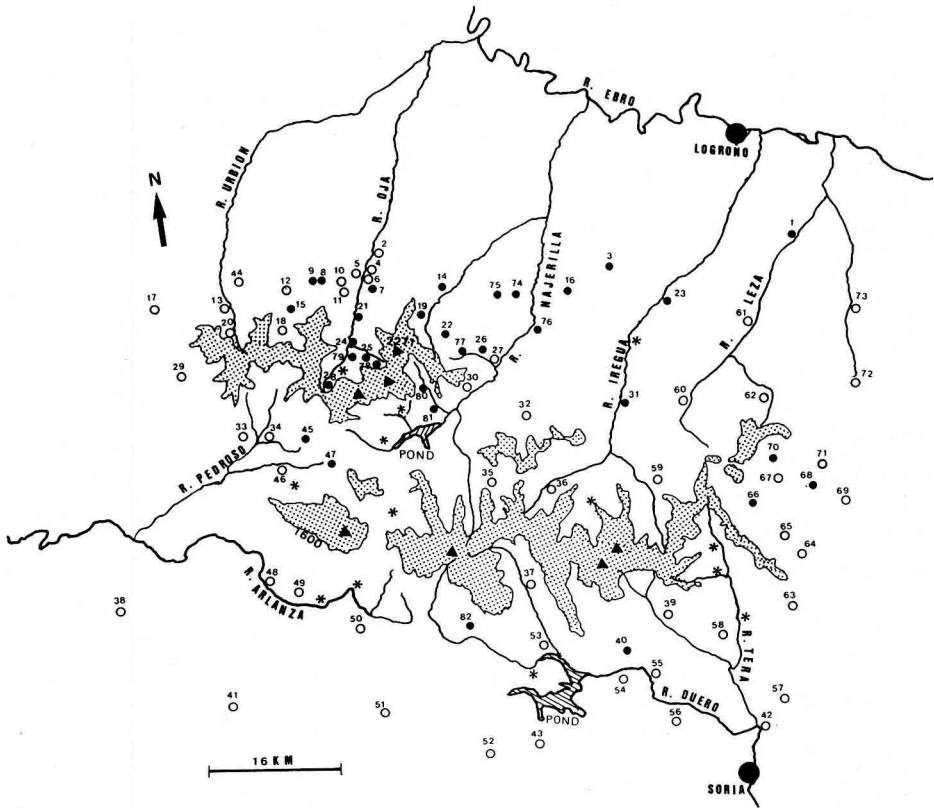
Fig. 1. Sampling zone for allopatric and sympatric populations of *Cepaea* (○ *Cepaea nemoralis*; ✳ *Cepaea hortensis*; ● mixed populations; ▲ altitude upper 1600m).

A total of 7 235 snails was collected, of which 5 220 were *Cepaea nemoralis* and 2 015 were *Cepaea hortensis*. Fifty allopatric and 32 sympatric populations were found for *Cepaea nemoralis* (Table I), while for *Cepaea hortensis*, there were 13 allopatric and 32 sympatric. For the purpose of analysis, only 23 sympatric populations of *nemoralis* and 26 of *hortensis* were considered. The difference in the number of sympatric populations of the two species is due to the fact that some populations had a very small number of individuals. Samples were scored according to the criteria of Lamotte (1951), Cain and Sheppard (1954) and Arnold (1968). For each sample, data on vegetation, pH, soil characteristics, climate, distance from the sea and altitude were collected.

The Factorial Correspondence Analysis (FCA) was done using the SPAD ("Système Portable pour l'Analyse des Données") package (Lebart *et al.*, 1977).

Table I. Numbers of individuals of *Cepaea nemoralis* phenotypes in Spain.

Locality	A-S	Y5	YM	YU	YF	YO	P5	PM	PU	PF	PO	TO	ALT
1 Ribaflecha	S	0	0	0	0	0	17	6	8	8	9	48	600
2 Ojacastro	A	21	6	29	3	2	19	26	20	14	0	140	800
3 Castroviejo	S	9	0	0	1	2	42	0	1	6	9	70	900
4 Ezcaray Ent.	S	25	5	8	13	1	37	13	6	28	0	138 *	800
5 Zorraquin	A	34	3	13	10	1	22	3	12	28	0	130 *	880
6 Ezcary Bel.	A	17	2	2	4	2	49	12	11	27	2	111 *	820
7 Ezcaray Pos.	S	5	1	1	1	0	32	5	0	4	0	49	820
8 Pradilla 1	S	7	7	4	1	0	20	7	5	0	2	54	1260
9 Pradilla 2	S	1	4	5	0	2	20	23	8	0	2	65	1260
10 Valgañon 1	A	23	0	8	5	3	33	22	2	12	12	124 *	920
11 Valgañon 2	A	9	21	8	0	9	0	11	1	0	2	61	1100
12 Fresneda Sier.	A	11	0	20	5	9	38	5	8	14	19	130 *	1000
13 Santa Cruz Urbion	A	20	2	4	2	2	29	27	10	12	3	111	960
14 El Rio	S	9	6	1	6	1	19	7	1	10	2	62	800
15 Fresneda Sier. 3	A	0	1	0	0	1	20	25	1	1	2	51	1040
16 El Pedroso	S	0	0	4	0	0	3	3	7	1	1	19	740
17 Villorobe	A	9	2	0	5	0	18	8	0	4	7	53	1080
18 Fresneda Sier. 6	A	0	2	0	0	1	4	14	2	0	2	26	1200
19 Rio Cardenas	S	1	1	7	0	0	4	8	10	0	4	35	1160
20 S. Cruz Urbion 4	A	0	1	1	0	0	20	60	12	3	2	99	1020
21 Zaldierna	S	1	3	0	0	0	13	10	0	0	1	25	900
22 Tobia 10	S	1	5	1	0	0	7	20	1	0	5	40	1120
23 Anguiano	S	12	5	18	3	1	20	8	13	7	3	90	600
24 Posadas 1	S	2	0	0	1	1	3	1	1	7	0	16	980
25 Altuzarra 1	S	1	0	3	2	0	21	13	0	9	1	50	1060
26 Valvanera 1	S	0	0	0	0	0	4	6	8	0	3	21	780
27 Valvanera Cruce.	A	8	2	27	0	4	17	4	30	1	5	98	720
28 Posadas 2	S	4	0	0	1	0	15	11	12	4	0	47	1100
29 Pineda Sier.	A	11	6	0	2	0	21	1	4	50	1	96	1200
30 Najerilla 8	A	8	1	2	2	5	27	3	3	6	1	38	800
31 Pradillo	S	1	3	2	1	1	13	10	4	7	6	48	900
32 Brieva Cameros	A	4	0	0	0	0	17	0	0	7	5	33	960
33 Riocabado Sier.	A	5	1	0	2	0	41	9	17	10	9	94	1120
34 Barbadillo Herr.	A	3	1	0	1	0	39	19	0	12	7	82	1120
35 Viniegra Arriba	A	11	1	1	0	8	18	1	1	7	7	55	1200
36 Montenegro Camer.	A	1	1	1	0	1	15	44	0	5	28	96	1260
37 El Quintanar	A	2	0	0	0	1	40	20	0	8	22	93	1240
38 Santo D. Silos	A	1	0	0	1	1	9	0	0	5	2	19	1000
39 Valdea Vellano Ter.	A	24	3	0	25	18	15	1	10	24	10	130	1120
40 El Royo	S	10	1	0	2	14	53	0	0	7	32	114	1060
41 Navas Pinar	A	4	0	0	2	1	18	0	0	10	4	39	960
42 Garray	A	12	0	2	1	2	37	0	11	6	14	85	1050
43 Abejar	A	20	0	0	18	0	10	0	0	7	0	55	1150
44 Pradoluengo	A	7	1	0	18	0	8	5	1	12	0	52	1000
45 Monterrubio	S	4	5	1	4	0	3	12	0	2	1	32	1200
46 Huerta Abajo	A	1	0	0	0	0	6	10	0	7	0	24	1120
47 Huerta de Arriba	S	8	0	0	5	2	44	2	3	17	7	88	1200
48 Palacios 1	A	11	10	1	2	1	7	9	8	1	4	54	1030
49 Palacios Pue.	A	1	2	1	2	0	5	17	0	8	0	36	1050
50 Canicosa	A	16	4	0	4	0	21	2	0	17	0	64	1090

Table I. (continued).

Locality	A-S	Y5	YM	YU	YF	YO	P5	PM	PU	PF	PO	TO	ALT
51 Navaleno	A	8	0	0	4	1	18	0	0	13	0	44	1100
52 Cabrejas	A	12	0	0	17	1	14	0	0	20	0	64	1140
53 Vinuesa	A	1	0	0	0	0	23	8	0	4	19	55	1110
54 Vilviestre	A	12	0	0	0	4	13	0	0	3	18	50	1040
55 Hinojosa	A	7	0	0	12	1	11	2	0	11	7	51	1040
56 Pedrajas	A	25	0	0	3	2	61	0	0	5	0	96	1070
57 Buitrago	A	37	0	0	52	1	24	0	0	47	0	161	1020
58 Rebollar	A	13	0	0	16	0	14	0	0	5	0	48	1130
59 San Andres	A	11	0	1	8	4	30	1	14	18	9	96	1230
60 Laguna Cameros	A	7	0	2	0	0	22	9	4	10	6	60	960
61 Terroba	A	1	0	0	4	1	53	4	1	10	7	81	760
62 Avellaneda	A	0	0	0	0	0	2	10	0	1	0	13	1060
63 Arevalo	A	21	0	1	6	6	9	0	6	5	3	57	1210
64 Valloria	A	9	1	0	1	13	7	3	0	2	13	49	1200
65 Vizmanos	A	6	0	1	4	1	7	0	10	21	9	59	1200
66 Santa Cruz Yanguas	S	3	0	0	3	5	22	1	7	26	10	77	1190
67 Vollar Maya	A	6	0	0	2	2	31	0	0	29	6	76	1210
68 Villar Rio	S	8	0	2	11	2	17	0	2	13	7	62	1000
69 La Cuesta	A	39	16	0	24	2	26	7	0	29	0	143	1120
70 Diustes	S	0	0	0	0	0	10	8	15	4	1	38	1190
71 Yanguas	A	12	0	0	1	54	17	0	1	19	1	69	970
72 Munilla	A	15	0	0	28	2	7	1	0	50	1	104	800
73 Robres Castillo	A	18	1	4	5	0	11	2	3	10	1	55	720

(*Samples with brown phenotypes; A-S = Allopatric or sympatric population; Y5 = Yellow 12345; YM = Yellow 00300; YU=Yellow 00000; YF = Yellow fusion bandeds; YO = Yellow others; P5 = Pink 12345; PM = Pink 00300; TO = Total; ALT = Altitude in meters...)

RESULTS

Cepaea nemoralis is more common and more widespread, than is *Cepaea hortensis*. Each species is polymorphic in the region. For *Cepaea nemoralis*, the area sampled was divided into two zones, the north and south-facing slopes of the Iberian Mountains (Table II). Phenotype differences appeared, principally in the patterns of bands (Fig. 2), whereas, for coloured, no differences were apparent.

We examined allopatric and sympatric populations in each zone. In the southern zone there were no significant differences in either species. In the north-facing slopes, allopatric populations of *Cepaea nemoralis* exhibit, a significant increase in yellows, banded yellows and effectively banded yellows (Table II), while in the sympatric zone the pinks are more frequent.

In allopatric populations of *Cepaea hortensis*, unbanded yellow, effectively unbanded and unbanded phenotypes were significantly more frequent than in sympatric populations, while in the latter, effectively banded, banded and yellow 12 345 were more frequent in the northern zone (Table II).

When frequencies are compared between species in sympatry and in allopatry in each zone, the number of significant differences are much the same for allopatric and sympatric comparisons in the south. In the north, however, allopatric comparisons produced many fewer significant differences than sympatric ones.

Table II. Average frequencies of different phenotypes of *Cepaea nemoralis* and *Cepaea hortensis* in northern and southern zones and comparison between allopatry and sympatry.

Morph	North CN	South CN	North CH-A	North CH-S	South CH-A	South CH-S	North CN-A	North CN-S	South CN-A	South CN-S	CHA-CHA North	CHS-CHS North	CNA-CNA South	CHS-CHS South
YE12345	9.46 *	14.16	9.16 **	40.00	50.94	39.68 *	12.38 *	6.54	15.38	7.86		**	**	*
Y 00345	0.46	1.99	0.00	0.15	0.65	0.48	0.92 *	0.00	2.15	1.17		**		
YE00300	3.81	2.04	1.22 *	0.00	0.26	0.83	3.47	4.14	1.90	2.75				
YE00000	5.81 **	0.62	49.69 **	12.18	0.48	2.43	6.16	5.47	0.54	1.06		**	*	*
YEFUSION	4.38 *	8.59	29.70	29.30	33.11	43.42	6.42	2.35	8.91	6.93			*	
YEHYALOZ	0.26	0.31	3.69	2.68	8.73	2.09	0.41	0.11	0.09	1.46		*	*	
YEOTHER	1.07	1.49	0.00	0.10	1.27	1.02	1.15	0.98	1.51	1.41		**	**	**
PI12345	27.83	30.47	0.41	1.01	0.28	3.31	23.56	32.11	30.30	31.36	**	*	**	**
PI00345	1.62 **	6.02	0.00	0.00	0.00	0.28	2.75	0.99	5.96	6.32		**	**	
PI00300	19.95 **	8.35	0.00	0.15	0.28	0.00	18.82	21.07	7.97	10.35		**	**	
PI00000	9.39 *	4.02	3.66	10.29	3.71	3.79	7.21	11.57	3.02	9.20		*	**	*
PIFUSION	11.32 *	18.31	0.41	2.84	0.28	2.66	13.21	9.43	18.72	16.16	**	*	**	
PIHYALOZ	0.27	0.36	0.00	0.41	0.00	0.00	0.00 *	0.55	0.37	0.79				
PIOTHER	3.79	3.25	0.00	0.40	0.00	0.00	2.99	4.60	3.17	3.67		**	**	**
YEBANDED	19.44 *	28.59	44.21	72.21	87.52	94.96	24.75 *	14.12	21.59	29.95	**	**	**	**
PIBANDED	64.79	66.76	0.81	4.81	6.24	0.85	60.83	68.75	68.16	66.49		**	**	**
BANDED	84.23 **	95.35	45.03 *	77.02	95.81	93.77	85.59	52.88	96.44	89.74				
UNBANDED	15.77 **	4.65	54.97 *	22.98	4.19	6.23	14.41	17.12	3.56	10.26		**	**	**
EFYEBAND	14.91 *	24.25	39.31	69.38	85.32	84.12	19.95 *	9.88	25.80	16.20		**	**	
EFPIBAND	42.95 *	52.02	0.81	4.25	0.57	5.96	39.75	46.14	52.19	51.19	**	**	**	**
EFYEUNBAN	10.34 *	4.97	54.59	15.01	10.12	5.84	10.97	9.72	4.69	6.45		**	**	
EFPIUNBAN	31.24 **	18.76	3.66	10.84	3.99	4.07	28.29	34.19	17.33	26.16		*		
EFBANDED	57.86 **	76.27	40.12 *	73.63	85.89	90.09	59.70	56.01	77.99	67.39		*		
EFUNBANDED	42.14 *	23.73	59.88 *	26.37	14.11	9.91	40.30	43.99	22.01	32.61	**	**	**	**
YELLOW	25.25	29.21	93.90	84.39	95.44	89.96	30.91 *	19.59	30.49	22.64	**	**	**	**
PINK	74.18	70.78	4.47	15.09	4.56	10.04	68.04 *	80.33	69.51	77.36	**	**	**	**

(CN = *Cepaea nemoralis*; CH = *Cepaea hortensis*; A = Allopatric; S = Sympatric; Samples with $n < 10$ were omitted from the analysis. YE12345 = Yellow 12345; YE00345 = Yellow 00345; YE00300 = Yellow 00300; YE00000 = Yellow 00000; YEFUSION = Fusion banded yellow; YEHYALOZ = Hyalozonate yellow; YEOTHER = Other yellow; PI12345 = Pink 12345; PI00345....; YEBAND = Banded yellow; PIBAND = Banded pink; EFYEBAND = Effectively banded yellow; EFPIBAND = Effectively banded pink; EFYEUNBAN = Effectively unbanded yellow; EFPIUNBAN = Effectively unbanded pink; EFBANDED = Effectively banded; EFUNBANDED = Effectively unbanded)
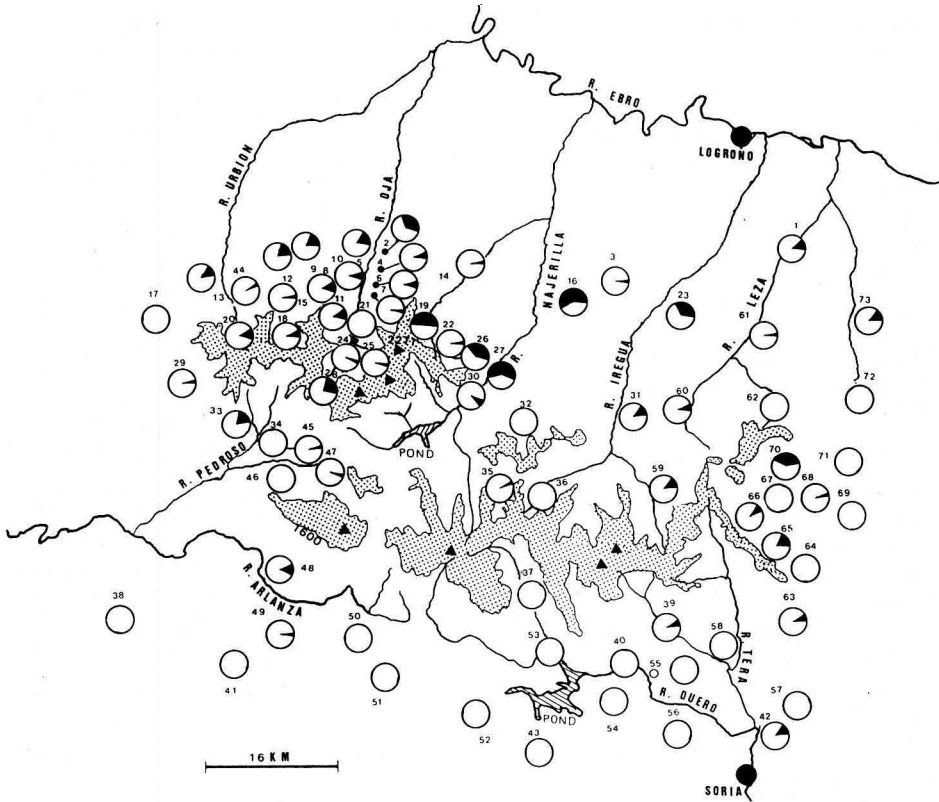
Fig.2. Geographic distribution of *Cepaea nemoralis* unbanded phenotypes (Black area unbanded phenotypes frequencies).

There were no significant differences of phenotypic frequencies related to soil characteristics, pH or vegetation. However, there were significant differences in the altitude of populations between northern and southern slopes (Table III).

There was a series of significant correlations ($P < 0.05$) between morph frequencies and altitude in *Cepaea hortensis*, but not with very high correlation coefficients. In the northern zone, the unbanded yellow and effectively unbanded yellow phenotypes were positively correlated with altitude. In the southern zone, yellow 12 345 and 12 345 were negatively correlated, whereas, fusion-yellow and fusion-banded were positively correlated. *Cepaea nemoralis* phenotypes, positively correlated with altitude, include pink 00300 and yellow 00300 in the North.

Trush predation was found in only five populations, of which, three were allopatric and the other two, sympatric (Table IV). In two populations, the predation is not selective, and in the remaining three, the most heavily predated are the fusion banded or effectively banded for *Cepaea nemoralis*, (San Andrés, banded shells, $\chi_3^2 = 8.12$; Vizmanos, colour shell, $\chi_1^2 = 4.98$, effectively banded shell, $\chi_1^2 = 4.39$; Diustes, banded shell, $\chi_3^2 = 8.06$), while for *Cepaea hortensis*, there is no selective predation.

Table III. Mean altitude of allopatric and sympatric populations of *Cepaea nemoralis* and *Cepaea hortensis* on the north and south-facing slopes of the Iberian Mountains.

	Northern	*Southern*	*Probability*
Sympatric CH	877 m	1140 m	*P*=0.016
Allopatric CH	1133 m	1168 m	ns
Sympatric CN	929 m	1110 m	ns
Allopatric CN	946 m	1097 m	*P*=0.001

Table IV. Phenotypic frequencies (%) of alive and depredated *C. nemoralis* and *C. hortensis*.

Locality		*Alive*						*Depredated*					
		Y	5	UB	FB	OT	TO	Y	5	UB	FB	OT	TO
59 San Andrés	CN	25.0	42.7	15.6	27.1	14.6	96	23.7	46.5	12.3	36.8	4.4	114
61 Terroba	CN	5.0	75.0	0.0	5.0	20.0	20	8.2	63.9	1.7	21.3	13.1	61
65 Vizmanos	CN	20.3	22.0	18.7	42.4	16.9	59	4.8	21.4	11.9	61.9	4.8	42
66 Santa Cruz	CN	18.8	35.4	12.5	31.3	20.8	48	6.9	27.6	3.4	48.3	20.7	29
	CH	100.0	6.2	0.0	93.8	0.0	64	100.0	0.0	0.0	100.0	0.0	36
70 Diustes	CN	0.0	26.3	39.5	10.5	23.7	38	3.7	18.5	14.8	37.1	29.6	27
	CH	100.0	14.3	6.1	77.6	2.0	49	100.0	8.8	0.0	94.2	0.0	34

(Y = Yellow shells; 5 = 12345; UB = Unbandeds; FB = Fusion bands; OT = Others; TO = Total; CN = *C. nemoralis*; CH = *C. hortensis*).

In our study, each population is composed of 16 different phenotypes. Up to now, we have made comparison phenotype by phenotype. This gives an idea of what is happening with just one phenotype at a time in each species, but causes a loss of perspective with respect to what is occurring overall. Therefore, we looked for an analysis where the 16 phenotypes and all the populations could be introduced, and whose results would be easy to interpret; an analysis which fulfills all these demands is Factorial Correspondence Analysis (FCA).

Two large groups of *Cepaea nemoralis* and *Cepaea hortensis* were separated (Fig. 3), so that the populations of two species would be sufficiently different to be grouped into two different areas in the figure. Within *Cepaea nemoralis*, there was a subgroup including the sympatric populations, although in this case, the separation was not as clear as between species.

FCA represents phenotypes and populations and also keeps the proximity relationship (*i.e.* the *Cepaea hortensis* populations are close to phenotypes yellow 12 345, fusion banded yellow and hyalozonate), which indicates that, in *Cepaea hortensis*, these are the most frequent phenotypes.

This separation may also be observed in the cluster (Fig. 4), made by nearest neighbour/paired sample analysis. The two species are separated by a level of affinity of 0.423. Within *Cepaea hortensis*, there is a separation of populations
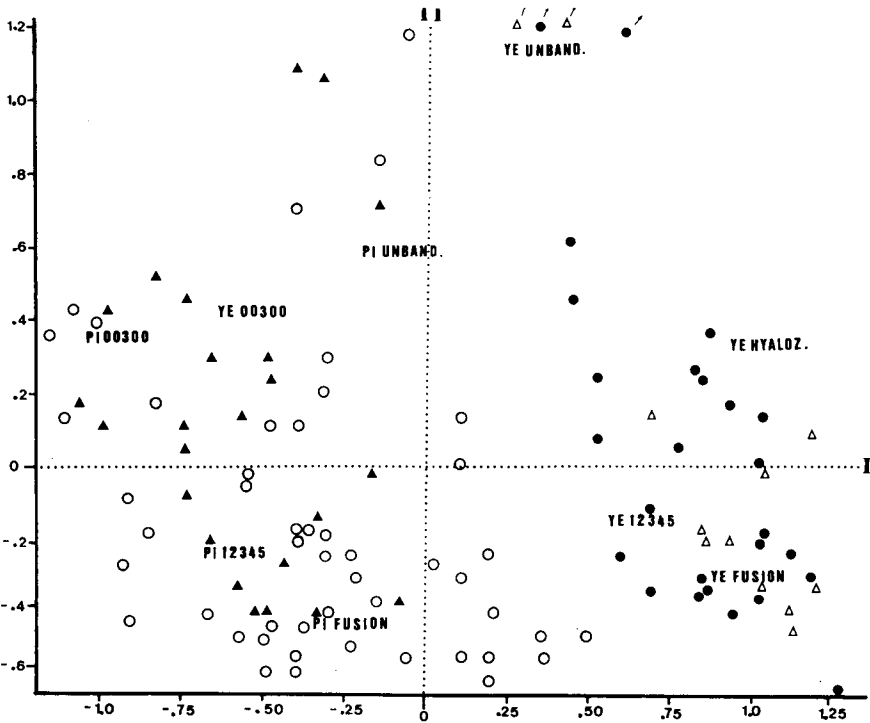
Fig. 3. Simultaneous representation of *Cepaea nemoralis* and *Cepaea hortensis* populations and phenotypes sympatry and allopatry on axes 1 and 2, obtained through Factorial Correspondence Analysis (FCA). (o *Cepaea nemoralis* allopatric; ▲ *Cepaea nemoralis* sympatric; ● *Cepaea hortensis* allopatric; △ *Cepaea hortensis* sympatric).

at 0.165 with a high proportion of unbanded yellow. For *Cepaea nemoralis*, there is a group at 0.102, where the majority of populations are allopatric.

DISCUSSION AND CONCLUSIONS

In our area, *Cepaea nemoralis* populations seem to be divided into two zones corresponding to the north and south-facing slopes of the Iberian Mountains. Marked climatic differences characterize the two zones. The southern zone is drier and hotter with more severe climatic conditions than in the northern zone. The observed differences in the phenotype frequencies could be produced by climatic selection or by geographic isolation, due to the Iberian Mountains.

When analysing the passage from allopatry to sympatry within each species, changes may be observed in the frequencies of colour patterns and shell banding. On north-facing slopes of the Iberian Mountains, in sympatric populations of *Cepaea nemoralis*, the effectively banded yellows and other yellow morphs decreased. With regards to colour, pink shells increased in sympatry, while yellow phenotypes decreased. For *Cepaea hortensis*, the banded phenotypes also increased in sympatric populations, while the unbanded diminished. This is similar to Arthur's (1978, 1980,
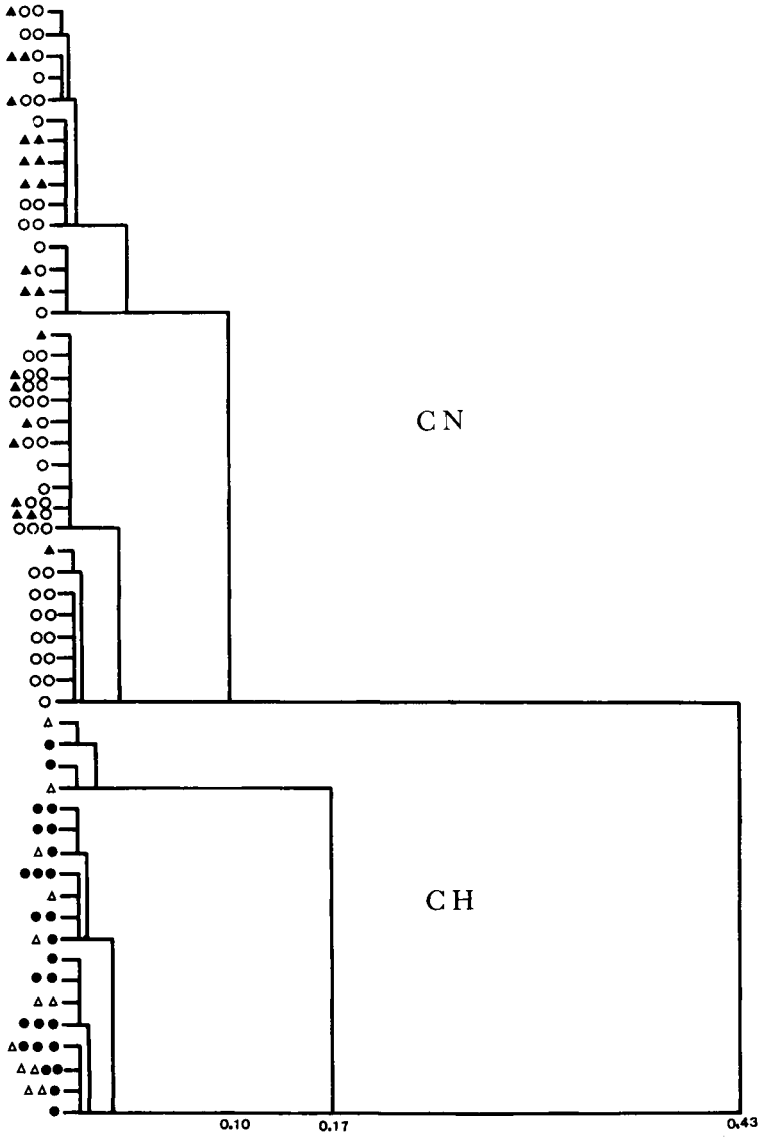
Fig. 4. Cluster of populations of *Cepaea*. Dendogram of affinity is made by nearest neighbour/paired sample analysis (See figure 3).

1982a) observations. The gene for shell colour of *Cepaea hortensis* does not seem to be affected.

Why are there such frequency differences between allopatric and sympatric populations? Some authors have proposed visual selection as the main cause (Clarke, 1962a, b, Carter, 1967; Bantock *et al.*, 1976). In our case, this does not seem to be so, since trush predation is very slight, and not significant. Others authors have suggested interspecific (Arthur, 1978, 1980) or climatic selection (Cameron, 1970 a, b, c, Arthur, 1980), although it is very difficult to separate the two (Arthur, 1982a). Climatic selection may be important in our southern populations, as there are no differences between the morph-frequencies of the allopatric or the sympatric populations within a species, while in the north there are differences. Another argument in favour of this kind of selection, is that the *Cepaea hortensis* populations sampled are marginal, and may be in environmentally limiting conditions. Moreover, the sympatric populations of *Cepaea hortensis* in the southern zone are significantly higher in altitude than those in the north, as happens with allopatric populations of *Cepaea nemoralis*.

For sympatry, there are more significant differences between the two species in the north, than in the south. However, for allopatry, they are higher in the south. Allopatric populations present more differences in morph-frequencies probably due to differences in niches or adaptative strategies. It is known that *Cepaea nemoralis* and *Cepaea hortensis* have different strategies to reach similar darkening of the shell (Jones *et al.*, 1977).

In the northern zone, the allopatric populations in both species have few significant differences in their morph-frequencies. That implies that there is little effect of climatic selection on the northen slopes, with a greater importance of interspecific competition, since the differences between species increase in sympatry. The phenotypes of *Cepaea nemoralis* or *Cepaea hortensis*, which present significant differences between allopatry and sympatry, would suffer interspecific competition. A possible strategy would be displacement of morph-frequencies towards phenotypes infrequent in the other sympatric species, in an attempt to make the two species appear very different as far as their phenotype frequencies are concerned (*i.e.*, within the phenotypes which suffer displacement, if one species has high frequencies of a phenotype, the other species tends to decrease its frequency when it passes from allopatry to sympatry, thus increasing the differences between the morph-frequencies of both species). This is reflected in the FCA (Fig. 3), where sympatric populations of *Cepaea nemoralis* appear on average farther from *Cepaea hortensis* than allopatric populations. Also sympatric populations of *C. hortensis* appear, on average, farther from *C. nemoralis* than the allopatric populations, although genetic flow between same species populations may exist. However, Cowie and Jones (1987) showed that there is competition and habitat separation in *Cepaea*, but found no evidence of an interspecific interaction that might be a precursor of character displacement in experimentally mixed population of *C. nemoralis* and *C. hortensis*. They consider that the competition may reflect a balance between invasion and extinction. On the other hand, Arthur (1982a) observed differences between allopatry and sympatry, possibly due to climatic factors, since allopatric populations of *Cepaea nemoralis* had less vegetation density and more sunlight. The data of Cameron and Dillon

(1984), also show differences in wooded habitats. In our study, we did not observe such a difference.

This leads us to believe that, in the south, the limiting factor is climatic, while in the north, there may be a mixture of climatic factors and competitive displacement.

Taking into account these results, climatic selection may be acting upon one or both species and competitive selection can be detected in the species or phenotypes not subject to climatic selection, although it is not clear whether there is an interaction between the two.

We agree with Arthur (1982a), that there is no reason why unbandeds should be weaker interspecific competitors, or why climatic selection should be the cause of the frequency changes when passing from allopatry to sympatry. We think rather, that a phenotype will be a stronger or weaker competitor depending on the frequency it has in the other species. This is an extension of the concept of selection depending on frequencies to a two species situation (see Arthur, 1982b). Frequency dependent selection had already been noted for mixed colonies, but from the point of view of selection (Clarke, 1962b, Bantock *et al.*, 1976). There are cases where differences have not been observed in morph-frequencies between allopatric and sympatric populations; this may be due to interaction between various selective forces which neutralise character displacement, or to an equilibrium in the mixed populations.

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