VISUAL SELECTION IN THE LAND SNAIL *ARIANTA ARBUSTORUM*

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1. INTRODUCTION

DURING the last twenty years there have been considerable advances in the understanding of the ecological genetics of polymorphic land snails. Cain and Sheppard (1950) were the first to show systematic patterns in the distribution of the colour and banding morphs of *Cepaea nemoralis* L., and considered that these could not be ascribed to random factors such as genetic drift or the founder effect. They suggested that predators were exerting visual selection which resulted in populations of *C. nemoralis* matching the background of the habitat in which the snails were living. Further work by these authors (1952, 1954) and by Sheppard (1951, 1952) showed that Song Thrushes (*Turdus ericetorum* Turton) were the agents mainly responsible for this selection. Subsequent workers have provided further examples of visual selection in populations of land snails from other areas of England (e.g. Currey, Arnold and Carter, 1964; Arnold, 1965; Greenwood, in prep.). Goodhard (1958), (1962), Carter (1965) and Cameron (1968) established that similar effects occur among populations of *Cepaea hortensis* Mull.

These two species have a complex series of loci controlling the shell-character polymorphism, and consequently the analysis of the selective forces acting upon these loci is difficult. A less complex species might facilitate the separation of the interactions between visual selection and other selective forces such as climate.

An example of such a species is the European gastropod *Arianta arbustorum* L. This paper, which is the first of a series, examines the variation in natural populations of *Arianta*, and reports upon the results of a survey undertaken to examine the effects of predation upon some populations of the species in Derbyshire, England.

2. MATERIAL AND METHODS

(a) *Arianta arbustorum*

A. arbustorum is a polymorphic helicid, approximately 20 mm. in diameter. Its genetics have been studied by Oldham (1934) and Cook and King (1966) from whom the following data are taken. It appears to be dimorphic for colour, yellow being recessive to brown. The condition "yellow" is not caused by the presence of a yellow pigment as in *Cepaea*, but is the consequence of the absence of brown pigment. It is therefore similar to the variety *albina* of *Helix aspersa* L. (Taylor, 1914) and perhaps to "yellow-white" in *C. nemoralis* (Cain, Sheppard and King, 1968).

There is only one band, which is in the position 3 of von Martens (see Cain and Sheppard, 1950). Presence of the band is dominant to its absence.

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The banding locus is closely linked to that controlling shell pigmentation, and Cook and King (1966) estimated a recombination frequency of 0.7 per cent. Thus, colour and banding genes tend to be inherited as a supergene.

The shell of *A. arbustorum* is typically mottled with whitish flecks; this condition being dominant to unmottled. The flecks are formed by small opaque patches lacking pigment, and the thin periostracum gives them a characteristic yellow tint. On a yellow snail, the shell is translucent between the flecks, and the animal appears more uniformly coloured than does a brown which is patterned with pale straw-coloured flecks on a darker background. In the region covered by this study, unmottled individuals were very rare (<0.1 per cent.) and the character is not included in the analysis which follows.

(b) *The area of the survey*

Carboniferous limestone in the counties of Derbyshire and Staffordshire in Northern England extends from Castleton in the north to Ashbourne in the south: a distance of approximately 22 miles. For most of its length this region is 8 or 9 miles wide. It is dissected by several major rivers, and their many tributary streams, which run typically in steep valleys, often with limestone outcrops and cliffs. These valleys are known as the Derbyshire Dales.

The rainfall is high in this part of England. The annual figure for Buxton (in the west) is 48.4 inches, at Chatsworth, less than 12 miles east, it is 32.6 inches. This represents a drop of almost a third over a few miles. There are also sharp differences in rainfall between the high, exposed surfaces and the sheltered valleys close at hand.

The steep slopes and thin soil allow rapid drainage, which prevents leaching on the sides of the valleys. On the flat areas above the dales, the soil is deeper, drainage is slower, and some leaching takes place. On some parts of the flat tops the removal of calcium carbonate and the accumulation of non-calcareous clay residue gives a heavy brown soil several inches thick. This forms permanent pasture and is unsuitable for *Arianta* and *Cepaea*. These snails are only found in the valleys and the present paper deals with populations found along the rivers Wye and Derwent.

(c) *The Wye Valley*

The river Wye flows across the limestone massif in Derbyshire from west to east (see fig. 1). It thus flows down the gradient of precipitation. As there are changes in the morph-frequencies of *A. arbustorum* which appear to be associated with rainfall (Parkin, in prep.), it is necessary to divide the valley up into units sufficiently small to be exposed to approximately the same major climatic conditions. The Wye valley between Buxton and Bakewell has already been divided by popular use into four approximately equal units, and these are used in the ensuing analysis. The subunits are from west to east: Wyedale, Cheedale, Millersdale and Monsaldale, and are shown in fig. 1.

The habitats which occur fall into six major types, in one of which—broken stone and scree—*Arianta* was only found on three occasions, with fewer than five shells in each. The remaining five habitats are described below.

Short Grass. Limestone turf not more than 12 cm. high, in which the majority of the vegetation is grass. This usually occurs on the exposed,

FIG. 1.—The map shows the geographical features of that part of the valley of the river Wye, Derbyshire, covered by the present survey. Land over 1000 feet is shown cross-hatched, and the contours are at 100-ft. intervals. The scale represents 1 km. The top left-hand corner of the map is at the United Kingdom Ordnance Survey Grid Reference SK 070 740, and the top right hand corner at SK 190 740.

well-drained southwards-facing sides of the valleys, or on high sides around rocky outcrops. In general, this is not a favourable habitat for *Arianta*, and most samples contain only *C. nemoralis*, with occasional *Helicigona lapicida* L.

Long Grass. This habitat grades continuously with the next, but is defined as containing mostly grass (not less than 12 cm. high) with only a few isolated dicotyledons. It usually occurs on the more shady northwards-facing slopes, but in the west, where rainfall is high, the south-facing sides also support this habitat.

Mixed Herbage. This term covers any habitat with vegetation more than 12 cm. high and containing a predominantly mixed flora. Included are stands of vegetation such as brambles (*Rubus* sp.), Coltsfoot (*Tussilago farfara* L.), and Dog's Mercury (*Mercurialis perennis* L.).

Tall Herbage. In the bottom of valleys or on patches of level ground where the soil is thin and stony, nettles (*Urtica dioica* L.) and Willowherb (*Epilobium* sp.) grow in a highly characteristic way. The stems are at least 30 cm. high and straight with the leaves clustered at the top, and each plant stands an inch or two clear of its neighbour.

Woods. In the west, the woods are dark and gloomy. The understorey is frequently Dog's Mercury or scattered nettles and moss, with frequent areas of bare earth, stones and leaf litter from the previous season. Ash (*Fraxinus excelsior* L.) predominates, with some Sycamore (*Acer pseudo-platanus* L.). Further to the east, the trees become more scattered with grass underneath, and the species are replaced by Oak (*Quercus* sp.), with Hawthorn (*Crataegus monogyna* Jacq.) and Hazel (*Corylus avellana* L.) scrub along the edges of the woods, even on north-facing sides.

(d) *Methods*

Random samples were taken from small areas (with maximum diameters of about 30 metres) to ensure that each represented a homogeneous population. This upper limit of area was chosen because *Arianta* is similar in size to *Cepaea*, and because the panmictic unit in the latter species is believed to be about 30 metres in diameter (Lamotte, 1951; Murray, 1962).

The *Arianta* were scored for colour and banding. If the lip of the shell was fully formed, the animal was regarded as being adult, otherwise as juvenile. When a shell was broken, only pieces which were the major part of an individual were used in the analysis; fragments were discarded. Samples which contained five or more scorable individuals of *A. arbustorum* are included in this paper. This restriction excludes all samples taken from short and long grasslands in Cheedale and Monsaldale from the paper.

(e) *Variation in brown*

There is a considerable amount of variation in the amount of pigment in brown shells, resulting in a gradation from very pale, almost straw-coloured, individuals with only a trace of pigment behind the lip, to those coloured a rich dark purplish brown. The brown *Arianta* have therefore been divided into two categories: pale individuals (called "buff") and dark brown ("chocolate"). There is inevitably a certain amount of subjectivity here, as the two categories are not discontinuous. However, scoring was found to be repeatable to within 1 or 2 per cent.

The data from the samples of *Arianta* are presented in table 1. Table 2

TABLE 1

The data from the samples of Arianta arbustorum (which contained five or more individuals which could be scored for colour and banding) collected in the valley of the river Wye

Column 1 gives the reference number of the sample which is shown in fig. 1, and Column 2 shows the National Grid Reference of the sampling point within square SK. Column 3 indicates the habitat from which the sample was taken. Columns 4-9 give the number of individuals in the six phenotype classes: yellow, buff and chocolate, unbanded and banded. Columns 10 and 11 show the total number of non-yellow snails, and of *Arianta* itself, respectively. The last two columns indicate the frequency of yellow shells in the samples, and the proportion of buff shells among the brown snails.

1	2	3	4	5	6	7	8	9	10	11	12	13
No.	Grid. ref.	Hab.	YU	YB	BfU	BfB	ChU	ChB	Bf & Ch	T.	% Yell.	% Buff
Wy 9	085726	SG	1	0	0	0	0	22	22	23	4.35	0
Wy 24	100705	SG	2	1	0	0	0	10	10	13	23.08	0
Wy 34	097724	SG	0	0	0	0	0	8	8	8	0	0
Wy 64	114726	SG	3	4	0	0	0	13	13	20	35.00	0
Wy 5	109724	LG	12	3	0	11	0	45	56	71	21.13	19.64
Wy 6	110724	LG	4	2	0	6	0	21	27	33	18.18	22.22
Wy 26	102725	LG	0	0	0	0	1	6	7	7	0	0
Wy 35	100724	LG	0	0	0	1	0	28	39	29	0	3.45
Wy 36	105726	RH	9	1	0	5	0	26	31	41	24.39	16.13
Wy 37	102725	RH	5	2	0	0	1	22	23	30	23.33	0
Wy 53	105725	RH	20	1	0	4	0	25	29	50	42.00	13.79
Wy 54	105725	RH	19	2	0	21	0	55	76	97	21.65	12.63
Wy 55	107725	RH	4	0	0	0	0	17	17	21	19.05	0
Wy 58	112725	RH	4	3	0	5	0	22	27	34	20.59	18.52
Wy 60	112725	RH	4	1	0	1	0	28	29	34	14.71	3.45
Wy 62	113726	RH	1	0	0	3	0	17	20	21	4.76	15.00
Wy 3	104724	TH	10	0	0	1	0	9	10	20	50.00	10.00
Wy 15	091724	TH	12	0	0	0	0	108	108	120	10.00	0
Wy 42	102725	TH	1	0	0	3	0	14	17	18	5.56	17.65
Wy 8	084726	W	7	0	1	4	0	36	41	48	14.58	12.30
Wy 10	085726	W	7	0	0	0	0	83	83	90	7.78	0
Wy 11	087726	W	2	0	0	0	0	95	95	97	2.06	0
Wy 12	087725	W	0	0	0	0	0	57	57	57	0	0
Wy 14	088723	W	5	0	0	0	0	108	108	113	4.42	0
Wy 27	088721	W	0	0	0	0	0	16	16	16	0	0
Wy 28	089722	W	2	0	0	0	0	28	28	30	6.67	0
Wy 29	090722	W	0	1	0	0	1	16	17	18	5.56	0
Wy 30	091722	W	4	0	0	0	0	16	16	20	20.00	0
Wy 31	092723	W	7	2	0	3	2	49	54	63	14.29	5.56
Wy 32	093724	W	0	0	0	0	0	12	12	21	0	0
Wy 33	095724	W	2	0	0	0	0	19	19	21	9.52	0
Wy 56	108724	W	3	0	0	0	0	30	30	33	9.09	0
Wy 57	111725	W	0	0	1	0	0	27	28	28	0	3.57
Wy 59	112726	W	2	0	0	0	0	18	18	20	10.00	0
Ch 22	113727	RH	4	2	0	3	0	16	19	25	24.00	15.79
Ch 38	116727	RH	14	8	0	7	1	39	47	69	31.88	14.89
Ch 23	115727	TH	36	7	1	35	0	78	112	155	29.03	30.36
Ch 34	119728	TH	9	0	0	1	0	14	15	24	37.50	6.67
Ch 35	120728	TH	6	2	0	0	0	22	22	30	26.67	0
Ch 36	121728	TH	4	1	0	1	0	20	21	26	19.23	4.76
Ch 37	112729	TH	2	1	0	1	0	9	10	13	23.08	10.00
Ch 44	123730	TH	1	2	0	2	0	20	22	25	12.00	9.09

TABLE 1—*cont.*

1	2	3	4	5	6	7	8	9	10	11	12	13
No.	Grid. ref.	Hab.	YU	YB	BfB	BfU	ChU	ChB	Bf & Ch	T.	% Yell.	% Buff
Ch 26	124734	W	1	1	0	0	0	31	31	33	6·06	0
Ch 27	126734	W	1	0	1	1	0	23	25	26	3·85	8·00
Ch 32	122732	W	1	0	0	0	0	17	17	18	5·56	0
Ch 33	118727	W	3	1	0	1	0	20	21	25	16·00	4·76
Ch 39	122735	W	0	0	0	0	0	9	9	9	0	0
Ch 40	122735	W	1	0	0	1	0	21	22	23	4·35	4·55
Ch 41	122733	W	1	0	0	0	0	13	13	14	7·14	0
Ch 43	124733	W	2	1	0	2	0	22	24	27	11·11	8·33
Mi 12	139731	SG	4	0	0	2	0	1	3	7	57·14	66·67
Mi 13	143732	SG	4	8	1	7	0	30	38	50	24·00	21·05
Mi 16	150733	LG	4	0	0	0	0	15	15	19	21·05	0
Mi 2	135733	RH	1	0	0	0	0	7	7	8	12·50	0
Mi 1	137733	TH	0	0	0	0	0	6	6	6	0	0
Mi 10	129733	TH	7	0	0	0	0	1	1	8	87·50	0
Mi 14	145732	TH	6	4	3	0	0	42	45	55	18·18	6·67
Mi 23	144735	TH	8	3	0	2	0	17	19	30	36·67	10·53
Mi 24	162729	TH	13	0	0	0	0	27	27	40	32·50	0
Mi 25	165731	TH	2	0	0	1	0	3	4	6	33·33	25·00
Mi 27	166728	TH	5	0	0	1	0	13	14	19	26·32	7·14
Mi 28	169727	TH	3	1	0	0	0	14	14	18	22·22	0
Mi 9	134733	W	1	0	0	0	0	14	14	15	6·67	0
Mi 11	135733	W	2	0	0	0	0	17	17	19	10·53	0
Mi 21	167731	W	1	2	0	0	0	33	33	36	8·33	0
Mi 22	167727	W	0	0	0	1	0	20	21	21	0	4·55
Mo 24	180712	RH	4	0	0	1	0	44	45	49	8·16	2·22
Mo 33	176701	RH	1	1	0	3	0	26	29	31	6·45	10·34
Mo 35	168702	RH	2	1	0	4	0	28	32	35	8·57	12·50
Mo 11	183717	TH	1	0	0	3	0	11	14	15	6·67	21·43
Mo 34	178700	TH	1	1	0	5	0	19	24	26	7·69	20·83
Mo 45	182697	TH	2	0	0	5	0	24	29	31	6·45	17·24
Mo 10	185715	W	2	0	0	3	0	23	26	28	7·14	11·54
Mo 13	176723	W	0	1	0	0	0	40	40	41	2·44	0
Mo 31	172702	W	3	0	0	0	0	24	24	27	11·11	0
Mo 32	173702	W	2	0	0	1	1	41	43	45	4·44	2·33
Mo 39	190695	W	0	0	0	0	0	18	18	18	0	0
Mo 43	180696	W	0	0	0	0	1	8	9	9	0	0
Mo 44	181696	W	0	0	0	2	0	11	13	13	0	15·38
Mo 46	184696	W	0	0	0	1	0	29	30	30	0	3·33
Ma 3	282594	LG	3	0	—	—	0	9	—	12	25·0	—
Ma 12	282581	RH	1	1	—	—	0	5	—	7	14·3	—
Ma 24	285570	RH	0	0	—	—	0	12	—	12	0	—
Ma 9	284577	TH	5	0	—	—	0	34	—	39	12·8	—
Ma 13	286582	TH	14	1	—	—	0	21	—	36	38·9	—
Ma 18	262565	TH	2	0	—	—	0	42	—	44	4·6	—
Ma 8	283537	W	0	0	—	—	0	38	—	38	0	—
Ma 11	289574	W	0	0	—	—	0	25	—	25	0	—

TABLE 1—*cont.*

1	2	3	4	5	6	7	8	9	10	11	12	13
No.	Grid ref.	Hab.	YU	YB	BfU	BfB	ChU	ChB	Bf & Ch	T.	% Yell.	
Ma 14	273570	W	1	0	—	—	0	24	—	25	4.0	—
Ma 15	270569	W	0	0	—	—	0	9	—	9	0	—
Ma 17	275572	W	3	0	—	—	0	40	—	43	7.0	—
Ma 19	269566	W	0	0	—	—	0	11	—	11	0	—
Ma 20	277573	W	0	0	—	—	0	6	—	6	0	—
Ma 21	279754	W	0	0	—	—	0	41	—	41	0	—
Ma 22	282574	W	0	0	—	—	0	18	—	18	0	—
Ma 23	265565	W	0	0	—	—	0	8	—	8	0	—
Ma 30	297590	W	0	0	—	—	0	8	—	8	0	—

illustrates the composition of two samples chosen merely because they contain large numbers of snails. The genetics of buff is not known, but it is possible that it could be the heterozygote between yellow and brown. Cook and King (1966), however, consider dominance to be complete, and the data of table 2 support this since buffs are significantly fewer than would be expected from the Hardy-Weinberg equilibrium ($P < 0.001$).

TABLE 2

The composition of two samples of A. arbustorum from the valley of the river Wye

	Wydale 54			Cheedale 23		
	Unbanded	Banded	Total	Unbanded	Banded	Total
Yellow	19	2	21	36	7	43
Buff	0	21	21	1	33	34
Chocolate	0	55	55	0	78	78
Total	19	78	97	37	118	155

There is no discernible difference in the proportion of unbanded between buff and chocolate, and this is typical of the data as a whole. They differ markedly from yellow in being associated with the banded condition. The continuous variation in brown could result from a series of modifiers adjusting the expression of the major gene.

3. CORRELATION WITH BACKGROUND

(a) *Distribution of yellow*

The woods in Derbyshire are primarily Ash, and for a considerable part of the year the ground below the trees is bare or covered with a carpet of leaf litter from the previous season. This gives a brownish background even in the areas where Dog's Mercury grows, for little grows between these plants. The grassland and other non-woodland habitats are green for much of the year, more so than in areas away from limestone. The change in colour during the winter months is to a dull straw, and the background is still paler than the adjacent woodland.

The proportion of yellow-shelled individuals in the series of samples from woodland has been compared with that from the non-woodland habitats in the same dale, using the U-test (Mann and Whitney, 1948). The results of these comparisons are shown in table 3, where the observed values of U are laid out beside the expected values, with the latter's variance. The value of P reflects the probability of there being no difference between the

frequency of yellow in the woodland and non-woodland habitats of the dale under consideration. The 17 samples from the area around Matlock, which lies about 9 miles to the east of Bakewell, can also be included here. The shells in these collections are too faded to permit accurate scoring for the shade of brown, so the columns in table 1 listing the number of buff shells have been left blank. There are 11 woodland and 6 non-woodland samples and, as shown in table 3, there is a significant excess of yellow shells in the non-woodland samples. Yellow snails are significantly more common in the non-woodland samples than in the woodland collections from the same dale.

TABLE 3

A comparison of the frequency of yellow and pale brown individuals in samples of Arianta arbustorum taken from woodland and non-woodland

		Obs. U.	Exp. U.	P.
(a) Yellow	Wyedale	73.0	142.5	0.02
	Cheedale	1.0	32.0	0.01
	Millersdale	3.5	24.0	0.01
	Monsaldale	9.0	24.0	0.03
	Matlock	7.5	33.0	0.01
(b) Buff in brown	Wyedale	79.0	142.5	0.02
	Cheedale	10.5	32.0	0.02
	Millersdale	15.0	24.0	0.28
	Monsaldale	7.0	24.0	0.02

This result is comparable with the findings of the workers referred to earlier, who showed that yellow unbanded *C. nemoralis* and "effectively yellow" (Clarke, 1962) *C. hortensis* were at an advantage on green backgrounds, and dark snails—whether pink, brown or with fused bands—were favoured in woods.

(b) *Distribution of buff*

If visual selection is the cause of the difference in the proportions of yellow individuals in the populations, buff shells should be advantageous in localities where yellows are favoured. Conversely, on the dark brown background of woodland floors, chocolate would be favoured at the expense of buff.

Table 3 shows the results of comparing the frequency of buff in the brown shells from the series of samples from the two habitat types in each dale. The samples from Matlock have been omitted since it was not possible to score them accurately for the shade of brown. There are significant differences for Wyedale, Cheedale and Monsaldale, but for Millersdale there is a 28 per cent. probability that the result is due to chance. The four results are effectively separate experiments and as they are all in the same direction (namely, more buffs in non-woodland habitats) the method of Fisher (1950) can be used to combine the probabilities. This gives χ^2 of 25.8 with 8 degrees of freedom, which is significant at the 1 per cent. level. There can therefore be little doubt that buff-shelled *Arianta* are more abundant in populations from non-woodland localities than woodland ones.

(c) *Analysis of predated material*

Morris (1952) showed that it is possible to distinguish thrush-broken *Cepaea* shells from those broken by rodents. The two predators produce

differences in the position and nature of the fracture of the spire. The shell of *Arianta* is sometimes thin and fragile so that it collapses when assailed, rendering identification of the predator difficult. For this reason, shells are merely recorded as "predated in the present section". Some other samples can be added. Two are from woodland localities around Bakewell. *Arianta* was absent from the non-woodland habitats examined in this part of Derbyshire. The other additional samples are from woodland habitats in the mouths of some side-ales of the main valley of the river Wye.

Scoring each sample separately for the number of yellow and brown individuals which had been killed by predators, or not, yields data which can be examined directly for evidence of differential selection. Using Cochran's (1954) method for combining a series of contingency tables using weighted differences in proportion gives no evidence of yellows being selectively predated in woodlands ($P \simeq 0.25$).

There is considerable heterogeneity between samples from similar habitat within some of the dales, so that data from the separate samples perhaps should not be combined. However, the number of each colour morph taken by predators from a population will be the combined results of a series of factors. Firstly, birds search entirely visually, whereas mammals may use their sense of smell to locate a snail. The former will therefore predate selectively, the latter may not, and no attempt has been made to distinguish between these types of predation. Secondly, differences in the relative proportions of snail-eating birds and mammals will result in differences in proportions taken. Thirdly, Allen and Clarke (1968) have shown that birds have colour preferences, and search images become superimposed upon these. Separate birds will have different preferences and images, resulting in variations in the proportion of yellows taken in separate localities. Finally, the background, while falling clearly into "woodland" or "non-woodland" will vary in colour, giving different backgrounds. These will all combine and interact to give differences in the proportion of yellow and brown available and taken, and consequently the heterogeneity between sites is not too disturbing.

Bearing this in mind, the samples from woodland and non-woodland habitats have been combined for each dale into table 4. The unpredated shells include both live individuals and unbroken dead shells: there is no difference in the proportion of yellow between these two classes. A higher proportion of yellow than brown shells have been predated in woodland. In non-woodland, the converse holds and brown are more heavily predated except among the populations around Matlock. Sheppard (1951) found that as the season progressed and the background of a wood became greener, so the Song Thrushes took a progressively higher proportion of pink *C. nemoralis* compared with yellow. The present result where yellow shells are at a greater disadvantage in woodland, and a lesser in non-woodland, is a significant one ($P < 0.01$ —one tailed sign test) and agrees with that of Sheppard.

4. DISCUSSION

The principal predators of *Arianta* involved in the present analysis are probably Song Thrushes, which hunt visually, and small mammals which possibly find their prey by scent rather than by sight. Predation appears to be a far more important cause of death in woodland, for the proportion of

TABLE 4
Data accumulated by date, showing the number of yellow and brown adult shells broken by predators or whole in the samples from Wye valley

Area	Woodland				Non-woodland			
	Predated	Not predated	Total	% Predated	Predated	Not predated	Total	% Predated
Wyedale	Yellow	36	6	42	85.7	27	101	26.7
	Brown	375	134	509	73.7	161	438	36.8
	Total	411	140	551	74.6	188	539	34.9
Cheedale	Yellow	3	1	4	75.0	25	86	29.1
	Brown	68	39	107	63.6	61	208	29.3
	Total	71	40	111	64.0	86	294	29.3
Millersdale	Yellow	9	2	11	81.8	24	34	70.6
	Brown	69	30	99	69.7	71	97	73.2
	Total	78	32	110	70.9	95	131	72.5
Monsaldale	Yellow	9	5	14	64.3	2	13	15.4
	Brown	110	118	228	48.2	15	95	15.8
	Total	119	123	242	49.2	17	108	15.7
Bakewell	Yellow	1	0	1	100.0	—	—	—
	Brown	11	8	19	57.9	—	—	—
	Total	12	8	20	60.0	—	—	—
Matlock	Yellow	3	1	4	75.0	6	21	71.4
	Brown	109	87	196	55.6	40	99	59.6
	Total	112	88	200	56.0	46	120	61.7

predated shells is higher in this habitat. This is also the opinion of Greenwood and Pedder (in prep.) who have undertaken a similar survey of *Cepaea* spp. in the same area. They were able to distinguish between thrush and rodent predation in their material, and considered both to be higher in woodland habitats, but rodents slightly less so than thrushes.

Cain (1953) has presented evidence that rabbits (*Oryctolagus cuniculus* L.), as colour-blind mammals, predate selectively by visual tone, and favour pink rather than yellow *C. nemoralis* on short downland turf. This has also been shown by Murray (1962) for "rodents". There were very few rabbits in the area of the Wye valley covered by the present survey during 1964-67, so that species can probably be ruled out as an important predator of present-day populations of *Arianta*. However, should other species of small mammals use vision rather than scent, they would probably show similar discrimination. Under such circumstances, yellow (*i.e.* pale) individuals would still be at a selective disadvantage in woodland. In greener habitats the brown morphs might be cryptic under some situations such as in the bottom of tufts of grass and in shady corners, so the selective differential would be less marked.

This expectation is partially borne out in the results reported above, for the proportion of yellow shells is higher in the predated than the non-predated material in all six sets of woodland data. In that from non-woodland, there is one area where brown shells are less predated than yellow, and the proportions of the two colour classes which have been predated are more similar than in woodlands.

Visual selection for crypsis will be operative wherever predators take snails after seeking them out by eye. The effects will depend upon the intensity of other selective forces. Thus, over large areas of Britain, populations of *C. nemoralis* exhibit area effects (Cain and Currey, 1963) where the frequency of a particular colour or banding variety is high or low over a wide area compared with the panmictic unit, and despite changes in habitat. Carter (1967) has shown that even here fluctuations may occur in the shade of shell colour, varying with habitat within a single area effect. He also showed (1967) that, where one factor was invariable within the confines of an area effect, other factors might vary in a manner consistent with visual selection.

Cain and Currey (1968) have shown that when the Song Thrushes were all killed by a severe winter, some morph frequencies of *C. nemoralis* in a grassland population within an area effect changed towards those in an adjacent nettle patch where predation had consisted of non-visual removal of buried snails in winter, and the removal of individuals from the periphery in summer when the confines were too dense for the birds to penetrate. The apparently simpler polymorphism of *Arianta* renders the detection of area effects more difficult, and of visual selection more easy than in *C. nemoralis*. In this part of Derbyshire, *C. nemoralis* appears to be varying between complex area effects with a superimposition of visual selection upon some of them (Greenwood, pers. comm.).

Since the yellow variety remains in the woodland populations despite this selection against it, it must be favoured at some stage of the life-cycle. Cook and King (1966) found no evidence of mutation occurring at the colour or banding loci, so mutation pressure is unlikely. The yellow variety could be held in the population by some form of environmental selection. This has been postulated for *Cepaea* by Lamotte (1951), Arnold (1968) and

Cameron (1968) among others and associations between the occurrence of unbanded yellow *Arianta* and areas of high rainfall in northern and western Scotland have been shown by Cain, Cameron and Parkin (1969). Similar effects can be detected within Britain as a whole as well as in the area covered by the present paper (Parkin, in prep.).

A further force which has been postulated as capable of maintaining the frequencies of the shell-character genes of molluscs is frequency-dependent visual selection or apostatic selection (Clarke, 1962). If a predator is able to develop a specific search image for a particular morph, it might miss differently coloured or patterned members of the same species during its search for food. This situation might occur in *Arianta*. The yellow unbanded form is totally distinct from banded brown, and apostatic selection could operate to maintain the yellow variety in woodland. It is difficult to show this type of selection in natural populations, and the data from Derbyshire are not adequate for investigating this matter.

5. SUMMARY

1. *Arianta arbustorum*, a British land snail, is polymorphic for colour and banding. The banded condition is usually associated with brown shell colour; unbanded individuals are yellow. There is variation in the shade of brown from pale to dark.

2. Among populations of *A. arbustorum* inhabiting the Wye valley in Derbyshire, yellow individuals are common in non-woodlands. Pale brown shelled snails are similarly commoner than dark brown in non-woodlands. Dark brown is the predominant form in woodland areas.

3. The frequency of predated shells within a colour class shows a higher proportion among the yellow shells than the browns in woodland. The converse is found in non-woodland habitats for four of the five areas considered.

4. It is argued that visually discriminating predators are selectively removing yellow snails from the woodland populations, resulting in the differences in distribution of the morphs found in the two habitat classes.

5. The results are compared with those obtained in studies of *Cepaea nemoralis* and *C. hortensis* and their significance discussed.

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