Ecogenetics of a Population of Cepaea nemoralis (L.) Subject to Strong Area Effects

A. J. Cain and J. D. Currey

Phil. Trans. R. Soc. Lond. B 1968 **253**, 447-482
doi: 10.1098/rstb.1968.0007

STUDIES ON *CEPAEA*

III. ECOGENETICS OF A POPULATION OF *CEPAEA NEMORALIS* (L.) SUBJECT TO STRONG AREA EFFECTS

By A. J. CAIN* and J. D. CURREY†

* *Department of Zoology, University of Manchester*
† *Department of Biology, University of York*

(*Communicated by P. M. Sheppard, F.R.S.—Received* 13 *February* 1967)

[Plate 33]

CONTENTS

On the discovery of area effects in morph frequency variation in the snail *Cepaea nemoralis* on the Marlborough Downs (Cain & Currey 1963*a*) an intensive study with mark–release–recapture methods of a population subject to these effects was begun. The area investigated was divided into four quarters (downland grass) and two nettlepatches; the snail population is continuous through the area. Frequent visits were made during the snails' active season in 1962, 1963 and 1964; in 1965 and 1966 a single large sample was collected, marked and released in the spring. Five-banded shells are absent. The scoring of mid-bandeds with reduced bands being difficult, attention was concentrated on the principal colour morphs, yellow, pink and brown. Thrushes were predating the snails heavily in 1962, but the hard winter of 1962/3 removed them, and they have not yet returned in any numbers; the snail population does not seem to have been affected by this hard season.

Throughout the period of investigation, the density of snails in the nettlepatches has been about ten times that in quarters 2, 3 and 4. Quarter 1 has less than half the density in the other quarters, and differs markedly from them and the nettlepatches in morph frequency, although it resembles quarter 2 strongly in vegetation. It is likely, therefore, that the snails are extremely localized in their wanderings, the more so as we had to collect from each division, take the samples away to be marked, and scatter them on release, each at random in its own division. Our estimates of migration from one division to another also suggest strong localization and perhaps homing.

The total population in the area is about 3000 adults. Subpopulations have decreased in all divisions from 1963 to 1965. Adult survival rates are high, about 0·65 per year; no differential survival of the colour classes has been found, but much more data are needed.

Predation by thrushes in 1962 was heavy in the summer, but not in proportion to snail density; the nettlepatches were proportionately much less predated, probably because of their dense growth of herbage. Winter predation, by contrast, was almost entirely in the nettlepatches, then showing expanses of bare earth.

A check on our own efficiency of collecting shows that we are taking non-random samples in the quarters (downland grass) but not in the nettlepatches. We find pinks rather more conspicuous than yellows, but dark browns much less conspicuous than either. As the snails' bodies in this area are very dark, yellows appear green, pinks dirty straw-colour. It seems unlikely that browns are really more cryptic visually than yellows. Possibly their behaviour is different. The samples of predated shells taken by the thrushes agree very closely with our samples, and it appears that they also are predating with a bias (missing browns) in the quarters but not in the nettlepatches.

Morph frequencies show no sign of alteration in the period of investigation, except that in 1963 and 1964 there was a drop in percentages of browns in quarters 2, 3 and 4, apparently not continuing in 1965 and 1966. (The compensatory increase is shared equally between pinks and yellows.) This could well be due to the sudden cessation of selection by thrushes, but the rate seems excessive if there was selection only on adults. There is no obvious relation between morph frequencies and population density.

The growth in size of the juveniles in our samples has been studied through the snails' active season. It is clear that they take two years to reach maturity (i.e. to form the lip terminating the adult shell). This finding and the survival rates give a minimum generation interval of four years, and the actual period may be close to five in this area.

1. Introduction

The striking area effects in both colour and banding discovered by us on the Marlborough and Lambourn Downs and on part of Salisbury Plain (Cain & Currey 1963 *a–c*) appear to be caused by natural selection (Cain & Currey 1963 *a*, *d*) of a sort different from the visual selection observed or inferred by various authors (see Cain & Sheppard 1954; Cain & Currey 1963 *a*; Currey, Arnold & Carter 1964), and often opposed to it in direction. For a study of the selection acting on a given population, a detailed knowledge of its ecology and age structure is desirable. We have therefore begun an intensive study from these points of view of the most strongly marked area effects on the Marlborough Downs. This paper gives the results of five seasons' work. Numerical stability, generation time and survival rates have been investigated, as well as selection by predators; and differences in density, morph frequency, incidence of predation, extent of selection and activity in relation to weather and season have been found between subpopulations in nettlepatches and in downland grass. Selection by ourselves in gathering samples differs in the nettlepatches and in the grassland, as does that exerted by thrushes. The ecogenetic importance of what might well be considered minor differences in background and habitat is demonstrated.

2. Ecology of the population

(2·1) *Locality*

Area effects on the Marlborough Downs were mapped by Cain & Currey (1963 *a*). They include a large area in the southern half of the Downs in which there are no five-banded shells (the modifier M^3 is at saturation) and there is generally a very high frequency of brown unbandeds even on open downland. We decided to work in the middle of this

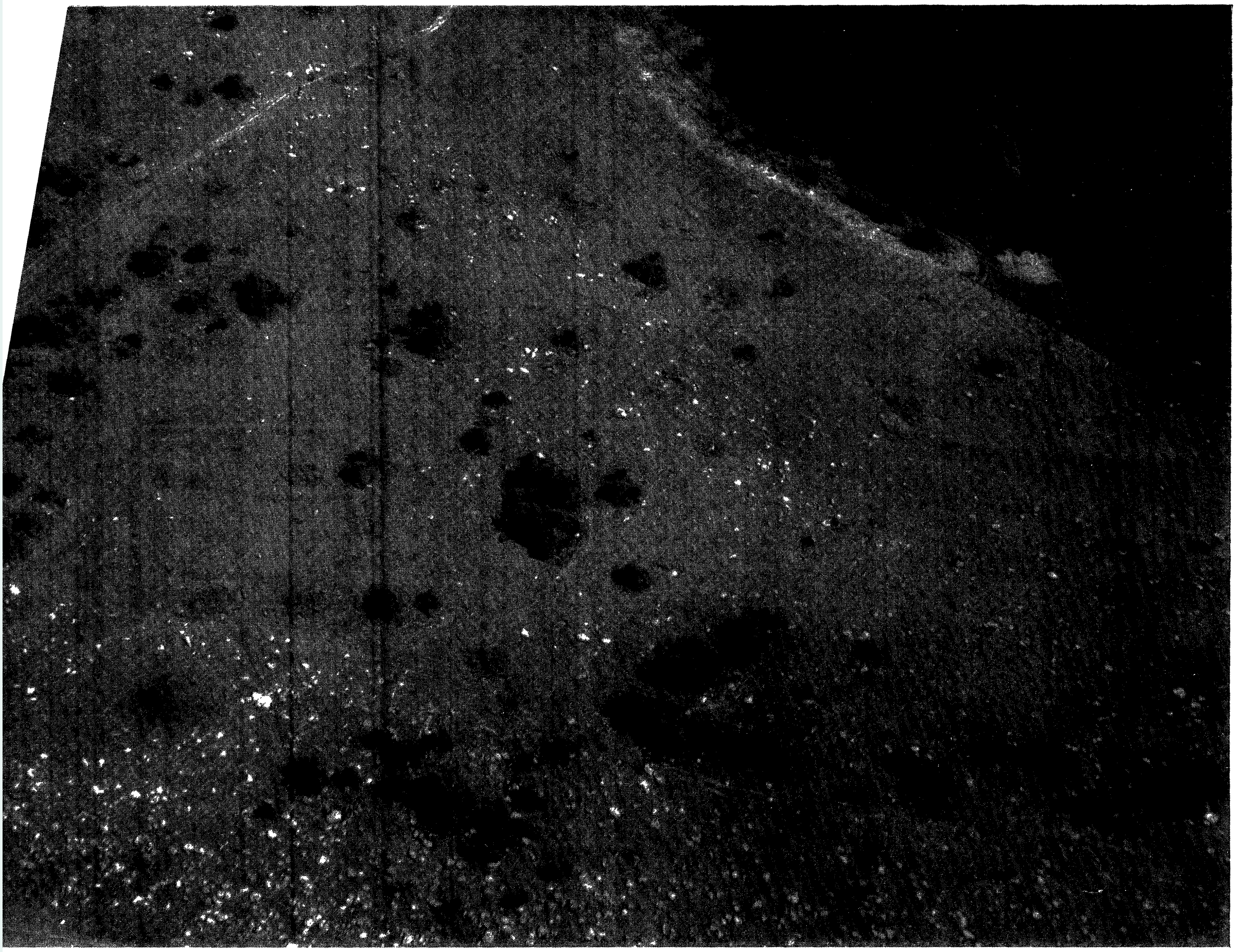


FIGURE 12. Aerial view of part of Fyfield Down looking north-east. The rectangular arrangement of banks and ditches in part demarcates the area investigated. Woodland in the top right corner of the picture is part of Wroughton Copse (compare Cain & Currey 1963*a*, pl. 1) and *C. hortensis* occurs in the vegetation at its edge. White objects, sarsen boulders. The large, more or less rectangular enclosure contains quarters 1 and 2 (the smaller one adjoining it to the north-east is outside the area worked). The grey patches in the edge of the enclosure nearest the bottom of the picture are nettlepatches 1 and 2, and the bank projecting more or less at right-angles from the edge between the nettlepatches runs along the border between quarters 3 and 4. The lowest border of the area investigated runs across the group of largest sarsens, parallel to the bank containing the nettlepatches. Sarsens are clearly more abundant in quarters 3 and 4 than in 1 and 2.

area (Cain & Currey 1963*a*, figures 5 and 6) where yellows and pinks are more abundant than at its edges and all three colours occur at frequencies high enough to be handleable statistically from practicable samples. Moreover, in the middle, large numbers of thrush-predated shells were found scattered on and around the numerous sarsen boulders, and the relative importance of visual selection and selection producing area effects could be investigated. Unfortunately only one season's work on thrush predation was possible, since the hard winter of 1962–3 killed off or drove away the birds, and very few have been seen since. Our working area (grid reference SU 1370) is near the middle of the Nature Conservancy's Fyfield Down nature reserve and reasonably well protected from interference.

The general topography, geology and vegetation of the Marlborough Downs are described briefly by Cain & Currey (1963*a*) and their plate 1 shows the general features of that part of the reserve in which the working area lies. The area itself is shown in the present figure 12 (plate 33). It is a stretch of open downland grass, roughly rectangular, sloping gently to the south-west with the lower edge about 100 yards from the foot of the steep slope of Overton Down and making part of the gently sloping side of a rather narrow valley, very asymmetrical in cross-section. It is partly demarcated by ditches and banks probably belonging to a medieval farm (P. Fowler, personal communication). There are no trees within the area but scattered thorns and elders, sometimes aggregated into small thickets, are rather frequent around it. About half-way up the slope the area is crossed by a slight bank on which are two nettlepatches. A plan of the area with dimensions and names of divisions is given in figure 1. Since the total surface is about 36 500 sq. ft. (figure 1) we divided the grassland into four 'quarters' to be investigated separately, and we also took the nettlepatches separately as being probably ecologically distinct; our work has in fact shown great differences in snail ecology between the nettlepatches and grassland, and between parts of the grassland.

Quarter 1 contrasts with all the other divisions in having a much lower density of *Cepaea*, and in having a high proportion of the yellow morph. In appearance, however, it is remarkably similar to quarter 2 having, as compared with quarters 3 and 4, very few sarsen boulders and rather lush tussocky grass: quarters 2, 3 and 4 agree fairly well in population density and in morph frequencies, but in 3 and 4 there are large numbers of sarsens, which the thrushes use as anvils, and the turf in parts is short; the lowest edge of these two quarters has very few snails. The principal difference between the two nettlepatches and the grassland areas as far as *Cepaea* is concerned is the far higher density of snails in the patches (and a very different predation régime).

Cepaea nemoralis is the common snail in the working area and for some distance around. *C. hortensis* comes no nearer than the edge of Wroughton Copse (about 400 yards). The only other common molluscs are the big black slug *Arion ater* (L.) and the grey slug *Agriolimax reticulatus* (Müller) which are generally abundant.

The area is used as rough grazing, almost entirely by sheep which walk through it daily, grazing as they go. Rabbits were formerly extremely common (P. M. Sheppard, personal communication); a very few still exist and sometimes a myxomatosed individual is found. Occasionally they scrape shallow burrows in the nettlepatches. Hares are common but we have no evidence that they take snails. Moles are frequent and produce fresh heaps of turned soil which are used by *Cepaea* for egg-laying. There are no signs of small rodents in the working area, and trapping by the Warden of the reserve (Mr N. King) was wholly unsuccessful. The only birds likely to be of importance to the present study are missel thrushes (*Turdus viscivorus*) and song thrushes (*T. philomelos*), both common in 1962, the missel thrush especially so. It is not certain, and inquiry of various ornithologists has produced no results, whether the missel thrush cracks snails as does the song thrush.

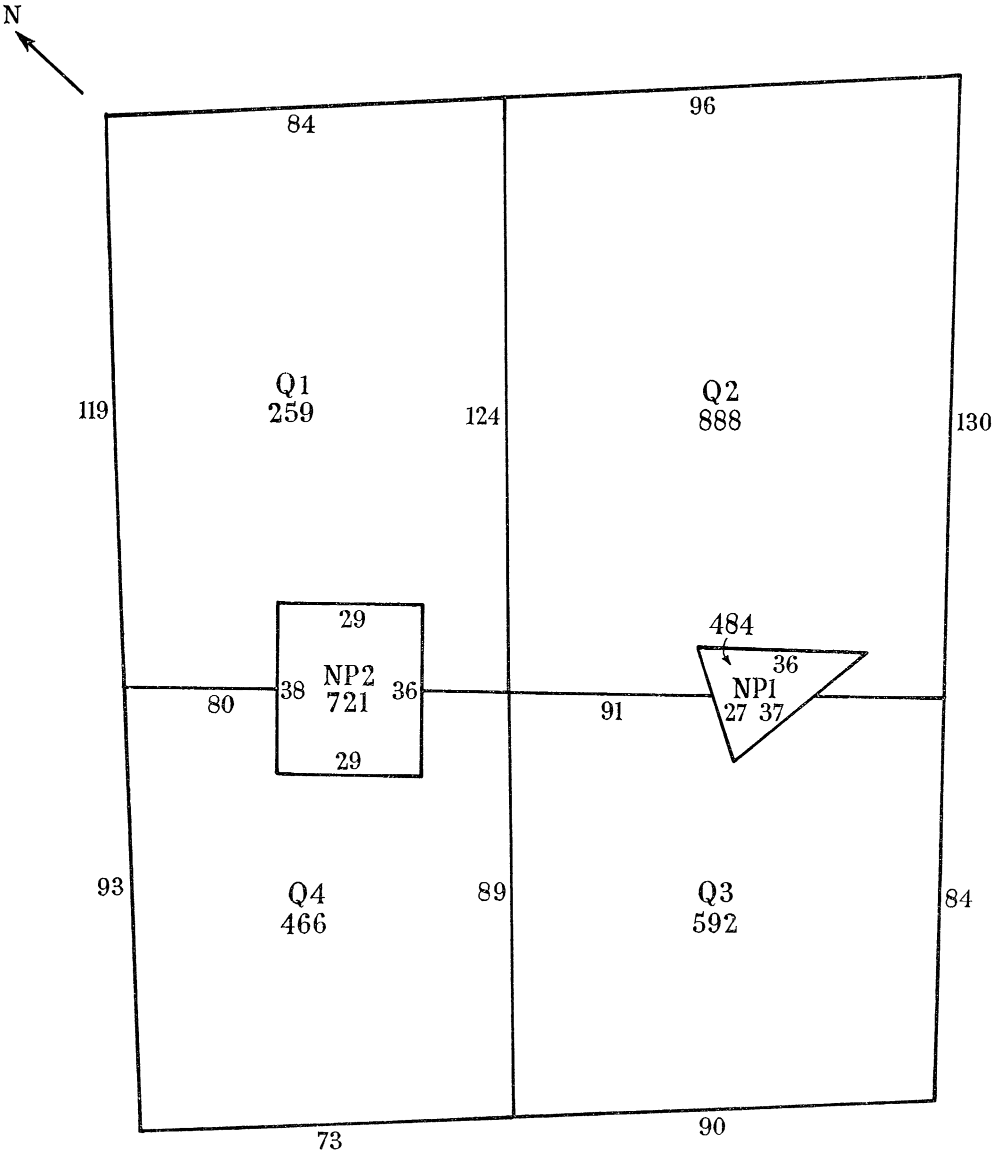


FIGURE 1. Plan of the area investigated, Fyfield Down Nature Reserve, with our divisions. Q = quarter, NP = nettlepatch. Dimensions in feet. For each division is shown the population size in 1963 (Jolly year-samples).

The widespread occurrence of marsh thistle *Cirsium palustre* (L.) Scop. and meadow saxifrage *Saxifraga granulata* L., especially the former, in the little valley and around and on the working area suggests a dampness that is more likely to be due to climate than to soil or water-table. No records of weather are available for the period covered in this paper.

(2·2) *Methods*

(i) *Advantages and disadvantages of* Cepaea

Compared with other animals, such as birds, small mammals, and Lepidoptera, which have been used for mark–release–recapture studies, *Cepaea* has some advantages. The shell of the adult is comparatively easy to mark. (Slugs, for example, are much more difficult, having no external hard parts.) Individual numbering is possible, and unless broken into small pieces by a predator, the shell remains with legible marks after death. *Cepaea* is hermaphrodite with reciprocal fertilization and without protandry or protogyny, so that differences of behaviour of the sexes need not be considered. It can be sampled by simple hand-collection, without the need for traps and the consequent development of trap-avoiding or trap-seeking behaviour which is a severe complication in some studies of small mammals (Leslie, Chitty & Chitty 1953) and birds (Lack 1946). Reading of the marks need cause little disturbance to the individual, not at all comparable with that caused to small birds when they are netted for ring numbers to be read. The marks are firmly attached to the individual during its lifetime and, being close to the lip, they are usually readable even after the shell has been broken by a thrush. The species occurs in favourable localities at high densities (§ 2·5), so that quite large samples are obtained, and as there is little wandering (§ 2·6) a high proportion of each population can be marked. Survival rates during the year appear to be high (§ 2·5) and multiple recaptures very common, which is not the case with the short-lived imagines of many insects, e.g. the moth *Panaxia dominula* (Fisher & Ford 1947). The life-history is simple, without profound metamorphosis giving a series of stages with very different ecologies and selection pressures, as in many insects. It is likely, however, that habits in the first few weeks after hatching differ from those of the adults.

There are also definite disadvantages. Marking juveniles in a permanent and inconspicuous manner is very difficult, and scoring of very small juveniles for morph frequencies is usually impossible. The principal disadvantage, however, is the snails' habit of burying themselves in the ground. This means that a large proportion, in bad weather from the snail's point of view close to 100%, is not available at any one time for sampling. Where, as in the present study, selection pressures of a few per cent are in question, impossibly high densities may be required for adequate samples; and the high survival rate makes it difficult to detect differential survival of morphs. Very small juveniles are rarely seen in the field and are delicate. It is impossible to dig up the buried snails since this would wreck the habitat for a long-term study. As the snails are crepuscular and nocturnal, sampling in the very early morning will increase the catch, but in the evening when the light is failing, highly biased samples are taken. The use of a sweep net at night has not been found successful in downland grass, nor in thick beds of herbage.

(ii) *Marking methods used*

In 1962, two methods were used, drilling holes in the shell (Murray 1962), and painting with cellulose paint small areas of the shell from which the periostracum had been removed with a file. Cellulose paint had been used with success by Ford (1945) for marking the wings of Lepidoptera and by Sheppard (1951) for *Cepaea*. Paint marks seem satisfactory for a single season's work, but at the end of 1962 we were already finding a few individuals with the paint cracking off; for animals as long-lived as *Cepaea* more permanent marks are desirable. Moreover, a succession of colours was needed to mark dates of capture and it was difficult to confine the gaudy series of paint spots to the underside of the shell where they would not normally be seen by the visual predators.

Marking by drilling holes in the shell was used by Murray (1962). The holes are filled in with white calcareous matter by the animal and remain permanently discernible, and different positions can be used to express numbers. If the total number of holes on a shell is to be kept small to avoid weakening the shell, the amount of information expressible is reduced. Moreover, careful positioning of the holes to reduce ambiguity of reading is possible with five-banded shells in which the bands serve as markers but is less easy on unbanded or mid-banded ones. The technique is a good one, producing quite inconspicuous marks, but laborious to apply, especially if the holes are to be positioned carefully and the shell is unbanded or mid-banded. We therefore used holes in 1962, but only to show the quarters or nettlepatches in which a snail was first found, and colours to give the date of each capture or recapture.

As these methods were unsuited for distinguishing large numbers of snails individually, we tried engraving numbers on the shell with a diamond. This technique has proved satisfactory over several years, with little sign of wear affecting the numbers. The periostracum is removed with a file to make sure that the diamond is cutting the calcareous layers of the shell. The area used is just behind the lip, a part held by the thrush in breaking the shell and therefore not often itself broken. Almost all fully adult shells can be numbered. A very few have brittle outer layers or an abnormally thin shell, but almost none have been unmarkable. Snails very newly adult which have not yet thickened the last-produced segment of the shell are not markable. The number must be read with a strong lens, especially on badly grown or damaged shells with irregular corrugations. The snails occasionally radulate the shells, making shallow excavations, but these are small compared with the numbers and are not a serious hazard to their legibility. So far, over 3 600 shells have been numbered and only about two became really difficult to read. A combination of the number, colour and banding, and often of the 1962 drill-holes and surviving colour marks, plus individual peculiarities of the shell, makes identification easy. The numbers are far less conspicuous than colour marks, and more like natural scratches or other wear on the shell than are drill holes.

Engraving the shell does not seem to disturb the animal abnormally. Disturbance by bringing the snails into the laboratory for marking is more likely to have some effect, and is considered in the next section.

(iii) *Sampling interval*

With a slow-moving long-lived species such as *C. nemoralis*, sampling cannot take place every day because the released samples must be given time to redistribute themselves. To test whether redistribution is satisfactory, one can examine the relative representation of two successive releases in the first recapture after the second release. If there is no indication that the snails of the second release are recaptured in a different proportion from those of the first release in the following recapture, the interval between them allows

TABLE 1. TESTS FOR REDISTRIBUTION OF RELEASED SNAILS

area	1st recapture: χ^2 and degrees of freedom	P	direction	smallest expected class	2nd recapture: χ^2 and degrees of freedom	P	direction	smallest expected class
data for recaptures on 31 May 1962 and 18 June 1962 of releases 26 April+3 May, and 21 May 1962, 10 and 30 days first recapture, 28 and 48 days second recapture								
Q2	0·00, 2	1·0	+	4·6	0·0045, 1	0·98 > > 0·95	+	16·7
Q3	0·90, 1	0·5 > > 0·3	–	6·7	0·043, 1	0·9 > > 0·8	–	20·8
Q4	6·10, 1	0·02 > > 0·01	–	6·2	0·0002, 1	0·99 > > 0·98	+	8·5
NP1	3·48, 1	0·1 > > 0·05	–	30·5	0·298, 1	0·7 > > 0·5	–	17·9
NP2	0·833, 1	0·5 > > 0·3	+	35·7	0·077, 1	0·8 > > 0·7	–	28·0
data for recapture on 18 June 1962 of releases on 21 May and 8 June. 10 and 28 days								
Q2	0·000338, 1	0·99 > > 0·98	+	5·5				
Q3	1·455, 2	0·483	–	2·2				
Q4	2·749, 2	0·253	+	2·2				
NP1	1·39, 1	0·3 > > 0·2	–	5·9				
NP2	0·46, 1	0·5	+	9·8				
data for recaptures on 18 May 1963 and 31 May 1963 of releases 23 April and 8 May. 10 and 25 days first recapture, 23 and 38 days second recapture								
Q2	0·739, 2	0·691	–	2·2	0·000, 2	1·0	–	2·0
Q3	12·43, 2	0·00202	–	3·7	0·893, 2	0·64	+	1·9
Q4	2·59, 1	0·2 > > 0·1	–	8·4	4·59, 1	0·05 > > 0·02	–	8·4
NP1	0·061, 1	0·8 approx.	–	19·7	0·75, 1	0·5 > > 0·3	–	16·9
NP2	0·0023, 1	0·98 > > 0·95	–	26·8	0·69, 1	0·5 approx.	+	21·3
data for recaptures on 31 May 1963 and 26 June 1963 of releases 8 May and 18 May. 13 and 23 days first recapture, 39 and 49 days second recapture								
Q2	0·567, 1	0·5 > > 0·3	+	10·1	0·160, 1	0·9	–	12·5
Q3	0·640, 2	0·726	–	3·3	7·192, 2	0·027	–	4·3
Q4	0·631, 1	0·5 > > 0·3	+	5·9	2·19, 1	0·2 > > 0·1	–	6·7
NP1	0·117, 1	0·8 > > 0·7	+	18·4	0·0064, 1	0·98 > > 0·95	–	14·2
NP2	5·19, 1	0·05 > > 0·02	–	30·0	0·142, 1	0·7	–	24·8

for redistribution unless the snails of both releases are equally disturbed. This can be checked by looking at their representation in a second recapture.

As considerable numbers of any releases are buried at any given recapture time, it is necessary to work with large releases and recaptures. All suitable ones are listed in table 1, with the results of tests for discrepancies in proportion of recaptures of releases of two previous dates. The direction of the discrepancies observed is given (+ means that more of the more recent releases were recaptured than of the more distant) and the size of the smallest expected class in each comparison. Single values of P are for exact probability calculations and the χ^2 is calculated from these as in Fisher (1946). For the first recapture after the second release we have:

	+	–			
quarters	5	7	summed χ^2, quarters (18 degrees of freedom)	28·8	$0·05 < P < 0·1$
nettlepatches	3	5	nettlepatches (8)	11·5	$0·1 < P < 0·2$
and for the second recapture:					
quarters	3	6	quarters (12)	15·1	$0·2 < P < 0·3$
nettlepatches	1	5	nettlepatches (6)	2·0	$0·90 < P < 0·95$

The only individual significant differences for the first recaptures are in the quarters, namely quarter 4 (1962, releases 26 April+3 May and 21 May, recapture 31 May) and quarter 3 (1963, releases 23 April and 8 May, recapture 18 May). Both are *deficiencies* in the recapture of the release just previous to it. For the later recaptures there are again two in the quarters and again deficiencies. The summed χ^2, however, is insignificant for the later recaptures and only approaching significance for the earlier ones. In no case is there a constant deficiency over two recaptures. A deficiency could be caused if snails disturbed by their temporary removal from the area were to secrete themselves and remain inactive, or were less active, for several days after return. It is unlikely that such an effect would continue for 30 to 40 days; moreover, the snails were kept in boxes before return for periods of several days in 1962, but were returned within 2 or 3 days in 1963, yet there is no sign of any greater deficiency in 1962. As the results show no consistent trends, the most that can be said is that in the quarters there may be a slight tendency for under-representation in the recapture of the most recent release. Where, as here, multiple recaptures are frequent, the effects of this, if any, will be minimized.

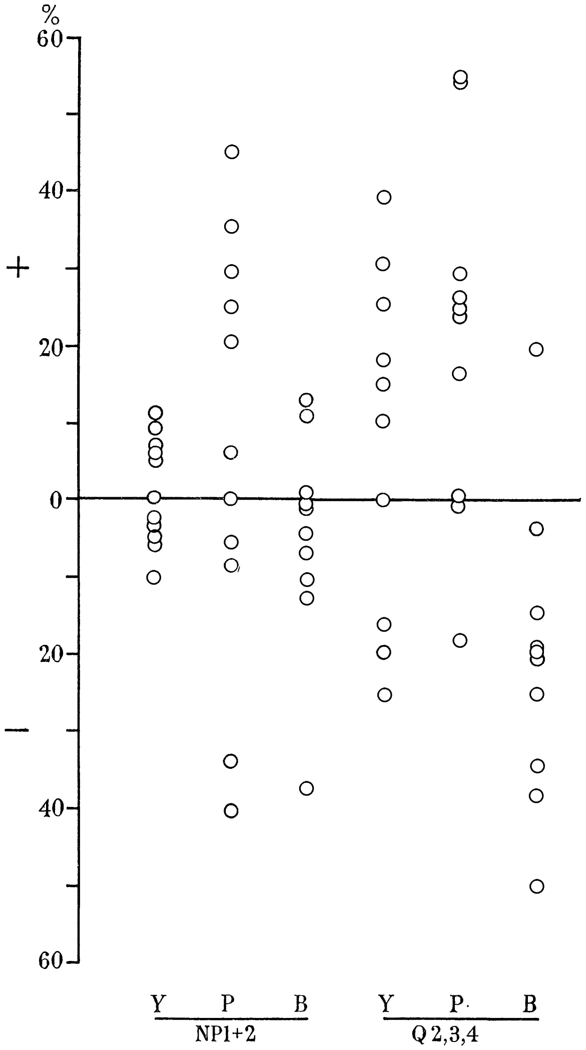


Figure 2. Biases of our recaptures of known releases. The ordinate gives the percentage discrepancy in each colour between snails released and those recaptured.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(iv) *Randomness of our samples*

Sampling by careful searching is sufficiently random for general surveys of morph frequencies in *Cepaea* when large variations of morph frequency are being investigated (Cain & Sheppard 1950, 1954; Cain & Currey 1963*a*, p. 4). When possible selection pressures of no more than a few per cent are in question, the goodness of the sampling must be examined. This can be done by releasing marked individuals and comparing the morph frequencies in recaptures with those in the samples released. A sufficient interval must be allowed for the released individuals to distribute themselves in the environment, but not so long that the effects of differential mortality might become appreciable. The results given (§ (iii) just above) indicate that a fortnight to a month are suitable, and those of § (2.5) that differential mortality in such a period is negligible.

Individual results for all the available data of sufficient size to be useful are given in table 2 and figure 2. The separate results give for the quarters and nettlepatches:

		yellows	pinks	browns
nettlepatches	+	5	6	3
	−	5	4	7
quarters	+	7	9	1
	−	3	1	9
totals	+	12	15	4
	−	8	5	16

These suggest no overall effect in the nettle patches but a deficiency of browns relative to pinks and yellows in the quarters. Both pinks and browns in the quarters show significant discrepancies (for both, *P* is 0·021) and the discrepancy for browns is significant in the totals (*P* is 0·020). On testing, there is no sign of heterogeneity between the various releases (*P* approximately 0·5 for nettlepatches and 0·9 to 0·8 for quarters). Combining the data, therefore, we get the following estimate of our percentage bias:

	yellows	pinks	browns
nettlepatches	+1·4 not significant	+2·6 not significant	−2·4 not significant
quarters	+12·5 significant *P* approx. 0·05	+16·3 significant *P* between 0·04 and 0·05	−20·5 significant *P* much less than 0·01

Consequently our samples from the quarters must be considered as biased to these extents. It will be noticed that although there is no significant bias in the nettlepatch samples, the discrepancies actually observed are in the same direction as those in the quarters. The biological significance of these results is discussed later (§ 3·1).

(v) *Methods of analysis for mark–release–recapture*

A discussion of different methods of analysis is given by Jolly (1963), who later (1965) produced a method based on a stochastic model. Parr (1965) has applied the Fisher–Ford method, Bailey's three-point test, Jackson's method and Jolly's stochastic method to a population of dragonflies and discusses their relative uses. In the present study we have used the Fisher–Ford method and Jolly's stochastic method to give a check upon each other. The Jolly method has the advantage of giving variances for all estimates, whereas

Table 2. Tests of our selection during sampling

		Q2, 3, 4			NP 1, 2			Qs			NPs		
year	releases and recaptures	Y	P	B	Y	P	B	Y	P	B	Y	P	B
1962	22, 24, 26 April releases	146	96	186	172	117	198	—	—	—	—	—	—
	8+11 May recaptures	44	27	40	107	63	118	+16·1	+8·5	−17·1	+5·4	−8·8	+1·0
	18 June recapture	18	10	10	24	14	24	+39·0	+17·4	−39·4	+9·6	−5·8	−4·7
1963	8 May release	69	44	68	131	90	174	—	—	—	—	—	—
	31 May recapture	7	6	3	24	21	31	+15·0	+54·3	−50·0	−4·8	+21·1	−7·5
	26 June recapture	15	6	9	18	16	22	+31·2	+17·7	−20·2	−3·2	+25·4	−10·9
	18 May release	85	73	106	81	76	130	—	—	—	—	—	—
	31 May recapture	8	11	12	13	7	22	−19·9	+28·2	−3·7	+6·5	−40·7	+12·0
	26 June recapture	6	7	12	11	10	18	−25·5	+1·1	+19·4	−3·1	+6·2	−1·3
1964	22 April release	112	80	133	142	86	175	—	—	—	—	—	—
	16 May recapture	9	8	9	23	14	28	+0·5	+25·0	−15·4	+0·4	+0·9	−0·8
	4 June recapture	12	16	14	23	19	27	−17·1	+54·8	−18·4	−5·4	+29·0	−10·1
	5 June release	101	76	123	69	47	69	—	—	—	—	—	—
	18 June recapture	21	18	17	12	11	7	+11·3	+26·9	−25·9	+7·2	+44·5	−37·5
	16 July recapture	27	16	21	15	6	15	+25·2	−1·2	−20·0	+11·8	−34·2	+11·8
	20 June release	106	80	106	78	44	62	—	—	—	—	—	—
	16 July recapture	29	23	16	13	11	10	+17·4	+23·4	−35·3	−9·9	+35·6	−12·8
	all releases	720	525	845	742	498	877	—	—	—	—	—	—
	all recaptures	196	148	163	283	192	322	+12·5	+16·3	−20·5	+1·4	+2·6	−2·4

the Fisher–Ford method does so only for death rate, which is assumed to be constant in the period investigated.

(2·3) *The population*

As the working area is inside the non-five-banded area effect, it has only unbandeds, and mid-bandeds, being saturated with the modifier M^3. All three main colour morphs yellow, pink and brown, are present. All the yellows appear to be dark yellows and there is no difficulty in distinguishing them from the other classes. The pinks are mainly pale pinks, with a small proportion of darks. A very few are extremely pale (faint pinks, Cain, Sheppard & King, this volume, p. 384) with very little pigment in the calcareous layers of the shell. Almost all the browns are very dark or dark, a few medium, and a very few pale. The last are not always easy to distinguish from the palest pinks. Of those we saw in 1963 and 1964—which stood a good chance of revision during the many recaptures in those years—and again in the spring of 1965 and 1966, we changed our minds on the scoring of only five faint pinks (to browns) in 870 pinks (0·6 %) and twelve faint browns (to pinks) in 1663 browns (0·7 %). The body colour in this population is remarkably dark, so that the yellows look greenish to deep grass-green. The pinks are a dull dirty straw-colour. The browns are nearly all so dark that the body colour has no effect on the appearance. Many shells have lost their periostracum at the spire; this hardly alters the appearance of yellows, produces a slight but often noticeable rose-pink flush in the pinks, and in the browns gives an often conspicuous bluish white patch. A few shells have lost all or nearly all the periostracum and show the colours just mentioned all over. For the purposes of the present paper we have used only the three classes, yellow, pink and brown.

There are three classes of banding present, unbanded 00000, plain mid-banded 00300, and mid-banded with the punctate form 00:00 (Cain *et al.*, this volume, p. 394; Cook, 1967). This produces a faint band with a dark blotch just before each varix and the lip. The band may be so reduced as to appear only as a single blotch by the lip (scored as a trace by Cain & Sheppard 1954) or may be easily visible along its whole normal length. Cain *et al.*, this volume, p. 394, have shown that genetically very reduced punctates may appear unbanded. Further, in this population variations in intensity of pigment above and below the periphery of the shell may often be seen in dark browns. The change occurs at the position of band 3 and it is often impossible to tell whether an apparent indication of the band is a reduced punctate band or merely due to the variation in ground colour. In yellows and pinks this difficulty does not arise; the normal mid-band unaffected by the punctate gene is heavily pigmented and varies only in width. It is just possible that we have confused literally one or two very narrow normal bands with punctate bands, but effectively the classes of normal and punctate bands are distinct in pinks and yellows. As we have difficulty in the browns, and as what little is known of visual selection on mid-bandeds suggests that they are closely similar to unbandeds (Arnold 1966; Lamotte 1951; Cain & Sheppard 1954), we have confined ourselves to the differences in colour morphs irrespective of banding.

(2·4) *Yearly cycle of activity*

Figure 3 shows the actual numbers of live snails found in the total area on each of the sampling occasions in 1962, 1963 and 1964. The activity of snails is very heavily affected by weather, so that there are considerable fluctuations, which are sometimes slightly exaggerated because on very unsuitable days we occasionally did not search the least populous quarters; this would have added only a very few snails, however. Collection was done in full daylight to reduce as much as possible our own visual bias; our experience, and Dr R. W. Arnold's (personal communication) is that collecting in the dusk produces an excess of yellows, which are so much lighter in tone that they stand out far more than the other colours. But these snails are mainly crepuscular and nocturnal in their habits, so that the samples are of that proportion of the population which was still out and active after dawn, usually late in the morning, or had stuck to leaves, grass or boulders instead of retiring underground. Murray (1962) found a very similar cycle of activity in 1959, 1960 and 1961 at Wittenham Clumps, Berkshire. The snails are much less active or perhaps much more strictly nocturnal in August, September and October than earlier in the year and there is usually a peak of activity in the late spring (May in all three of Murray's years, April and May in ours), when most copulating pairs seem to be found.

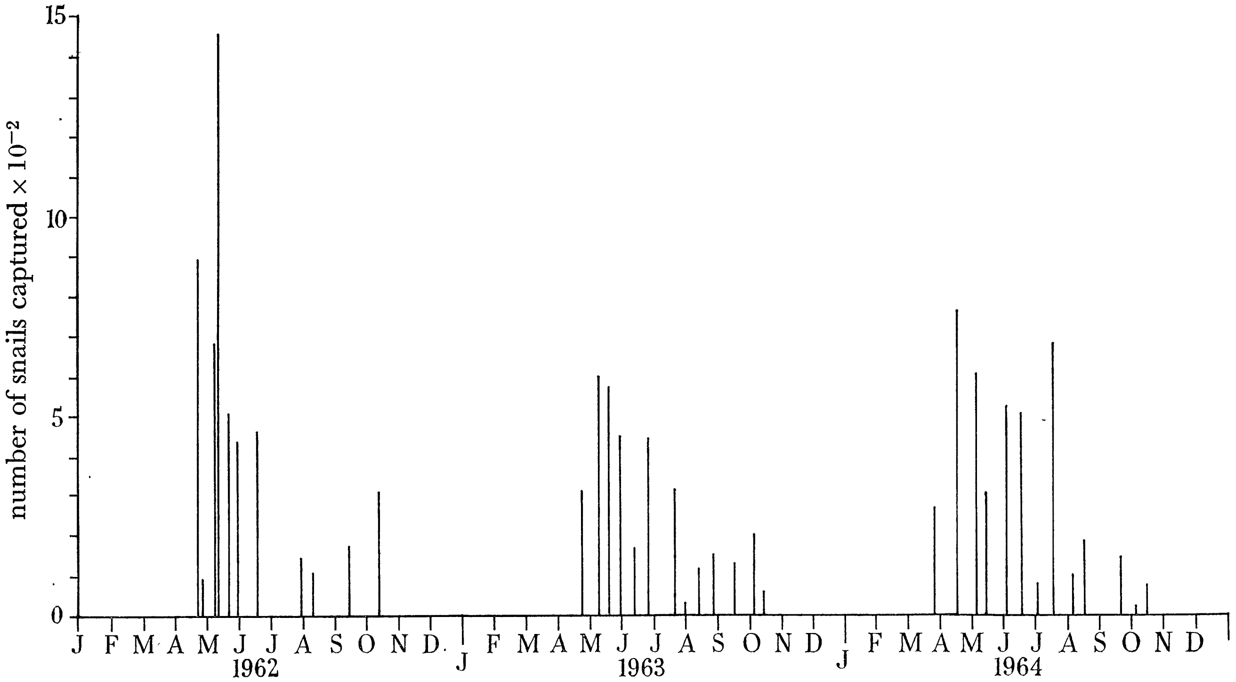


FIGURE 3. Number of snails captured on each sampling occasion as a measure of snail activity.

(2·5) *Population sizes, densities and survival rates*

(i) *Population sizes and densities in the different areas*

In figure 4 are shown all the estimates of population size for each quarter and nettle-patch for all sampling occasions from 1962 to 1965 for both Fisher–Ford and Jolly methods. In 1962 only the Fisher–Ford method was used; the figures given are based on samples with colours lumped for each area. In 1963 and 1964 both methods were used. In 1963, Jolly figures are given both for samples ignoring colours and for the sums of the separate estimates for each colour for each area; the agreement between them is good. The 1964 Fisher–Ford figures are by addition of separate colour estimates. In 1962, 1963 and 1964 we were able to visit Fyfield Down frequently through the active season; in 1965 and 1966 this was impossible, so we took (over a period of several days) one single large sample during the spring.

The agreement between estimates for the Fisher–Ford and Jolly methods is very good. Figures calculated for samples with colours lumped are subject to some bias because we did not sample the colours randomly (§ 2·2 (iv) above), but in practice they compare well with those from addition of separate estimates which are not subject to this bias; the latter are necessarily based on smaller samples and more inaccurate, and cannot be given for some occasions because no recaptures of a particular colour were obtained. There is little sign of any general trend in population size, except that the 1965 values for the

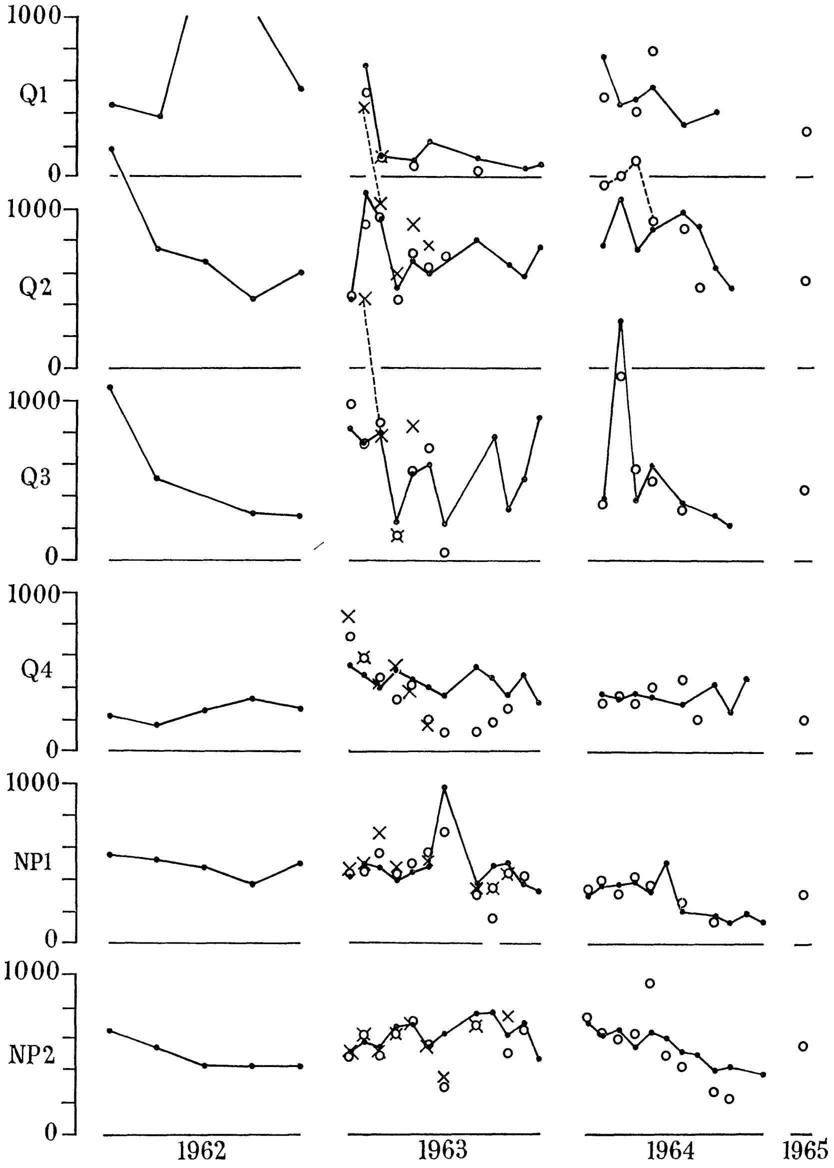


FIGURE 4. Estimates of population size for each division, 1962–5. Black dots, Fisher–Ford method (in 1964 by addition of separate estimates for each colour class). Circles, Jolly's method for the whole population, colour ignored. Crosses, Jolly's method, by addition of separate estimates for each colour class. A few aberrant estimates (∞ etc.) are omitted. Dotted lines join values falling outside a graph to the next value inside it.

quarters are rather consistently low compared with those for 1964, and these are sometimes lower than in 1963.

If we regard all captures in a single year as one sample, the sample size is much improved and trends might be more obvious. The resulting year estimates by the Jolly method are given in figure 5. Since in the year samples we are ignoring deaths within the period of sampling which is prolonged (except in 1965 and 1966 when effectively a single sample was taken) the resulting estimates are likely to be too high by a few per cent. For example, if we assume a population of 1 000 000 and a death rate over the year of 0·5, a single sampling occasion within the year will give $N = 1\,000\,000$, 2 give $N = 1\,032\,175$,

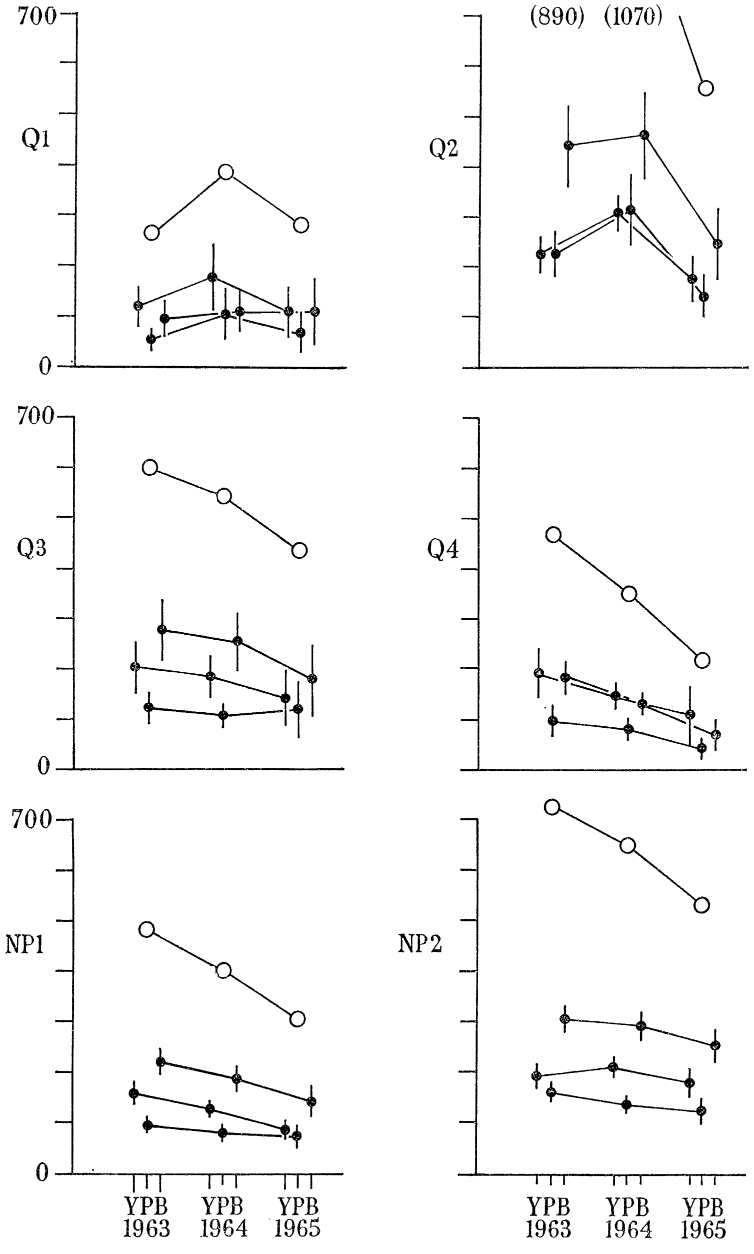


FIGURE 5. Population sizes from year samples (Jolly's method). Black dots, estimates for colour classes. Circles, totals by summing; numbers, for values off the graph. Vertical lines give twice the standard error on each side of the dot. Y.P.B. yellow, pink, brown.

and 4 give $N = 1\,039\,234$. Nevertheless, comparison of figures 4 and 5 shows a good agreement for 1963 and 1964 (the 1965 estimate is necessarily the same for both) and except in quarter 1 indicates a general decline in population size. A decline in frequency of browns in quarters 2, 3 and 4 (§ 3·2) is not of course, shown with as much clarity as in the direct comparison of morph frequencies, but can be seen in these quarters and not in the nettlepatches, as one would expect.

From figures 4 and 5 together it seems that there is some indication of population increase from 1962 to 1963 in quarter 4 and perhaps in nettlepatch 2, but otherwise no clear change. Between 1963 and 1964 all but quarter 1 and quarter 2 decline, and between 1964 and 1965 the population size drops in all. The densities of snails for 1963, 1964 and 1965 are given in table 3. Densities in 1962 were about those in 1963 except in quarter 4 where they were closer to that for 1965, and in nettlepatch 2 where they were slightly lower, perhaps about 5/m^2.

TABLE 3. DENSITIES OF SNAILS

	extent in		density (from Jolly year-estimates) in snails/sq.m		
division	sq.ft.	sq.m	1963	1964	1965
Q1	9385	872	0·30	0·45	0·33
Q2	11520	1070	0·83	1·00	0·52
Q3	7639	710	0·83	0·76	0·61
Q4	6379	593	0·79	0·59	0·36
NP1	437	41	11·80	9·83	7·46
NP2	1073	100	7·21	6·53	5·38

The close similarity of the quarters in density (quarter 1 being lowest as would be expected from the small samples obtained there), and their contrast with the nettlepatches throughout the period of investigation is striking and has important consequences when predation is discussed (§ 2·8). It is clear that so great a difference as is shown between each nettlepatch and its adjacent downland can be maintained only if the snails are highly localized and move around very little, or, if they move considerably there is either a strong attraction in the nettlepatches which causes them to return rapidly if they stray out, or a great hindrance to locomotion so that they move slowly, whether or not at random, when in them.

(ii) *Survival rates*

Survival rates calculated by Jolly's method and by the Fisher–Ford method for the morphs taken separately for each division and for the short sampling intervals used in 1962, 1963 and 1964 have too high a variance to be of use. The mean value for all these estimates by the Fisher–Ford method is 0·965, i.e. the death rate during the active season is about 3·5 % per week. Figure 6 shows the survival rates calculated by the Jolly method from year samples for 1962, 1963 and 1964. The median survival rate per year is about 0·55. In figure 4, taking the nettlepatches as with the largest samples, there is no indication of any drop in population size during the inactive seasons (about 5 months) including that one spanning the hard winter of 1962/3. This implies that most deaths occur during the active season. There are no significant differences between the colour morphs. The quarters show no trends and hardly differ amongst themselves; the nettlepatches, however, seem to agree in an improvement of survival rate, at least as between 1962 and 1964. Further observations are clearly needed. Even with these year samples, however, the variances of the estimates are still too large to allow us to pick up even comparatively large differences in survival rate between the morphs.

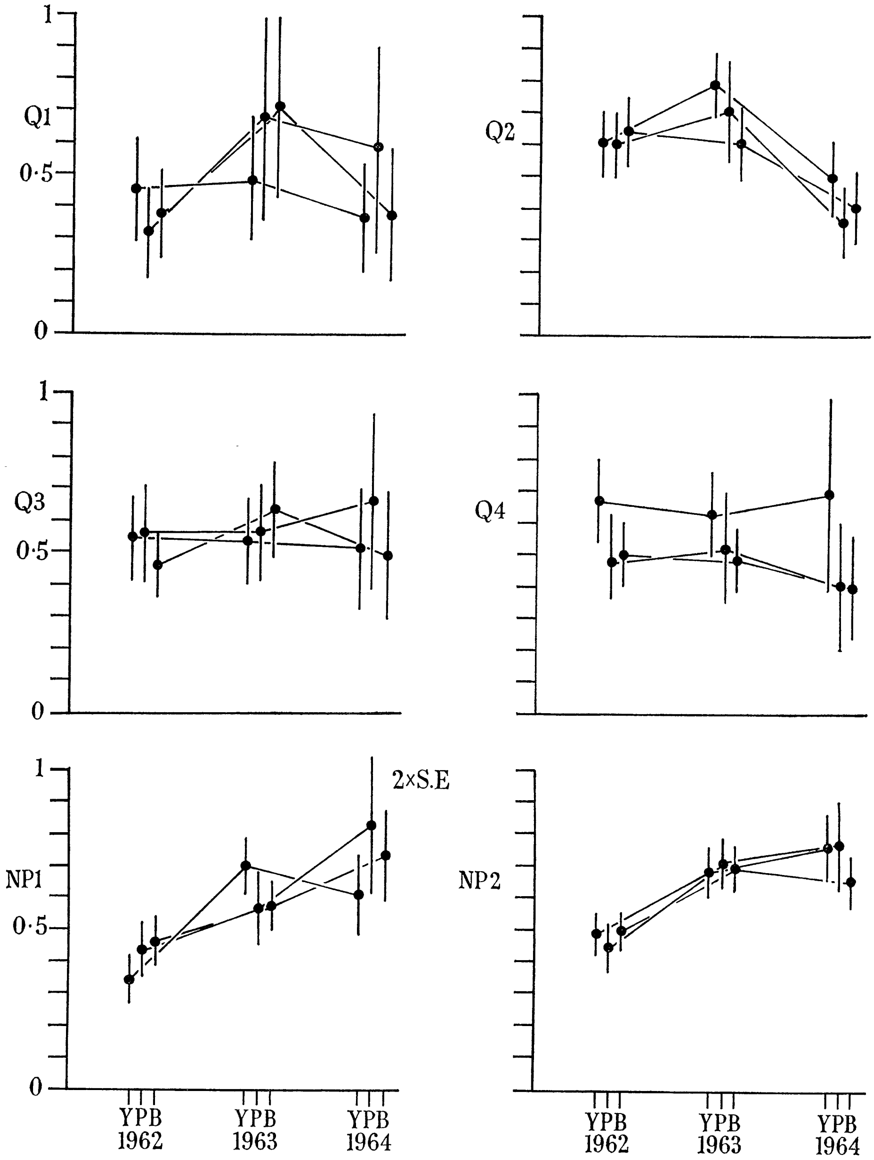


Figure 6. Survival rates from year samples (Jolly's method) for each colour class separately. Vertical lines give twice the standard error on each side of the dot.

(2·6) *Movement*

Both the Fisher–Ford and the Jolly methods for population size and survival work with a 'death-rate' which is rate of loss from the population because of both death and emigration. To estimate these separately, it is necessary to get an independent estimate of emigration, which is not easy to obtain from mark–release–recapture data from a series of samplings. As we have arbitrarily delimited populations which are in fact part of a continuous population, we have to estimate emigration, which may bias our estimates of both population size and survival rate for each of our areas; around the perimeter of the whole area investigated we expect loss of marked snails by emigration and very little replenishment by immigration (of marked snails that wander out and then return from outside).

Emigration of marked snails from a given area will have two effects. (*a*) The overall loss rate will be greater than the actual death rate in that area, irrespective of whether immigration is occurring or not, since the death rate is calculated from the re-appearance or not of individuals marked in that area only. (*b*) The apparent population size will be increased, but only if there is immigration of unmarked snails from outside, diluting the marked population. We have used the convention that marked snails on their first appearance in a different area from that in which they were marked are counted as unmarked and thereafter as belonging to the new area (unless, of course, they stray out again). In 1962 we marked by area and date, not individually, and could not identify snails that moved out of an area and later re-entered it: however, there were very few of these in subsequent years, and this class can be ignored.

C. nemoralis is likely to have restricted wanderings as compared with the width of one of our grassland areas (Lamotte 1951; Murray 1962). There is one complication caused by our method to be considered. We had to remove our samples from the areas in order to mark and record them, and on returning each to its area we scattered it at random; it was not possible to return each individual to the place where it was found. Therefore any snail which wandered into an area from which it might easily return but was caught by us in its new area, will very likely have been replaced in a part of that new area from which it could not return.

The situation we have investigated also differs from the ideal one in that:

(*a*) The death rate is probably not the same in all areas—but our evidence (preceding section) suggests that it does not vary greatly, and we have taken it as constant between areas in the following calculations but made no assumption about its variation with time.

(*b*) We do not recapture all the snails we release into any area, both because some die off and because on many occasions a high proportion of the snails are hidden.

(*c*) The probability of recapturing live snails certainly differs from area to area, and a snail that has moved to a different area may thereby alter its chances of being recaptured.

(*d*) We have only casual observations of snails migrating out of the whole area.

Difficulties (*b*) and (*c*) can be met if methods are devised which will indicate what number of snails of its class alive in the population each observed live snail represents. Two methods have been found, appendix 1, one of which, *A*, produces fictitious numbers for each class but the proportions of movers to non-movers is correct; the other, *B*, produces estimates of numbers taking death rates into account but needs 3 years' observations and can give no estimate for the final year's observations.

As an example, table 4 gives the % emigration for 1962–3 as determined by both methods. As agreement is good, method *A* has been used since it can give estimates for all working years. As the numbers of emigrants are small, they are lumped for all areas for 1962–4 in table 5 to give an estimate of differential movements by morphs. As will be seen from the table, there is no evidence that morph colour has any effect, (compare § 3.1).

Estimates of movement within the active season of one year have not been used because in the multiplying factor (Appendix 1), *M* will be most influenced by the earlier recaptures, since after only a short period from release there will be more snails to be recaptured than later when the proportion of dead is greater. The number of snails that have moved will, however, increase with the passage of time. If we take a period sufficiently far from that of release, we can treat the variation within it of the number of released snails still surviving and the number of migrants as approximately linear. A series of samples within this period can then be simply added; and as the number of migrants recovered on any one occasion is tiny we need to increase in this way the numbers dealt with to get any adequate estimate. Consequently we have used, for the years in which frequent sampling took place (1962, 1963 and 1964) only comparisons between years. Figure 7 and table 6 give the % movement in surviving snails for various periods. Considering the sizes of the samples on which they are based. the estimates for 1962–3 and 1963–4 agree well. Surprisingly, so do those of 1962–4. The emigration rate for 1962–4 should be rather less than twice that for 1962–3 or 1963–4. There is no indication in the present figures that it differs from them at all. With a migration rate m for period t_{01} or t_{12}, the proportion migrating in t_{02} is $m\ (2-m)$ which approximates to $2m$ if m is small. But this assumes that the migration rate is applicable to the whole population considered. If in the undisturbed snail population each individual wandered round in a very restricted locality so that only those close to an arbitrarily delimited line were liable to cross it, and the same individual might cross and recross frequently, then any sampling interval that was long compared with the time of wandering around each little locality would give the same migration rate. Our distribution will tend to increase the observed migration rate over longer periods since individuals

TABLE 4. ESTIMATES OF PERCENTAGE EMIGRATION BY BOTH METHODS FOR 1962–3

		method A	method B
quarter	1	25·2	35·2
	2	7·9	5·6
	3	9·4	11·7
	4	17·7	14·0
nettlepatch	1	6·7	8·6
	2	2·9	3·5

TABLE 5. TOTAL NUMBERS OF DIFFERENT COLOURS OBSERVED TO MOVE, 1962 BEGINNING TO 1964 END

	Y	P	B	total
Q/2, 3, 4	28	31	32	—
NP/1, 2	69	51	67	—
totals	97 (33·7 %)	82 (28·5 %)	109 (37·8 %)	288

TABLE 6. VALUES BY METHOD A FOR % MIGRANTS OF THOSE LEFT ALIVE AFTER VARIOUS PERIODS

	within 1963	within 1964	1962–3	1963–4	1962–4
Q1	18·3	9·6	25·2	21·9	24·4
Q2	4·2	12·3	7·9	4·9	6·3
Q3	4·7	11·1	9·4	9·7	11·2
Q4	8·8	20·6	17·7	12·8	7·7
NP1	14·2	18·4	6·7	17·0	13·9
NP2	3·2	5·9	2·9	8·0	10·8

will be less likely to obliterate a move in period t_{01} by a return move in a later period t_{12} and the estimated rate for t_{02} should be correspondingly higher.

Even with our disturbance, the emigration rates out of the nettlepatches are low, when we consider the density of the populations in them. There is clearly no reason to think of the nettlepatches as overpopulated areas exporting large numbers of snails into the surrounding grassland. Quarter 1, by contrast, seems to have a high emigration rate, which, unless due to some systematic error in our methods, may reflect the discomfort of a population in an unsuitable area, as indicated by the low population density.

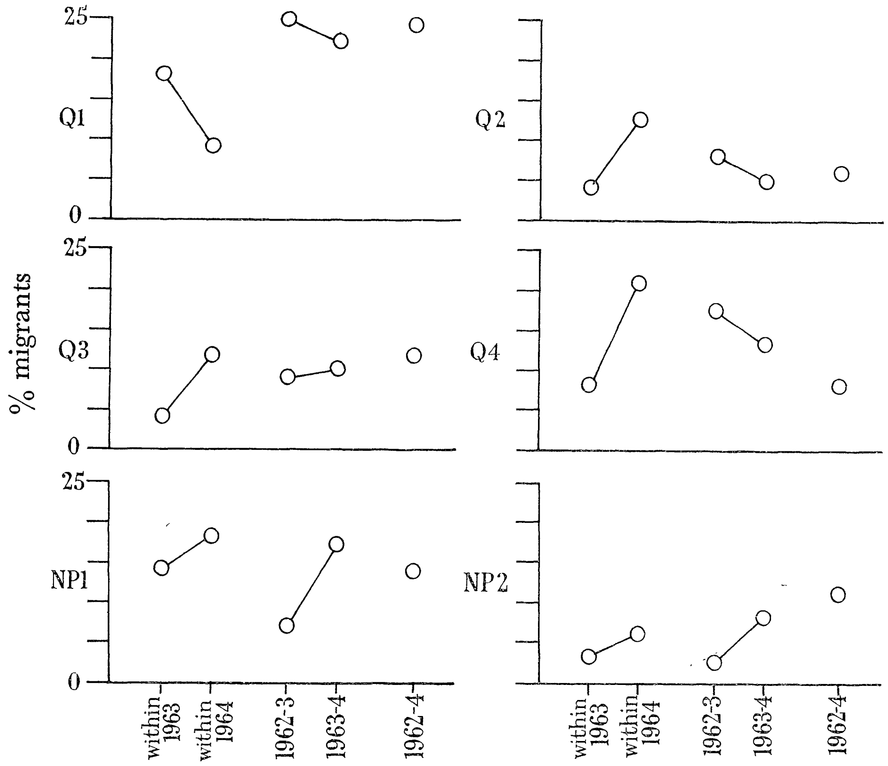


FIGURE 7. Percentage migration out of each division.

Compared with our estimates of overall death rate (figure 6) the emigration rates are not negligible during the years when we had to disturb the populations (table 6). Since there is no evidence of differential migration of morphs (table 5), nor of differential survival of morphs (figure 6 and p. 461) the only conclusion is that our calculated general survival rate of about 0·6 should be increased to about 0·7. The estimates of migration are of course only approximate both because of the small numbers of migrants observed and of approximations inherent in the method.

(2·7) *Generation interval*

It is essential in calculating selection pressures to consider them per generation. For *Cepaea*, which has overlapping generations, one must find the mean length of time from the origin of a zygote to when it has produced half the new zygotes that it will produce in its reproductive life (Clarke & Murray 1962*b*). We have observed the growth of particular year-classes of juveniles to maturity as defined by the formation and full thickening of a lip at the shell-mouth, and have determined the half-life of adults from this point onwards. This, strictly, is not quite what is required since there might be a non-reproductive period after lip formation. Wolda (1963, p. 427) found in outdoor cage experiments that just over one-half of the snails maturing in one particular season laid no clutches in the following active season. Apparently none laid a clutch in the first season in which they were still immature in May. Experience with breeding-pot cultures out of doors in Oxford (A.J.C.) also suggests that many snails maturing in the middle or towards the end of an active season wait until the next season before laying eggs; but the proportion of snails observed by Wolda which did not lay clutches in the next season after reaching maturity seems remarkably high. One would expect selection to act against it strongly since the half-life of adults reckoned from the formation of the lip is only about one year. The density of snails in Wolda's cages was about $69/m^2$ which is about five times higher than anything we have found in the wild (§2·5). If Wolda's findings do represent the situation in the wild, the generation interval determined below must be increased by about 6 months.

In the outdoor breeding pots at Oxford, *C. nemoralis* began to lay eggs about the beginning of June. We have seen no trace of eggs at Fyfield Down before the end of May; in 1964 snails laying eggs (in loose soil turned up by moles) were noticed for the first time on 2 June. Wolda (1963) states that the laying period at his Groningen colony was from the end of May to the beginning of August. The first hatchings, therefore, should be at the end of June or beginning of July.

Juveniles hatched in July 1963 and reared under laboratory conditions by Dr M. A. Carter were only 5 to 7 mm in size on 29 October 1963, and in the wild would then hibernate without further growth until spring. Figure 8 gives the sizes of all juveniles taken by us on each sampling occasion from 18 June 1962 onwards. The 1963 data give a clear separation of generations and it can be seen that the juveniles forming the peak for lower shell size on 18 July 1963 are too large to have been hatched in 1963; they must be of the 1962 class. The growth of this class can be followed through the rest of 1963 and the first half of 1964 until they became adult from 2 June to about mid-August of that year. This means that these snails were already 2 years old when forming their lips. In 1964 the separation of generations is less clear but a lower peak of size, of which there is some indication on 14 October 1963, can be seen from 2 June onwards, rapidly becoming the dominant peak. One minute juvenile seen on 16 July 1964 and a few at the end of the season belong to the 1964 class, as presumably do a very few at the lower limits of the distributions on 3 and 16 August.

In 1962 the situation is far less clear, partly from a lack of material in July and August because of unsuitable weather, and partly from the similarity between the samples collected on 18 June, 14 September and 12 October, unlike what was found in 1963 and 1964. However, the upper peak on 2 June 1964, which is similar to that on 18 June 1962, is of animals attaining maturity, and among the large number of predated shells picked up in early July 1962 there is a proportion of shells just become adult which can only be from the upper size-classes represented in the 18 June 1962 samples. It seems therefore that the September and October 1962 samples are not of individuals from June 1962 which have not grown during the summer but of a 1961 generation, not clearly represented in the inadequate samples of July and August 1962. It will be noticed that there are differences in modal size in 1963 and 1964 both between animals becoming mature and between those in the first samples of each year. Size might be expected to vary phenotypically in a cold-blooded animal; and if we assume, on the contrary, that the size on reaching maturity is constant enough to be useful in recognizing juveniles about to become mature, the assumption is contradicted by a comparison of the maturing classes in 1963 and 1964. Moreover, it would imply that if 1963 is taken as a standard year, then in 1962 the juveniles showed no growth through the active season and there was either an entire

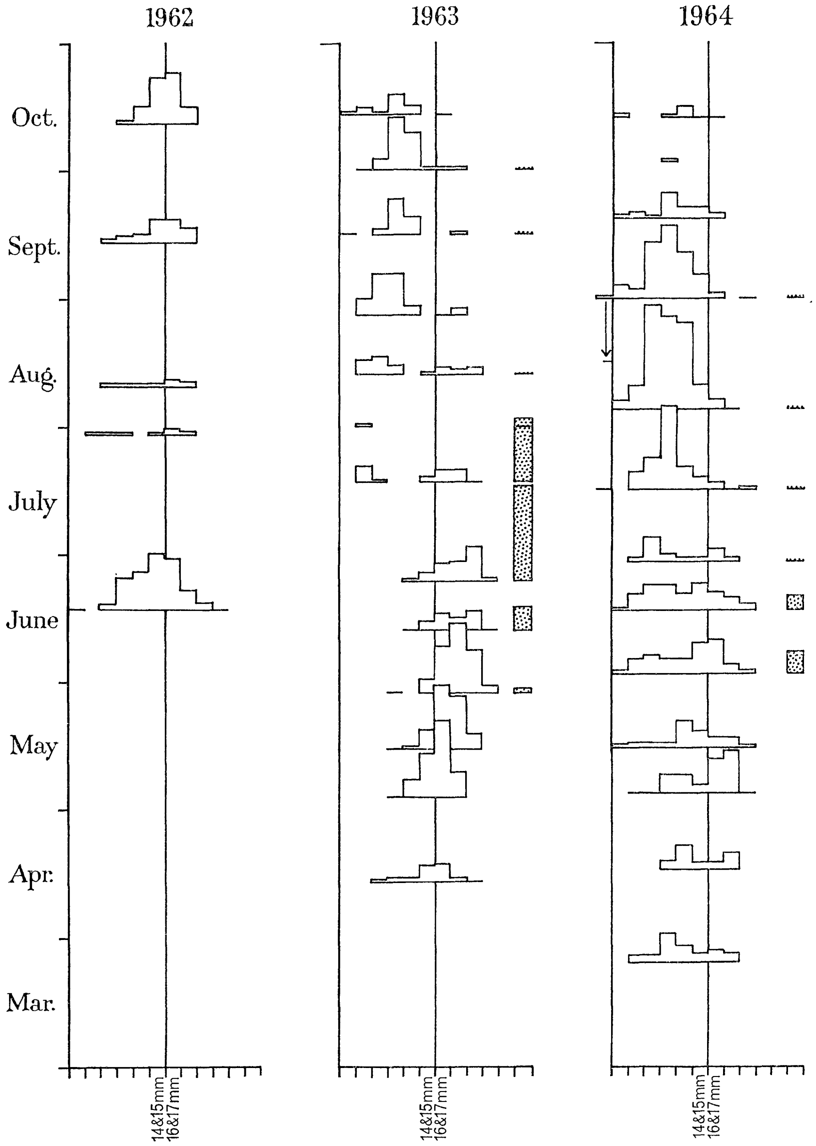


FIGURE 8. Size distributions of samples of juveniles. Juveniles grouped into 2 mm size-groups beginning at the left-hand end of each year-column with those of 4 and 5 mm, ending on the right with those of 26 and 27 mm. Size taken is maximum breadth of the shell. A reference line is drawn down each column between the groups of 14 and 15 mm, and 16 and 17 mm. Dotted columns, frequency of newly adult shells (with last part of body whorl and lip still not fully thickened) irrespective of actual size. Ordinate, time in months. The distance showing 1 month also shows a frequency of 80. One histogram (Aug. 1964) is displaced for clarity; the arrow shows the extent of displacement.

absence of the 1961 class, or only a very few of this class developed and these grew so rapidly in 1962 as to merge with the 1962 class. There remains the possibility that, since the minute juveniles are so rarely seen in the wild, they live buried in the soil and may hardly grow at all for a year. Wolda's data (1963, p. 455) for an artificial colony started out of doors at a definite date rule out this possibility, which is also not supported by observations on the hatching and growth of young both in rearing boxes indoors and in pot cultures out of doors at Oxford. Most of the evidence in figure 8, then, points definitely to an interval between hatching and lip-completion of 2 years, and the remainder is consonant with this period, which is also shown by Wolda's data from Groningen.

As shown in § 2·5, the half-life after lip completion does not differ greatly from one year. If the incidence of egg laying is equal in all age-classes after lip completion, then the generation interval is 3 years. If, as seems the case, the majority of snails with newly completed lips wait until the next active season before laying, this estimate must be extended by about 11 months, and if Wolda's findings are accepted as relevant in the wild, by a further half-year.

Our estimate of survival rate after lip completion is of course a mean of the survival rates of various age-classes according to the numbers in them. As yet we have not sufficient information to determine the variation of survival rate with age. With a mean adult survival of about 50% per year in a species which often survives for several years in captivity, it is unlikely that members of a wild population will survive to senility. An absence of senile members seems characteristic of wild as against laboratory populations generally (Lack 1954).

It seems then that the generation interval in our population must be close to 4 years at the least. Disturbing factors such as new adults laying fewer eggs than older ones might well add to this but we have no information on them. If, however, the survival rate is closer to 0·7 (§ 2·6), the generation interval is nearer to 5 years.

(2·8) *Predation*

We have direct evidence of four types of predator acting on Fyfield Down, namely thrushes, 'rodents', a beetle and a snail. Potential predators which might consume snails whole and leave no evidence are common in the district, especially partridges and pheasants, but we have no information on their activities.

One specimen of the snail *Oxychilus cellarius* (Müller) recorded as an egg-predator by Wolda (1963) was seen eating a *nemoralis* egg on 2 June 1964, on Fyfield Down. One *Phosphuga atrata* (L.) (Coleoptera, Silphidae) was found on 12 October 1962 in quarter 2 with its head buried in a juvenile brown unbanded. One other specimen was seen on 2 June 1964, This beetle is specialized for predating live snails. Nothing is known of its population size and activity in the wild. From its size it would seem to be a predator of juveniles rather than adults.

Predated shells picked up on 20 March 1964 in the nettlepatches and elsewhere, a good number of which must have been predated after 6 March 1964, show the signs of rodent predation as described by Morris (1954). Many were scattered in the nettlepatches, which also points to rodent rather than thrush predation. It is not possible to distinguish between predation by lagomorphs and by the larger true rodents. Although hares have been common on Fyfield Down during the first 3 years of this study at least, and rabbits have been seen in the nettlepatches occasionally, this is the only evidence we have found for rodent-type predation.

By far the majority of predated shells on Fyfield Down are clearly thrush-broken, almost all on sarsen boulders. In 1962 we saw large numbers of thrushes, sometimes up to 30 or 40, close to or occasionally in our working area. These were mainly missel thrushes (*Turdus viscivorus*) with a few song thrushes (*T. philomelos*). On relative numbers of the two species it seems that missel thrushes must be predating snails but we have no direct observations on their cracking the shells as do song thrushes. The hard winter of 1962/3 seems to have destroyed or driven away the thrushes that were so common in 1962, and since then we have had only a very occasional sight of any thrush species except for a few fieldfares (*Turdus pilaris*) in the late winter and early spring.

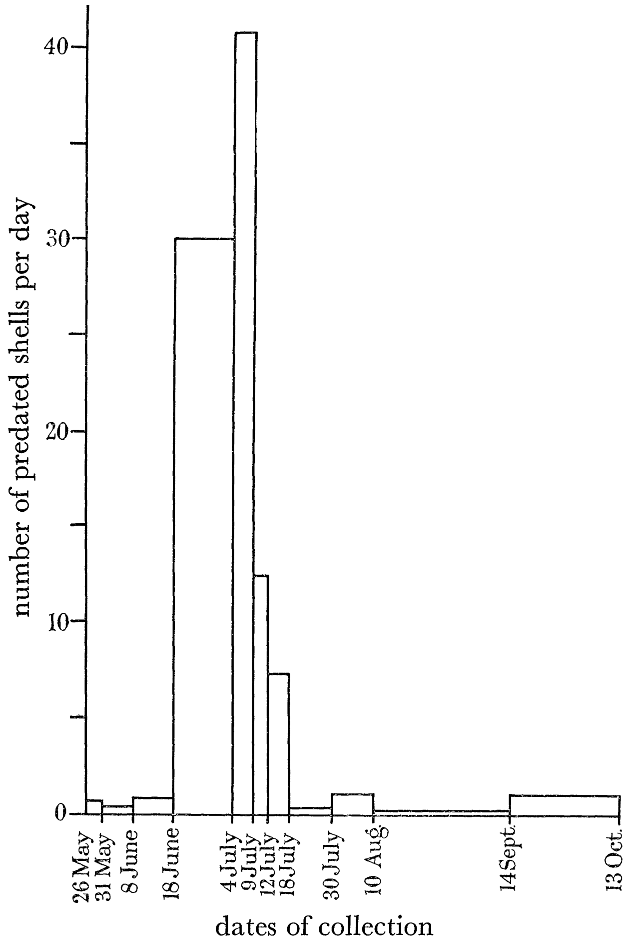


FIGURE 9. Thrush predation, March–October 1962. The area of each column gives the total number of predated shells for each period between collections.

Figure 9 shows the incidence of thrush predation for the period March 1962 to October 1962, giving all predated shells found inside our area (and the few marked predateds found outside). There is a clear peak in June–July. Few were found on 30 January 1963 because of the extensive snow cover and those obtained on 8 March 1963 are most likely snails predated at the end of December before the snow became thick everywhere. The incidence of predation has been discussed by Goodhart (1958), Davies & Snow (1965) and Wolda (1963); snails appear to be a reserve food taken when others are not available. The summer peak in figure 9 is almost certainly associated with unavailability of earthworms during dry weather; and the winter predation with a general lack of other foods in very cold weather.

Table 7. Predation pressure and snail densities, summer predation 1962

division	density per m²	marked localizable shells put out to and including 4 July 1962	nos. predated to and including 18 July 1962	% predated
Q1	0·30	219	7	3·2
Q2	0·83	528	21	4·0
Q3	0·83	358	41	11·5
Q4	0·79	292	21	7·2
		1397	90	
NP1	11·80	459	65	14·2
NP2	7·21	519	106	20·4
		978	171	

(Densities in 1963 are used, as this is the first year for which results based on year-samples are available, and inspection of figure 4 shows that population sizes were similar in 1962 and 1963.)

Table 8. Total numbers of live adult snails and percentage of population in each division taken by us during the main period of thrush predation, as an indication of relative availability above ground of the snails

	Q1	Q2	Q3	Q4	NP1	NP2
31 May 1962	13	50	43	38	128	153
%	2·9	7·7	7·8	9·5	25·6	25·5
18 June 1962	58	115	63	53	79	116
%	12·9	17·7	11·5	13·2	15·8	19·3
30 July 1962	11	10	3	4	51	80
%	2·4	1·5	0·5	1·0	10·2	13·3

The nettlepatches and quarters differ in both vegetation and density of the snail populations. The question arises of the thrushes' reaction to these two variables. If it were as easy to search in nettlepatches as in downland grass and if the snails were equally available above ground in both, one might expect that the far higher densities in the nettlepatches would be attractive, perhaps disproportionately so, to the predators. Taking the summer peak of predation first, the percentage predation and the densities in numbers of snails per square metre are given in table 7. Taking the means for quarters 2, 3 and 4 (since quarter 1 has only a few predateds) the expected percentage predation for the nettlepatches if predation were directly proportional to density would be about 85%. The high densities in the nettlepatches are therefore associated with disproportionately *low* percentage predation. This might be either because the snails are proportionally less available above ground in the nettlepatches or because the thrushes find it less attractive for some reason to search in them. Our experience in collecting suggests strongly that in general a higher proportion of the nettlepatch populations can be found above ground than of the populations in the quarters, as is shown by figures for our own collecting during the period of maximum predation by the thrushes, in Table 8. It would seem then, that the thrushes are not hampered by unavailability of the snails above ground but by some other difficulty, when predating in the nettlepatches. It might perhaps be expected that they would avoid dense beds of nettles and other herbage inside which there is little room to manoeuvre. If the predation is only at the edge of each patch, then its local intensity could be very high.

TABLE 9. INCIDENCE OF THRUSH PREDATION DURING THE PERIOD OF MAXIMUM PREDATION, 1962

division	predation to and including 4 July 1962	predation 5 July to 18 July 1962
Q1	4	3
Q2	11	10
Q3	20	21
Q4	15	6
NP1	51	14
NP2	54	52

It is remarkable that the incidence of predation varied sharply during the period of maximum predation in nettlepatch 1 (table 9). This might be accounted for if thrushes were nesting in the bushes nearby at the junction of quarters 2 and 3. Morris (1954) has noticed a clear avoidance of the immediate vicinity of an occupied nest, presumably because the noise of shell-breaking might attract the attention of nest predators which might then follow the thrush to the nest. However, an analysis of the incidence of predated shells on particular sarsens shows a general shift towards the central baulk between quarters 3 and 4, not merely a movement away from the bushes. Other such shifts occurred in predation of shells from nettlepatch 2 and quarter 4, in no constant direction. The thrushes seem inconstant in their use of anvils when, as here, there is considerable choice. Why they nearly stopped predating in nettlepatch 1, in the second half of the main period, is unexplained.

The thrushes on the open downs being very wary and having an excellent view of anyone approaching, no direct observation of their behaviour was possible. Observation of captive thrushes in aviaries (A. J. C. and Professor P. M. Sheppard) suggests that predation is visual only and that they will always stand on firm objects in preference to vegetation, including leaf litter. They will approach clumps of long grass from the side and peer in but make no attempt to search them or part the grass. It is likely, therefore, that in the quarters the thrushes look around for snails, often from the vantage point of a sarsen, and frequently see them part-obscured by grass. At the edge of the nettlepatches, however, they are likely to see clearly snails sitting on stems or leaves close to them; others further in and more obscured they would not attempt to reach. Consequently, the intensity of selection is likely to be greater in the grassy areas than in the nettlepatches, as we find.

In contrast to the summer peak, that in the winter is almost confined to the nettlepatches (64 localizable marked shells from the nettlepatches, four from the quarters). This is hardly surprising; in the depths of winter the nettlepatches offer quite large areas of comparatively bare ground with loose nettle litter and soft soil easily disturbed by the thrushes. The snails are present in abundance, just below the soil surface; hibernating

C. nemoralis often rest with the mouth upwards so that when the thin covering layer of soil is disturbed, the white winter epiphragm is conspicuous. In the open downland, however, the grass remains as a thick rough cover with dense root-mats, hard to dig into.

3. The polymorphism and selection

(3·1) *Selection of colour morphs by us and thrushes*

It was shown in § 2·2 that we ourselves in taking samples of live snails were exerting selection in the quarters but not significantly in the nettlepatches. The only season in which we have extensive thrush predation in the summer was that of 1962 (§ 2·8). The hard winter of 1962/3, while not apparently affecting the populations of adult snails, killed or drove away the thrushes and the total summer thrush predation in our area in 1963 was one shell and in 1964 four as against over 800 in the summer of 1962. Even in 1962 the totals of marked and localizable shells (i.e. referable to the nettlepatches or the quarters) when divided between nettlepatches and quarters and sorted into yellows, pinks and browns, would not be sufficient to produce a significant χ^2 when compared with the marked snails put out, even if considerable selection were being exerted by the thrushes. Table 10 gives the marked localizable shells put out and the recoveries as predated shells. Combining the quarters and nettlepatches gives too few predateds for a useful comparison —e.g. the quarters 2, 3 and 4 combined give on comparison with what is expected even if the thrushes are exerting the same biases as ourselves, $\chi^2_2 = 2{\cdot}35$, $P = 0{\cdot}3$. It is possible, however, to use the unmarked and unlocalizable predated shells as well, and some indication can then be obtained. The thrush-broken shells are found on or close to the anvils, often in little heaps, and with their jagged outlines and considerable display of the pale inner surface of the shell, are conspicuous; there is no reason to believe that we are selecting them at all, and an experiment by Arnold (1966) designed to test his own selection at anvils in beechwood showed no selection.

Table 10. Releases of marked localizable shells, and recoveries as predated shells. Releases to and including 4 July 1962, predateds to and including 18 July 1962

	releases			recoveries of predateds		
	yellow	pink	brown	yellow	pink	brown
Q1	84	59	77	—	1	6
Q2	163	142	227	8	6	7
Q3	111	75	172	11	9	21
Q4	104	51	138	9	3	9
NP1	158	93	205	22	13	30
NP2	168	127	228	34	31	41

There is no sign of any change in morph proportions in the predated shells during the period of predation (χ^2 with 4 degrees of freedom 2·5, P between 0·7 and 0·5) and they can therefore be lumped for the season. The proportions of marked and localizable shells in the predateds taken by the thrushes in the quarters and nettlepatches respectively are $\frac{101}{275}$ and $\frac{172}{273}$, i.e. 37 and 63 %. Our totals for live shells collected in 1962 are:

	Y	P	B	totals
quarters 2, 3 and 4	671	457	871	1999
nettlepatches	556	363	678	1597

Our estimate of our own selection for 1962, 1963 and 1964 is given in § 2·2 (iv). Correcting our observed totals for these biases and reducing to percentages, our estimate for the morph proportions in the live adult populations is

	Y	P	B
quarters 2, 3 and 4	28·6	18·8	52·6
nettlepatches	33·7	22·0	44·3

From recaptures on 18 June 1962, the last date of observation before the period of intense predation, we have an estimate of the proportions of marked to unmarked live shells in the different areas (table 11). The marked and localizable predated shells can be distributed directly to quarters and nettlepatches. If the thrushes were not selecting, the marked but unlocalizable predated shells should be distributed between the quarters and nettlepatches in the proportions in which they were predating marked localizables in these two habitats, i.e. 37 and 63 % respectively. The unmarked predated shells should be divided between quarters and nettlepatches in the proportions of unmarked shells in these habitats, i.e. 44·4 and 21·0 % respectively, but also in the proportions that the thrushes predate these habitats; the final distribution proportions, therefore, are these proportions multiplied together, i.e. 55·1 and 44·9 % for quarters and nettlepatches respectively. The assignment of predated shells is given in table 12.

Table 11. Proportions of marked to unmarked live shells in each division, from our captures of 18 July 1962

division	unmarked	marked	total	% marked
Q1	27	31	58	53
Q2	44	71	115	62
Q3	30	32	62	52
Q4	27	26	53	49
all Q's	128	160	288	55·6
NP1	17	62	79	78
NP2	24	92	116	79
both NP's	41	154	195	79·0

Table 12. Assignment of predated shells, beginning of predation 1962 to 13 October 1962

	Y	P	B	total
quarters localizable	31	20	50	101
other marked	19	14	25	58
unmarked	74	57	106	237
	124	91	181	396
nettlepatches localizable	56	44	72	172
other marked	32	25	42	99
unmarked	61	47	86	194
	149	116	200	465

From our estimates of the morph proportions in the quarters and nettlepatches we can then calculate the expected predateds on the assumption of no selection, from the totals just given in table 12. For the quarters we find

	Y	P	B	
observed	124	91	181	396
expected	113·3	74·4	208·3	396
discrepancy	+10·7	+16·6	−27·3	—

χ^2 2 degrees 8·29, *P* between 0·02 and 0·01.

and for the nettlepatches

	Y	P	B	
observed	149	116	200	465
expected	156·7	102·3	206·0	465
discrepancy	−7·7	+13·7	−6·0	—

χ^2 2 degrees 2·38, P between 0·4 and 0·3.

As with our own bias, therefore, there is a significant discrepancy in the quarters and not in the nettlepatches; moreover, in the quarters the signs of the discrepancies for each morph are the same as ours. (A direct comparison of marked and localizable predateds with the marked live shells put out in the quarters and available for predation is insignificant, as would be expected if the thrushes are exerting only our biases.)

It is certain, then, that we are taking biased samples of live snails and likely that the thrushes are also doing so with similar biases to ours. We have used of necessity rather different modes of searching in the nettlepatches and the quarters. We have searched intensively through the nettlepatches, bending the vegetation from side to side, seeing many snails but finding many more because they fall out of disturbed vegetation or are picked up off the ground below. In the quarters we have similarly searched the tiny areas of nettles, looked carefully at the broad-leaved plants, and have felt along the edges of the boulders; but because of the areas involved we have walked over most of the grass looking for snails, although often feeling around thick tussocks. The naïve visual element in our searching has certainly been much greater in the quarters than in the nettlepatches.

(3·2) *Changes in colour-morph frequencies* 1962 *to* 1966

Estimates of the frequencies of colour morphs can be obtained in two ways: (i) by calculation from our samples, which are affected by our own biases in collection and any differential morph activity; (ii) by comparing population size estimates for the colour classes; these are free from our biases in collection and from any due to differential activity, but have the disadvantages that no estimates can be given for the first and last sampling occasions by the Jolly method or for the first only by the Fisher–Ford method. Using year classes, the variances as percentages of the frequencies by the two methods are very similar. There is no reason to think that our biases have changed from year to year, and the backgrounds on which the snails were collected have remained constant as far as we can see throughout the working period. We can therefore use the frequencies calculated direct from our samples without correction for bias as comparative values to look for any changes in the period 1962 to 1965.

Figure 10 shows the frequencies by direct calculation for each of our divisions. Quarter 1 stands out immediately as having a far higher proportion of yellows and a lower proportion of browns than any other division. (The high variance is a reflexion of low population and therefore sample size). Quarters 2, 3 and 4 are similar to each other and show an apparent decrease in proportion of browns with time; nettlepatch 1 and 2 also agree closely with each other but show no indication of a trend. The data for quarters 2, 3 and 4 combined and for the combined nettlepatches are shown in figure 11.

It is immediately noticeable that the stability of frequencies in the nettlepatches contrasts with the highly significant decrease in browns between 1962 and 1964 in the three combined quarters, after which there is apparent stability. Taking the last two years together, there is a significant difference in the frequencies of brown in the quarters and the nettlepatches (χ^2 with 1 degree 7·22, *P* less than 0·01). Both pinks and yellows in the combined quarters have some signs of the increase compensatory to the decrease in browns.

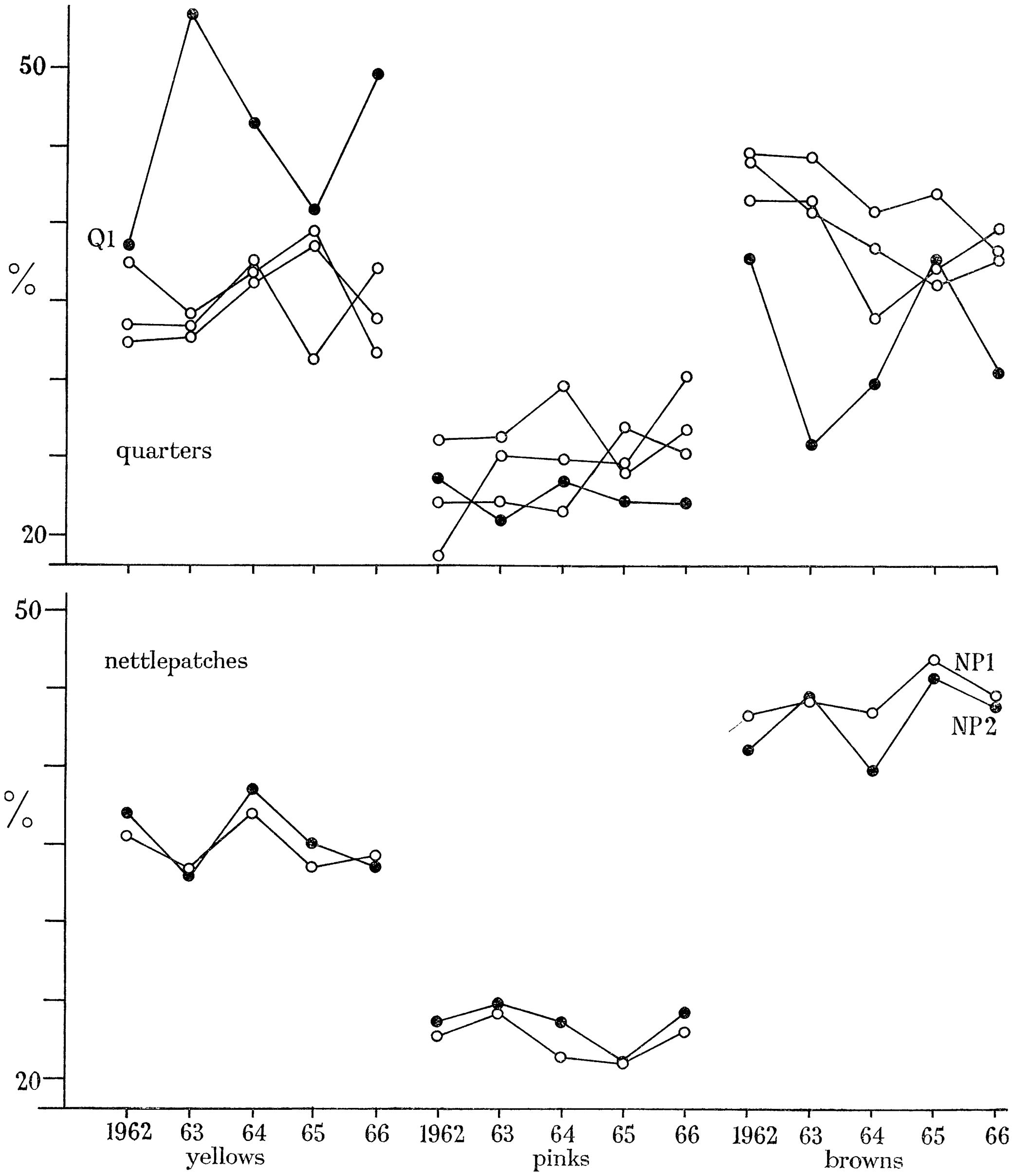


FIGURE 10. Percentage colour morphs for each division, for all captures and recaptures in each year. Black dots; upper diagram, quarter 1, lower diagram nettlepatch 2.

Thrushes appear to have been taking yellows and pinks preferentially (§ 3·1) and missing dark browns in the quarters but not in the nettlepatches, as we did ourselves. Thrush predation was strong in 1962, stopped abruptly because of the hard winter of 1962/3 and has not effectively been resumed. The incidence of morph frequency changes (in the quarters, not in the nettlepatches) and the direction are in agreement with what would be expected if thrushes were exerting selection in favour of browns on the grassland but not in the nettlepatches, this selection was removed, and the frequency of brown in the grassland forthwith began to decrease. Furthermore, our bias in collection is the same as the thrushes' in direction and general magnitude; indeed there is excellent agreement between the predated sample taken by the thrushes and the live samples taken about the same time by ourselves. We too are missing browns on the grassland by about 20 %, i.e. the proportion of browns in all colours in our recaptures is 20 % less than the percentage of browns in the sample released.

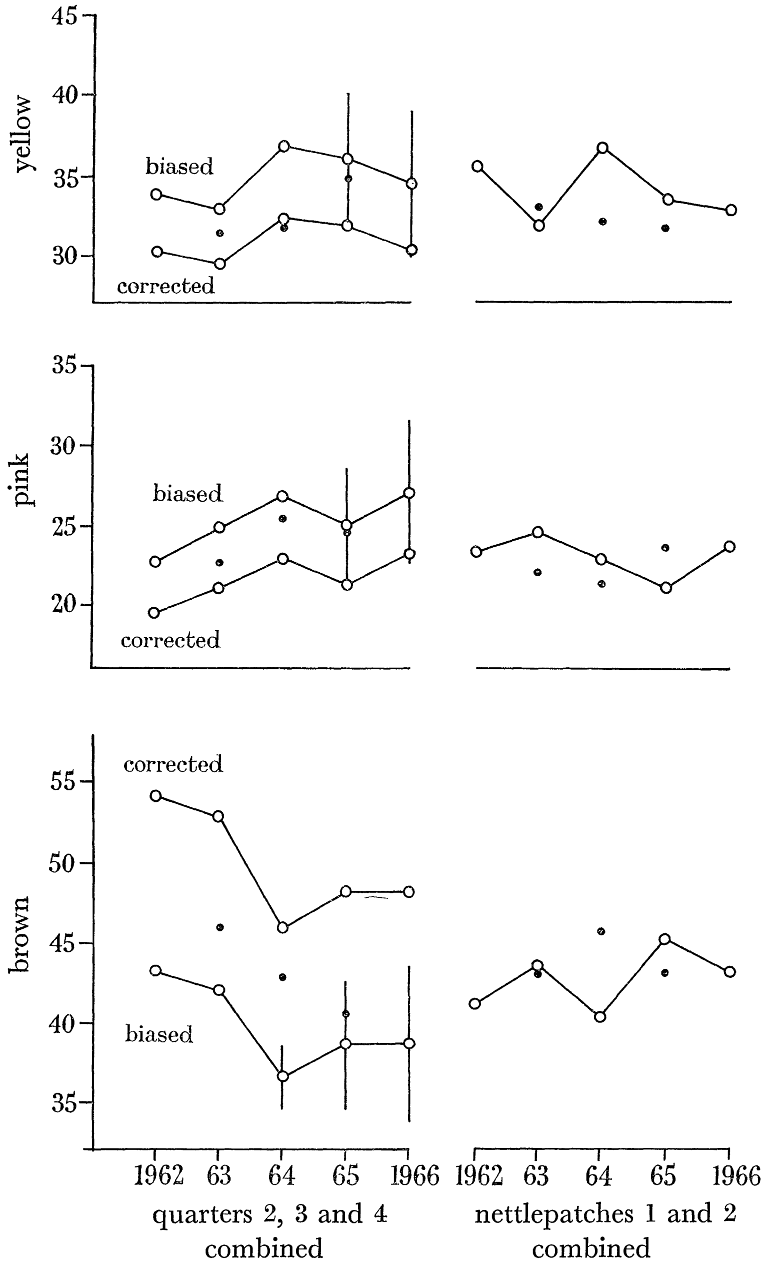


FIGURE 11. Percentage colour morphs, by year samples, for the quarters combined (except quarter 1) and the nettlepatches combined, both uncorrected and corrected in the quarters for our bias in collecting. Circles, percentage values direct from year-samples; black dots, percentage values calculated from independent estimates (Jolly's method) of population sizes of each colour class taken separately. Vertical lines show twice the standard error on each side of the circle, and for clarity, are given for the largest sample and for the two smallest sample-sizes in each colour.

If we correct the morph frequencies in our samples by our own bias of +12% for yellows, +16% for pinks and —20% for browns we get the time series shown in figure 11, from which it is seen that the decrease in the browns is bringing the frequency of browns in the combined quarters towards that in the nettlepatches, which shows no comparable signs of overall change (and needs no correction for bias). If as we believe the frequency in the nettlepatches has been only slightly disturbed by visual selection and is in equilibrium with whatever other selective forces are acting in the district generally to produce the area effects, we would expect the frequency of brown in the quarters to move towards the general equilibrium frequency for the district when visual selection stopped.

Values for morph frequencies calculated from morph population sizes by Jolly's method for 1963, 1964 and 1965 are also shown in figure 11. With only three points one cannot say much but those for quarters 2, 3 and 4 combined seem to support the results obtained from our samples. Almost all fall between the uncorrected and corrected values; this may perhaps suggest that our values for our biases are too great. Those in the nettlepatches agree well with our estimates. However, as the errors for the frequencies derived from Jolly estimates are large, it is necessary to wait until more values can be obtained before reaching any conclusions.

If our tentative conclusions about the similarity of visual selection by thrushes and by ourselves are correct, the selective differential of pinks and yellows combined, relative to browns, is about −27%. The thrushes predated up to 18 July 1962 in the quarters 83 shells out of 1178 put out to 4 July 1962, about 7% (table 7). The selection they exerted to 4 July 1962 was therefore about 2%, It is clear that the amount and rate of change in the frequency of browns observed in our (biased) samples from 1963 to 1965 is much too great to be explained merely by the cessation of 2% selection favouring them, and would require about 8% per year. However, we have no information on the rate of predation or selection of small juveniles by thrushes in 1962 nor of any rates before 1962, and the incidence and direction of change are to be expected from a cessation of selection by the thrushes.

4. Discussion

Even from the comparatively short period covered by this paper, several important points emerge.

(i) The remarkable differences in density, which have been maintained throughout the period, between the populations in the nettlepatches and those in the surrounding downland grass.

(ii) The difference in morph frequencies between quarter 1 and the rest, also apparently maintained (figure 10).

(iii) The differences in thrush predation régime from winter to summer between the nettlepatches and the quarters, with winter predation concentrated on the nettlepatches.

(iv) The difference in intensity of summer thrush predation in relation to density of population, being disproportionately light in the nettlepatches.

(v) The differences in visual selection shown both by us and apparently by the thrushes in relation to habitat, selection being strong in quarters 2, 3 and 4 and weak or absent in the nettlepatches. (The data for quarter 1 are too scanty for any conclusion.)

All the above points except (ii) show how different ecologically and genetically are the consequences for the snail populations of living in downland grass as contrasted with dense nettles. Previous work (e.g. Cain & Sheppard 1954; Cain & Currey 1963*a*; Currey *et al.* 1964) has shown the importance of the difference in background provided by woodland and non-woodland habitats for visual selection, but the more general effects of the difference, at first sight so trivial, between the two types of herbaceous habitat, tussocky grass and nettles, have not been appreciated.

(vi) The maintenance of differences in morph frequency and density over very short distances in spite of our disturbances of the snails by rescattering them in their divisions.

This suggests that the structure of the populations involves extreme localization. If a snail in the grassland needs primarily a place to bury itself which is within reach of food during an ordinary night's activity and such places are scattered over the grassland (as seems likely) it is possible that when we collect a sample, we leave a number of individual niches vacant and, on rescattering, the snails move from where they have landed only sufficiently to reinstate themselves in a suitable place. Since we have searched over each division and taken all the snails we found, and returned the same number (since none died during absence from the area) at random over the same division, the speed of settling down spatially may be high, even though the disturbed snails may well remain underground for longer than usual once they have found a place.

(vii) The constancy of values for percentage migration over a period of years.

In view of our disturbance of the populations in 1962, 1963 and 1964, this is a remarkable finding. It is hardly explicable by the snails returning rapidly each to a restricted area unless the previous pattern of individual distribution was partly restored after each disturbance.

(viii) The significant change in frequency of browns in the quarters but not in the nettlepatches.

The change so far (figure 11) is from about 43·0 to 38·5% in our biased samples, i.e. from about 53·0 to 48·0% when the bias is corrected. The mean value in the two nettlepatches is about 43·0%. As already pointed out, both the incidence of the change (on brown in the quarters) and the direction are as expected if it were caused by cessation of the thrush selection. The rate seems to be too high, but we have no information on the maximum predation by thrushes on adults, nor on any predation on juveniles. If the thrushes do not return in numbers, the percentage should eventually fall in the quarters to that of the nettlepatches; if they do, it should return to its value for 1962 or higher.

(ix) The unintentional experiment made by us on visual selection of snails in downland grass seeems to show that dark browns are inconspicuous on this background; the thrushes apparently agree.

The excellent agreement between samples taken by the thrushes and ourselves is perhaps not surprising; in the Oxford district where Sheppard (1951) was able to demonstrate visual selection in Wytham Woods (Cain & Sheppard 1954), and elsewhere (Cain & Currey 1963*a*; Currey *et al.* 1964), the correspondence between morph frequencies and type of background, both in shell colour and banding, is what we would expect from our own appreciation of the backgrounds and the snails, and although no work seems to have been done on thrushes, it is clear that various species of bird have colour vision like that of the higher primates (Walls 1942). What is surprising is the nature of the selection found at Fyfield Down, namely that dark browns are frequently overlooked and there is little difference between yellows and pinks. As already described, the yellows look very green, the pinks a dirty straw colour. In the downland grass at all times of the year there are a large number of dead stems and blades, so that the area at a little distance has a very brownish look, except only in the few patches of very short turf which is kept closely cropped and green by the sheep (and rabbits formerly). Snails of any colour which are seen crawling out on top of the vegetation are all fairly conspicuous; those of which only the shell is seen slightly or largely covered over by grass blades and stems, are the ones liable to selection, and there is probably little to choose between a green patch and a straw-coloured one glimpsed between grasses of mixed green and straw-colour. Only the reds are clearly more conspicuous, and there are few of them in these populations. If the backgrounds are considered merely as expanses of an average colour, the apparent crypsis of the dark browns is inexplicable; but of course among the tussocky grass there are numerous dark places, deep in the tussocks or down between them; any attempt to paint a realistic picture of the area without including tones as deep as those of dark-brown shells would be a failure. Scoring with a colour atlas suggests that to match the deep shadow between tussocks colour is less important than tone, and the dark browns are better than either the pinks or yellows. Cain (1953) compared shells on top of handfuls of deep green grass; his plate 1 suggests that dark browns are the best match on tone for interstices. Nevertheless, it is difficult to believe that dark browns will be more cryptic generally on this type of background than yellows and pinks with dark bodies.

If there are differences of behaviour between the different colour morphs, and our selection is partly or wholly due not to our own discrimination but to a differential availability of morphs: if browns, for example, were to skulk more than the other colours: the same effect would follow as from their greater crypsis. As we cannot partition the effect we have found between differential discrimination by predators (including ourselves) and differential exposure to predators by the different morphs, a study of the behaviour of *Cepaea* is desirable.

An unfortunate consequence of our bias is that we can make no use of morph frequencies in the juveniles we have seen as against the adults. Differences of morph frequency have been found, but they are in the direction expected if we miss juveniles more readily than adults, and therefore exercise stronger selection on them, which is very likely.

The effects of the hard winter of 1962/3 on birds are discussed by Dobinson & Richards (1964), who include notes on previous hard winters. They give references for statements that the 1962/3 winter was the coldest recorded in central and southern England since 1740, and possibly the snowiest for 150 years. Frosts were worst on the Berkshire/Wiltshire border (close to our area). High winds drifted the snow, which we saw covering the area, in places several feet deep. This was probably fortunate for the snails; at Oxford in places where the snow had been swept away, water pipes well below the surface were frozen solid (J. A. L. Cooke, personal communication). Dobinson & Richards, working from reports by bird observers scattered over the country, and from the results of analysis of British Trust for Ornithology nest record cards, state that the song thrush 'clearly lost a considerable proportion of its breeding population'. Seven reports were of its local extermination, of which five were in the west (Cornwall 1, Pembrokeshire 1, Somerset 2, Breconshire 1). The missel thrush they considered to have been 'generally reduced in its breeding strength but nowhere very severely hit; possibly suffered more in the western half of England than in the eastern . . .'. It certainly disappeared for some years from our immediate area.

They list as previous hard winters 1916/17 (very like 1962/3), 1928/29 (prolonged bad weather, not as severe as 1962/3), 1939/40 (very severe spell lasting all January), and 1946/47 (late start in February but lasting long). If, as is likely, it takes several years after each hard winter before thrushes recolonize the bleaker areas, then the mean visual selection is likely to be notably less on the Marlborough Downs than in the Oxford district in any 50-year period.

If no other influence but that of visual selection were acting on the polymorphism in *C. nemoralis*, one would expect from the present results that dark browns would be a common morph in almost every kind of habitat, since most of them offer a good stand of vegetation at ground level, with consequent shadows, and those that do not (leaf-litter in thick woodland) are shaded anyway. Brown, however, is a sporadic morph, restricted geographically, and probably affected by local climatic conditions (Cain & Currey 1963*a*; Carter, this volume). Its absence is frequently referable to causes other than visual selection.

(x) From figures 5 and 6 it is clear that there is little relation between population size and survival rate in the quarters, and in the nettlepatches there is an increase in survival rate with a falling population.

(xi) From figures 5, 6 and 11, there is no clear relation between morph frequency and population density. It is true that quarter 1 has the lowest density and a different morph frequency from any other division, but the nettlepatches, with very high densities, resemble in morph frequency quarters 2, 3 and 4 rather closely.

Apparently the factors which produce the principal differences in density in our area do not affect the polymorphism; or alternatively they do so only below a certain threshold density. No study on degree of polymorphism in relation to density which also allows for the disturbing influences of visual selection, area effects and migration is available for comparison.

Too little information is as yet available for detecting differential survival of morphs from the survival of individually known snails. Observation over several more years may increase it sufficiently. It is already obvious from the present work that to increase the samples by increasing the area covered is likely to lump populations heterogeneous for the very features being studied, and only an extension of time can increase our knowledge usefully.

Our work has shown what remarkable differences in ecology can exist between different parts of a continuous population of *C. nemoralis*, according to whether it is in nettlepatches or downland grass. These differences can have important consequences for the population genetics of each part. While samples taken considerable distances apart may be of use in showing overall trends of variation, as in our initial survey of the Marlborough Downs (Cain & Currey 1963*a*) or Lamotte's survey of France (Lamotte 1951) it is clear that studies as intensive as the present one will be necessary before a satisfactory interpretation of the morph frequency variation in *Cepaea* can be made.

We are deeply grateful to the Nature Conservancy for permission to work in the Fyfield Down area, and to Wardens Inigo Jones and N. King for personal encouragement, advice and help. Dr G. M. Jolly and Mr P. H. Leslie have given us much statistical help. We are thankful to Professor P. M. Sheppard, F.R.S., Dr R. W. Arnold, Dr L. M. Cook and others for criticizing this paper in draft, and to Dr R. W. Arnold for assistance with field-work. We thank the Director in Aerial Photography, University of Cambridge, for permission to reproduce as figure 12, plate 33 a photograph by Dr J. K. St Joseph. The greater part of this work was done as part of a programme of work on functional systematics supported by D.S.I.R. (now S.R.C.) to whom our grateful thanks are due.

Appendix 1. Methods of estimation of emigration

Method A

(i) For each division, for a particular year, find the whole number released N omitting those released on the last occasion in that year (which could not be recaptured within the year).

(ii) Find M, the total number recaptured at least once in that year, irrespective of which division they were found in. (Since the numbers seen migrating in any direction are small, they are lumped together at this point.)

(iii) Then N/M is the factor by which one multiplies the number actually seen immigrating into that division, to estimate the total numbers immigrating into that division—it is the catchability factor.

(iv) Consider in turn all the emigrants out of each division seen in each other division and multiply by the appropriate catchability factor.

For instance, if five emigrants from quarter 2 are seen in quarter 1, and N/M for quarter 1 is 1·5, then the estimated number of migrants from quarter 2 to quarter 1 is 7·5.

In this way the total emigrants into the other divisions can be calculated.

(v) Make appropriate corrections for the quarters because they will have migrants going outside the area of investigation. For instance, the emigration over the north-western side of quarter 4 is taken as equal to that over the south-eastern into quarter 3, the sides being equal in length and the habitat apparently uniform throughout. The migration out of the south-western edge of quarter 4 is into grassland only. That across the north-eastern is into grassland (quarter 1) and into nettles (nettlepatch 2).

If the estimated number of emigrants from quarter 4 to quarter 1 is x and the length of the border between quarter 1 and quarter 4 minus the length occupied by nettlepatch 2 is r, and the length of the south-western edge of quarter 4 is s, the estimated number migrating over the south-western border is xs/r.

(vi) Express the total emigration out of each division as a % of the total numbers released in that division.

Method B

Consider three sampling occasions 0, 1 and 2. Snails seen on both 0 and 2 can be divided into those seen also on 1, namely C_{012}, and those missed on 1, namely C_{0-2}. The fraction $C_{012}/(C_{0-2}+C_{012})$ is a measure of the catchability on occasion 1 which does not depend on any death rate (the rate for snails caught and those missed being taken as the same). This is the equivalent of M/N (not N/M) in method A. Take 0, 1 and 2 as year classes and proceed as for method A.

References

Arnold, R. W. 1966 Factors affecting gene-frequencies in British and Continental populations of *Cepaea*. D.Phil. Thesis, University of Oxford.

Cain, A. J. 1953 Visual selection by tone of *Cepaea nemoralis* (L.). *J. Conch.* **23**, 333–336.

Cain, A. J. 1965 Recent population studies on *Cepaea* at Oxford. *Proc. Ist Eur. Congr. Malac.* pp. 209–213.

Cain, A. J. & Currey, J. D. 1963*a* Area effects in *Cepaea*. *Phil. Trans.* B **246**, 1–81.

Cain, A. J. & Currey, J. D. 1963*b* Differences in interactions between selective forces acting in the wild on certain pleiotropic genes of *Cepaea*. *Nature, Lond.* **197**, 411–412.

Cain, A. J. & Currey, J. D. 1963*c* Area effects in *Cepaea* on the Larkhill Artillery Ranges, Salisbury Plain. *J. Linn. Soc. Lond.* (*Zool.*) **45**, 1–15.

Cain, A. J. & Currey, J. D. 1963*d* The causes of area effects. *Heredity* **18**, 467–471.

Cain, A. J. & Sheppard, P. M. 1950 Selection in the polymorphic land snail *Cepaea nemoralis*. *Heredity* **4**, 275–294.

Cain, A. J. & Sheppard, P. M. 1954 Natural selection in *Cepaea*. *Genetics* **39**, 89–116.

Cain, A. J., Sheppard, P. M. & King, J. M. B. 1968 The genetics of some morphs and varieties of *Cepaea nemoralis* (L.). *Phil. Trans.* B **253**, 383–396 (part I).

Carter, M. A. 1968 Area effects and visual selection in *Cepaea nemoralis* (L.) and *Cepaea hortensis*. *Phil. Trans.* B **253**, 397–446 (part II).

Clarke, B. C. & Murray, J. J. 1962*a* Changes of gene frequency in *Cepaea nemoralis* (L.). *Heredity* **17**, 445–465.

Clarke, B. C. & Murray, J. J. 1962*b* Changes of gene frequency in *Cepaea nemoralis* (L.): the estimation of selective values. *Heredity* **17**, 467–476.

Cook, L. M. 1967 The genetics of *Cepaea nemoralis*. *Heredity* **22**, 397–410.

Currey, J. D., Arnold, R. W. & Carter, M. A. 1964 Further examples of variation of populations of *Cepaea nemoralis* with habitat. *Evolution* **18**, 111–117.

Davies, P. W. & Snow D. W. 1965 Territory and food of the song thrush. *Br. Birds* **58**, 161–175.

Dobinson, H. M. & Richards, A. J. 1964 The effects of the severe winter of 1962/63 on birds in Britain. *Br. Birds* **57**, 373–434.

Fisher, R. A. 1946 *Statistical methods for research workers*. 10th ed. Edinburgh: Oliver and Boyd.

Fisher, R. A. & Ford, E. B. 1947 The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* L. *Heredity* **1**, 143–174.

Ford, E. B. 1945 *Butterflies*. London: Collins.

Goodhart, C. B. 1958 Thrush predation on the snail *Cepaea hortensis*. *J. Anim. Ecol.* **27**, 47–57.

Jolly, G. M. 1963 Estimation of population parameters from multiple recapture data with both death and dilution—deterministic model. *Biometrika* **50**, 113–127.

Jolly, G. M. 1965 Explicit estimates from capture–recapture data with both death and immigration —stochastic model. *Biometrika* **52**, 225–247.

Lack, D. 1946 *The life of the robin*. London: Witherby.

Lack, D. 1954 *The natural regulation of animal numbers*. Oxford: Clarendon Press.

Lamotte, M. 1951 Recherches sur le structure génétique des populations naturelles de *Cepaea nemoralis* (L.). *Bull. Biol. Fr. Belg.* (Suppl.) **35**, 1–239.

Leslie, P. H., Chitty, D. & Chitty, H. 1953 The estimation of population parameters from data obtained by means of the capture–recapture method. III. An example of the practical applications of the method. *Biometrika* **40**, 137–169.

Morris, D. 1954 The snail-eating behaviour of thrushes and blackbirds. *Br. Birds* **47**, 33–49.

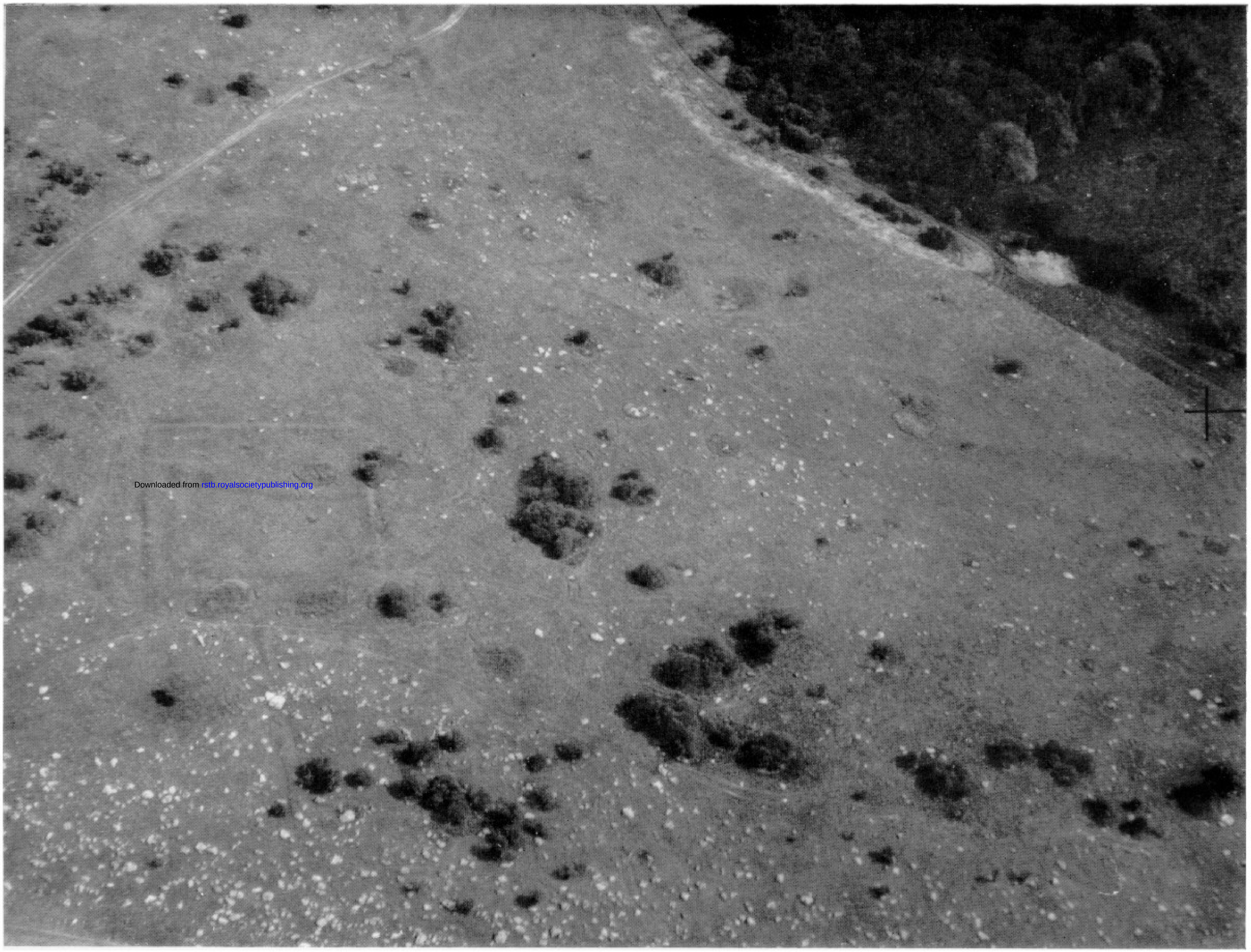
Murray, J. J. 1962 Factors affecting gene-frequencies in some populations of *Cepaea*. Thesis for D.Phil., University of Oxford.

Parr, M. J. 1965 A population study of a colony of imaginal *Ischnura elegans* (Van der Linden) (Odonata: Coenagriidae) at Dale, Pembrokeshire. *Field Studies* **2**, 237–282.

Sheppard, P. M. 1951 Fluctuations in the selective value of certain phenotypes in the polymorphic land snail *Cepaea nemoralis* (L.). *Heredity* **5**, 125–134.

Walls, G. L. 1942 *The vertebrate eye and its adaptive radiation*. Bloomfield Hills, Michigan: Cranbrook Press.

Wolda, H. 1963 Natural populations of the polymorphic landsnail *Cepaea nemoralis* (L.). *Arch. néerl. Zool.* **15**, 381–471.



Crown Copyright reserved.

FIGURE 12. Aerial view of part of Fyfield Down looking north-east. The rectangular arrangement of banks and ditches in part demarcates the area investigated. Woodland in the top right corner of the picture is part of Wroughton Copse (compare Cain & Currey 1963*a*, pl. 1) and *C. hortensis* occurs in the vegetation at its edge. White objects, sarsen boulders. The large, more or less rectangular enclosure contains quarters 1 and 2 (the smaller one adjoining it to the north-east is outside the area worked). The grey patches in the edge of the enclosure nearest the bottom of the picture are nettlepatches 1 and 2, and the bank projecting more or less at right-angles from the edge between the nettlepatches runs along the border between quarters 3 and 4. The lowest border of the area investigated runs across the group of largest sarsens, parallel to the bank containing the nettlepatches. Sarsens are clearly more abundant in quarters 3 and 4 than in 1 and 2.