A POSSIBLE CASE OF GENETIC DRIFT IN COLONIES OF THE LAND SNAIL *THEBA PISANA*

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1. INTRODUCTION

THE importance of random genetic drift, or sampling drift, in influencing the frequencies of different morphs in animal populations has been debated since Wright's (1931) early paper on the subject. After extensive work in France on the snail *Cepaea nemoralis* (L.), Lamotte (1952, 1959) concluded that although predation and environmental factors control to some extent the levels of the variable genes in the populations, there is in addition a considerable amount of variation which can be attributed to random factors.

Cain and Sheppard (1950, 1954) have shown that selection by predation depends on the plant cover in which the snails are found, and because of this predation differing habitats have populations with differing gene frequencies. They considered that the importance of random factors is negligible, and this view is supported by others (*e.g.* Cameron, 1969). The importance of environment has been acknowledged by many authors who have either shown a direct relationship between environmental factors and morph frequencies (*e.g.* Arnold, 1969), or suggested that unidentified changes of environment reacting with the genotypes of the snails determine the morph frequencies which are constant over large areas (Cain and Currey, 1963), or change within small distances (Wolda, 1969).

Goodhart (1963) has pointed out that " to prove that the Sewall Wright effect has been responsible for inter-colony variation, it must be shown that the effective breeding populations have been small enough for sampling errors to have been important, and that the observed variation is not due to differential environmental selection ". It is difficult in a natural habitat to ensure that there is no differential environmental selection, and virtually impossible to prove it, but in the present work specimens of *Theba pisana* were collected from a small area 800 m. × 80 m. and from sites occupied by only one species of plant, in order to reduce the variation of environmental factors to a minimum. Estimation of rate of movement of the snails and consideration of the terrain between colonies show that there is considerable isolation of colonies. Finally, calculations of the sizes of the populations indicate that random factors may indeed be very important in producing the considerable variations in morph frequencies that are found.

2. MATERIALS AND METHODS

Theba pisana (Müller) is a land snail which was first recorded in South Africa in 1881 (Barnard, 1951) and now occurs in great abundance in local

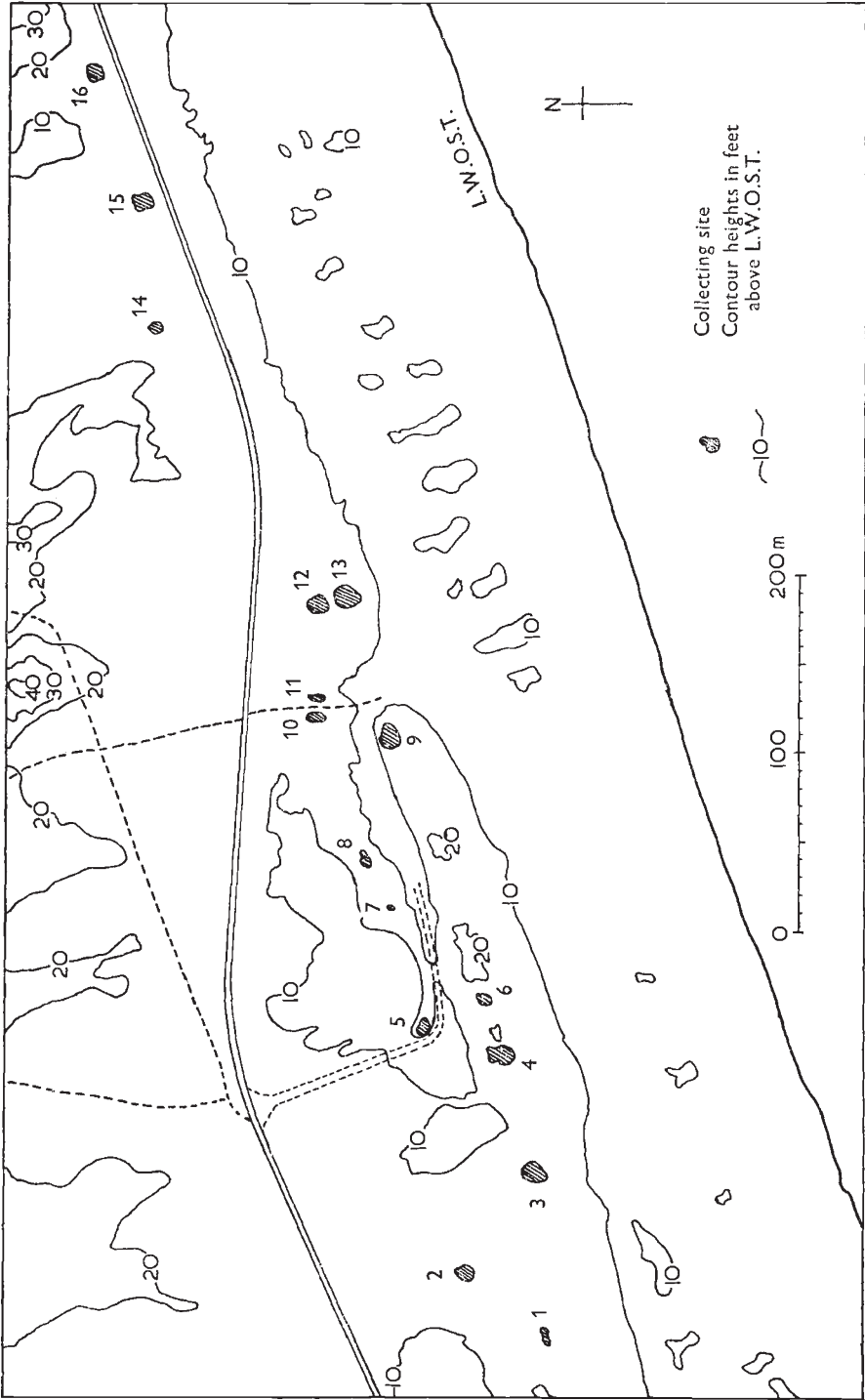* Present address: Cauldron Barn Farm, Swanage, Dorset.
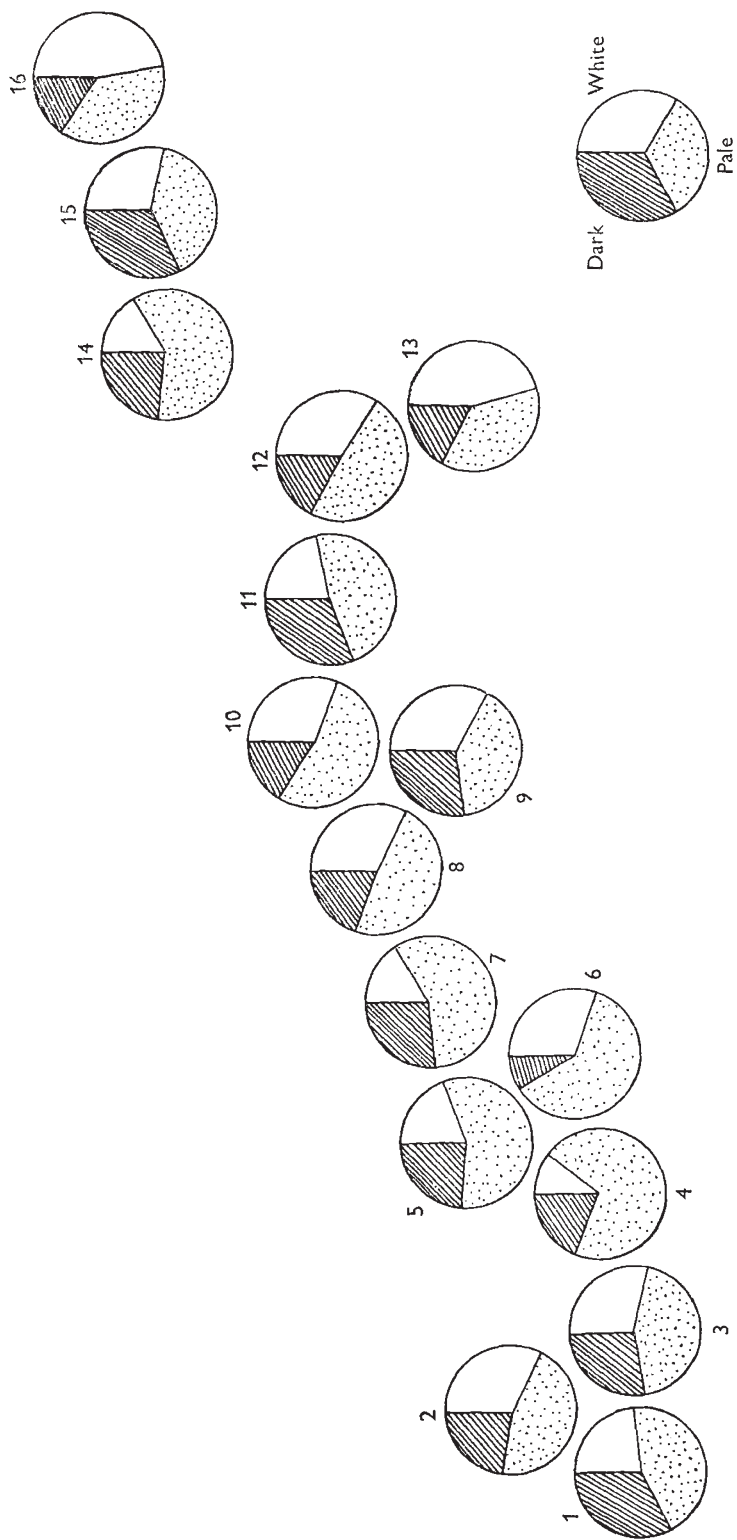
Fig. 1a.—The collecting area.

Fig. 1b.—Frequencies of shell colours at the collecting sites.

areas of the Western Cape Province. It feeds on a wide range of plants in many different habitats, but for this study the snails were collected only from *Tetragonia decumbens* Mill. growing on sand dunes along the coast of False Bay, 1 mile north-east of Muizenberg. The area within which all the collecting sites were found extends inland for 70 metres from a line 150 m. from the Low Water of Ordinary Spring Tide position (LWOST), and runs for 800 m. parallel to the coast. In this region the vegetation cover is not continuous and there are islands of vegetation surrounded by sand (plate Ia). *T. decumbens* forms large clumps in which the stems lie below the surface sending up numerous aerial shoots to an average height of 15 cm. The density of these shoots varies somewhat within the clumps. In order to test whether there is a significant variation from one collecting site to another, a square of wire 25 cm. × 25 cm. was cast at random and the number of shoots within the frame counted. Counts were made in four collecting sites which appeared to show the greatest difference in plant density. Scattered through the clumps are plants of the grass *Agropyrum distichum*, and in some of them are odd plants of *Carpobrotus edulis*, *Helichrysum crassifolium*, *Cnidum subfruti-cosum* and *Arctotheca populifolia*. Snails were only collected from areas where at least 95 per cent. of the plant cover consisted of *T. decumbens* shoots, and there was no additional plant but the grass *A. distichum*. The collecting sites, which are shown in correct scale in fig. 1a, have an average area of 70 m².

The size of the snail shell may have some influence on the interpretation of its colouring; for example, it appears that many that are initially white, later develop stripes near the mouth of the shell. For this reason only snails that fell within certain size limits were used. The criterion adopted to decide whether or not to accept a shell was the number of whorls present. Only those shells with four to five whorls were accepted (fig. 2).

The predators of *T. pisana* are not known, but as the snail is so abundant and so easy to see (by human standards, see plate II), the effect of any predators cannot be great. It is probable that availability of food, or water during the dry summer months, presence of shade or other factors are more important than predation in limiting population size.

However, in some areas collections of shells were discovered close to burrows of small rodents in dense growth of *Acacia cyclops* A. Cunn., on which the snails do not normally feed. These shells were without exception broken or gnawed, whereas most empty shells found near the food plant were intact. Thus it was possible to gauge the effect of this rodent predator by comparing the chewed shells with intact ones from a neighbouring clump of *T. decumbens*.

Polymorphism

The colouring of the shells of *T. pisana* varies in two respects. Firstly there is a wide variation in the striping of the shell. The background colour is white to pale fawn and laid down in this are stripes of brown to black pigment. The stripes are arranged in four longitudinal bands, each band consisting of one to five stripes, or sometimes none. The intensity of colouring of the stripes varies from black to a colour which is just perceptibly darker than the background colour of the shell. Furthermore, the stripes are sometimes interrupted to form a series of discrete dots, of varying size, or they may be fused together to form an undifferentiated broad band.

As there is such an enormous diversity of striping in the shells, it is necessary to classify them according to some arbitrary definitions. The " white " shells include those that are without pigment, and also shells which have stripes which go less than one whorl around the shell (plate Ib). Those shells that have stripes covering at least the basal whorl are grouped into the " pale " class only if the protoconch is without dark pigment. The " dark " group includes those shells in which the protoconch is dark brown or black. Besides having a darker apex, these shells invariably have the darkest stripes in the collection.
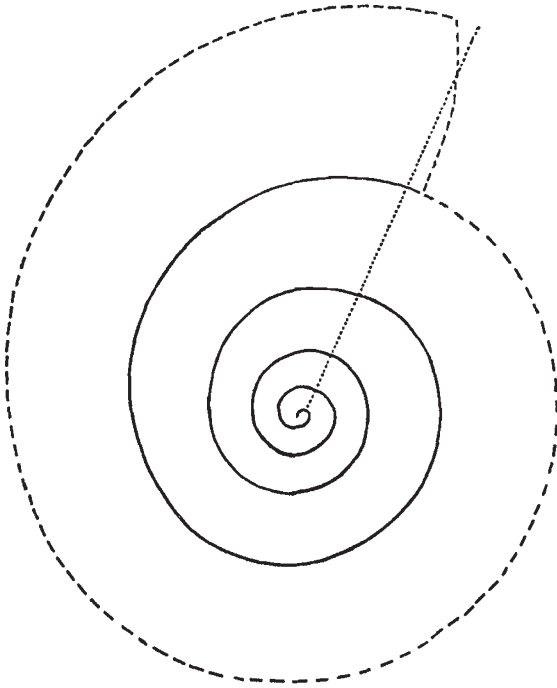

Fɪɢ. 2.—Shells were included only if the mouth lay within the position indicated by the dashed line. This was estimated by extending a line directly from the point of the apex, and if it crossed more or less than 4 whorls the shell was discarded.

Secondly, in addition to the striping characteristic, there is variation in the colour of the inner surface of the aperture and the base of the columella, which in some specimens show a rosy pink flush. But as it is difficult to differentiate accurately between different degrees of pinkness this factor has not been considered.

Rate of movement

A collection of 400 snails from one dune was made and a spot of enamel paint was placed on the shell of each. The marked snails were placed in a line 5 m. long on the dune in the centre of an area with fairly uniform cover of *T. decumbens*. At weekly intervals the vegetation in the vicinity of the starting-line was searched thoroughly for snails and the distance between each specimen and the starting-line was recorded in centimetres.

Size of colonies

The numbers in three colonies were estimated by the mark-release-recapture technique. The snails were marked as they were clinging to the plants; they were not detached lest this should result in increased mortality. In searching the colonies for snails to mark, an attempt was made to cover the entire area of each colony, so that the painted snails were approximately evenly distributed over the whole colony. An interval of at least a week was allowed for the snails to disperse, then a collection was made, and the snails were scored for presence and absence of paint. The snails were then distributed as evenly as possible over the colony so that they could be collected again subsequently. In one case all the snails collected were again painted, with a different colour, before being scattered. After a period of 17 weeks the paint marks were still visible.

3. RESULTS

Comparison between living and dead snails

In one collecting area a large number of intact shells was collected from the surface of the sand as well as from the stems of the plants, and these were then soaked in water for 24 hours so that the living snails emerged and they could be distinguished from the empty shells. When the bodies of the snails had been removed, the shells were classified (table 1). A χ^2 test gave $\chi^2 =$

TABLE 1

Shells collected from one area and classified according to whether they were alive or dead, and according to the colour

	Alive	Dead
White	19	18
Pale	85	80
Dark	25	39
Total	129	137

$3\cdot00$, $0\cdot20 < P < 0\cdot25$; so there is no evidence that the living and dead shells differ with respect to the proportions of the white, pale and dark individuals.

Predated shells

The gnawed shells collected from near the rodent burrows were compared in a 2×3 table with shells collected from a nearby patch of *T. decumbens* (table 2); $\chi^2 = 0\cdot91$, $0\cdot30 < P < 0\cdot50$. That is, there was no significant difference between gnawed and intact shells, and it may be concluded from these results that there is no evidence that predation by rodents is influencing the frequencies of the different morphs in the populations.

TABLE 2

Shells collected from two adjacent areas, one with gnawed shells, and the other with living snails

	Gnawed shells	Intact shells
White	8	18
Pale	26	41
Dark	33	47
Total	67	106

Comparisons between different colonies

Although the sites at which the snails were gathered lay within a small area, and the snails were collected from the same plant species, the proportions of the different colours of shells varied widely. In no case were less than 100 shells collected from any site, so there were sufficient numbers for statistical tests (table 3).

The frequencies of different coloured shells in each colony are shown diagrammatically in fig. 1b. There is no overall pattern visible, and there is no indication of a cline running through the collecting area.

A test of the overall homogeneity of the 16 different sites with respect to the numbers of white, pale and dark shells was made by calculating χ^2 for the 3×16 table. The very large value obtained ($\chi^2 = 132 \cdot 45$, $P \ll 0 \cdot 0005$) confirms that there are significant variations between the sites.

TABLE 3

Counts of snails from different sites

Site	White	Pale	Dark	Total
1	30	59	44	133
2	43	62	31	136
3	49	75	48	172
4	11	75	20	106
5	21	64	27	112
6	31	63	9	103
7	18	67	31	116
8	43	64	26	133
9	41	49	34	124
10	33	58	18	109
11	29	65	42	136
12	49	70	24	143
13	56	46	22	124
14	16	61	24	101
15	31	44	36	111
16	55	43	19	117

The densities of *T. decumbens* shoots varies between 8 and 32 shoots per 625 cm.^{2}. An analysis of variance of the results from 10 counts in each of four different collecting sites gave $F = 4 \cdot 6$, $P > 0 \cdot 05$. It may be concluded that the variation of density of shoots between different sites is not significantly greater than the variation within the sites.

Rate of movement

The results from measuring the distance moved by individual snails after 1 week and after 3 weeks from the start of the experiment are shown as histograms in figs. 3 and 4. The theoretical normal curves derived from the means and the standard deviations of the raw data are also shown. The histograms appear to follow the normal curves quite closely, except that they are leptokurtic in the central values. The degree of kurtosis (*Ku*) is calculated from the formula

$$Ku = \frac{n\Sigma r^4 f}{(\Sigma r^2 f)^2} \text{ (Dobzhansky and Wright, 1947),}$$

where n is the number of snails recorded and f is the frequency of the snails reaching a position r cm. from the starting position. The results of the calculations of *Ku* are entered in table 4. In a normal curve, $Ku = 3$.

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This figure is exceeded in the data collected on 13/2 and 20/2, however the test of Pearson (1931) shows that these values for *Ku* are not significantly higher than 3.

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TABLE 4

Results of analysis of movements of snails

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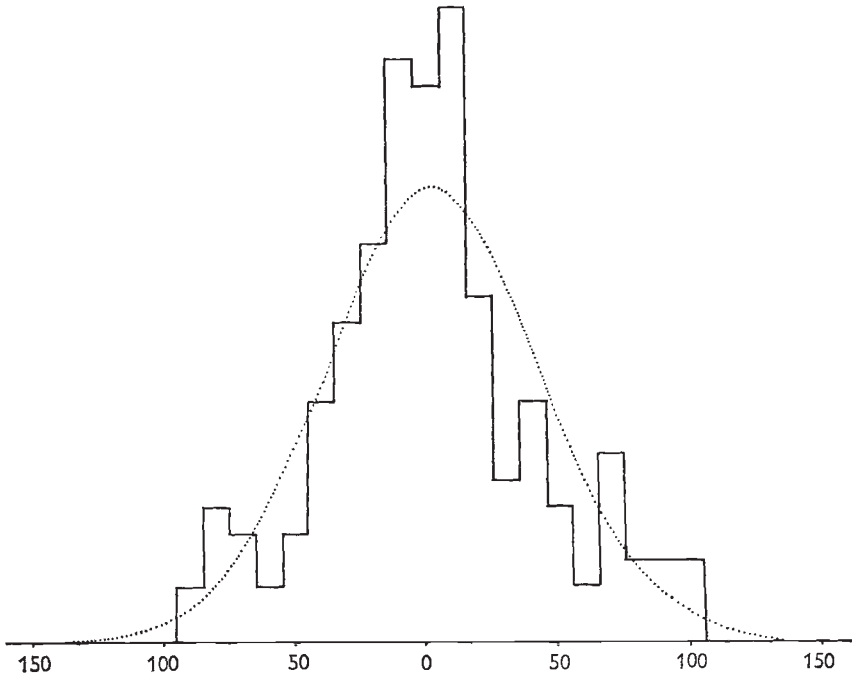| Date	Number of snails	Variance (m.²)	Variance increment	Ku
6/2/70	400 (start)			
13/2/70	171	0·159	0·159	3·55
20/2/70	161	0·231	0·071	3·65
27/2/70	173	1·052	0·821	2·97

FIG. 3.—Histogram showing distances moved by snails in one week. The distances shown on the abscissa are in cm. The normal curve with the same mean and standard deviation is shown as a dotted line.

The dispersal of animals that are moving at random may be compared to the diffusion of molecules in a solution. The diffusion coefficient of the molecule is found from the expression

$$D = \frac{\sigma^2}{2t}$$

and the same expression may be applied to the data of snail dispersion in order to get the " diffusion coefficient " of the snail. In table 5 this has been done for the data of *T. pisana* and also for Goodhart's (1962) figures, using his fixed mean data.
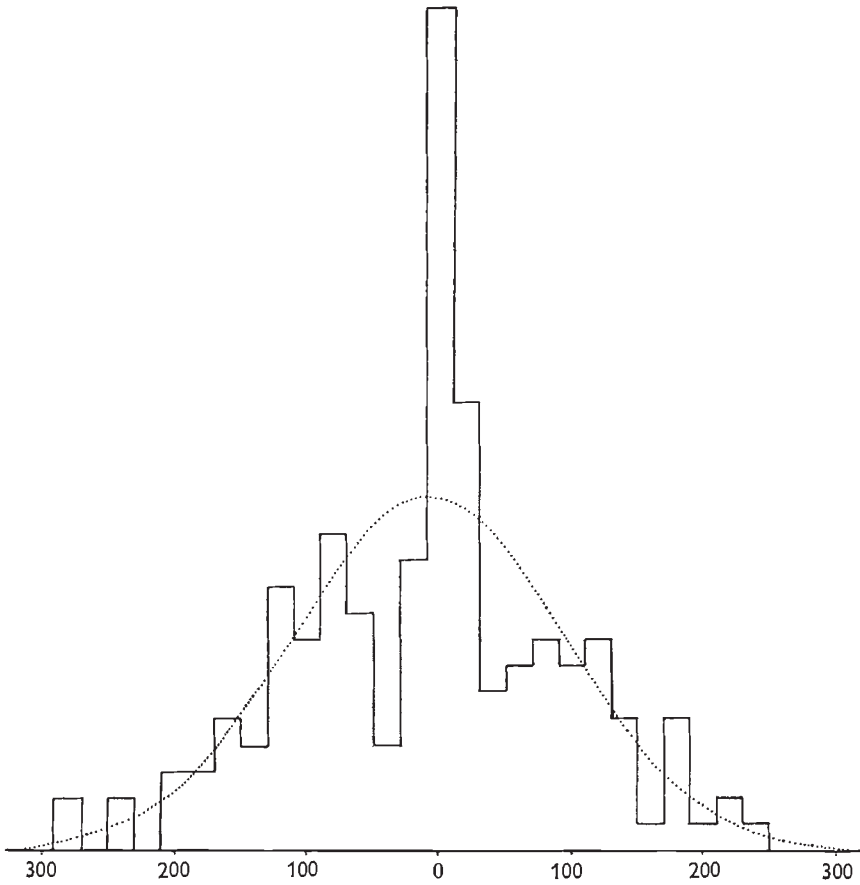
FIG. 4.—Distances moved by snails in 3 weeks.

TABLE 5

Rates of movement of T. pisana *and* C. nemoralis

Time (weeks)	Variance, σ^2 (m.²)	"Diffusion coefficient" $D = \dfrac{\sigma^2}{2t}$ m.²/week
	Theba pisana	
0–1	0·159	0·079
1–2	0·071	0·035
2–3	0·821	0·410
		Average 0·175
	* *Cepaea nemoralis*	
0– 4	4·01	0·501
4–14	2·09	0·104
14–51	4·27	0·058
		Average 0·221

* Data taken from Goodhart (1962).

It may be seen that the average " diffusion coefficient " for *T. pisana* is 0·17 m.²/week and for *C. nemoralis* it is 0·22 m.²/week. *T. pisana* is a slightly smaller snail although this probably has no bearing on their relative speeds.

The magnitude of the variances recorded for *T. pisana* in table 5 may be correlated with the rainfall. During the first week of investigation rain fell for about 12 hours and the variance is 0·16 m.²; in the second week no rain fell, giving a low variance of 0·07 m.², and the third week included 36 hours of intermittent rain giving a variance of 0·82 m.². The movement of the snails is clearly influenced by the periods of rain. Thus the figure calculated for the " diffusion coefficient " is an approximate one calculated over 3 weeks of the relatively dry summer. The movement in the wet winter months of the Cape Province may be more rapid, though Goodhart's (1962) figures reflect slower movements in the English winter because of the lower temperatures.

Size of colonies

Three sites were chosen for estimation of snail numbers. From experience in collecting it was known that one site (9) had an abundance of snails over a comparatively large area, and the other two sites (6 and 10) had far fewer snails. The results of the counts of the painted snails are entered in table 6.

TABLE 6

Numbers of snails painted and re-collected at three sites

| | Painted | | Collected | | | | Estimated |
Site	Date	No.	Date	Marked	Unmarked	Total	total No.
6	13/3/70	108	16/6/70	5	80	85	1836
9	6/2/70	300	13/3/70	47	890	937	5981
	6/2/70	300	16/6/70	17	417	434	7659
	13/3/70	937	16/6/70	80	354	434	5083
10	6/2/70	53	13/2/70	8	44	52	344
	6/2/70	53	13/3/70	18	112	130	383
	6/2/70	53	16/6/70	3	46	49	866

The final column has been estimated from the relationship:

$$\text{Total number in population} = \frac{\text{Number painted} \times \text{Total number collected}}{\text{Number of painted shells collected}}$$

(Jackson, 1936, p. 848). It may be noted that the estimates for sites 9 and 10 are higher when the snails were marked on 6/2/70 and collected on 16/6/70. This is probably due to the fact that some of the marked snails died or migrated away or for some other reason disappeared in the long interval between these two dates, thus resulting in an estimate that is too high. In order to get a more accurate estimate of the populations, the figures were corrected as described by Jackson (1936, p. 852) and the logs plotted. Extrapolation of the curves to zero time gave estimated populations of 5500 at site 9 and 300 at site 10. The areas of these sites are 168 m.² and 50 m.² respectively, so the concentrations of snails are 33 snails per m.² and 6 snails per m.². As these sites were chosen because they appeared to show extremes of snail density, these figures may be taken as the limits of variability of snail concentration for estimating the probable populations at other sites. The results are shown in table 7.

TABLE 7

Size of colonies

Site	Dimensions (m.)	Area (m.²)	Populations estimated from snail densities of 6 and 33 snails/m.².
1	10 × 4	40	240–1320
2	9 × 7	63	380–2080
3	12 × 15	180	1080–5940
4	12 × 14	168	1000–5540
5	10 × 5	50	300–1650
6	8 × 8	64	1800
7	5 × 4	20	120–600
8	10 × 5	50	300–1650
9	12 × 14	168	5500
10	10 × 5	50	300
11	8 × 5	40	240–1320
12	11 × 10	110	660–3630
13	14 × 12	168	1000–5540
14	7 × 6	42	250–1390
15	12 × 8	96	580–3170
16	10 × 10	100	600–3300

4. DISCUSSION

The frequencies of the characteristics studied vary widely from one sample of snails to another. The probability that the samples are from a homogeneous population is much less than 0·05 per cent., thus the variation evident in the samples reflects a very real variation in the populations from which they were drawn.

Cain and Sheppard (1950) have shown that the variation in morph frequencies of *Cepaea nemoralis* in different colonies is produced, in part at least, by the differential bird predation to which the morphs are subjected in different environments. It is not known whether birds eat *T. pisana*, but if they do it would be expected that the predation would not vary between colonies investigated as they were all found on the same species of plant. Predation by a small burrowing animal, probably a rodent, has been noted, but this is not selective with respect to the striping categories. In this respect the predation is similar to that of rodents on *C. nemoralis* as shown by Day and Dowdeswell (1968), though these authors point out that larger numbers might have shown a significant selective action.

A difference in environment between one colony and another could also change morph frequencies. Arnold (1969) has shown that riverside and hillside populations of *C. nemoralis* show different morph frequencies; altitude and proximity to the river may be contributing factors. In this study, however, all the colonies were found between the 10- and 20-ft. contours, so altitude must be of little significance. Distance from the sea could be of importance to snails, as spray and mists are carried in from the sea during the summer by the prevailing S.E. winds. But the 16 colonies lie in a belt only 70 m. wide between 150 and 220 m. from the LWOST line, so that distance from the sea is probably less important than local differences in micro-climate caused by other factors. These factors are difficult to analyse, and would include the exact configuration of the nearby dunes and their effect on the winds, the density of the plant cover and the angle of exposure of the dune to the sun. The strengths of the winds can not be measured and are probably so variable as to be unimportant. Although the plant shoots

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vary somewhat in length and number of leaves the results of counting shoots do give an approximation of the density of the plants, and the results tend to confirm the subjective impression that there is greater variation of plant density within the collecting sites than between them. The angle of exposure varies within each site as most sites are rounded and all show many aspects, which change as the sands drift, thus it is unlikely that this factor is of importance in influencing shell colour frequencies.

Before assuming that the variation in populations is due to random sampling errors it is necessary to consider whether the characteristics concerned are genetically controlled, whether there is sufficient isolation between the colonies to allow random drift to take effect, and whether the colonies are small enough for sampling errors to have been important.

The banding patterns of *C. nemoralis* have been demonstrated to be genetically controlled (*e.g.* Wolda, 1969) and similar inheritance has been found in *C. hortensis* by Murray (1963). By analogy it is almost certain that the striping of *T. pisana* is also a hereditary feature, though no work has been reported on the genetics of this snail.

The rate of movement of the snails was measured in vegetation, and the " diffusion coefficient " found to be 0·17 m.^{2}/week. This estimate is only approximate as the amount of movement is influenced by the rainfall and probably by other factors affecting humidity. However, if this figure is accepted then σ for 1 year is 4·2 m., that is about 30 per cent. of the snails will move this distance or more in 1 year. The distance between some colonies is as little as 50 m. but it would take about 35 years for 5 per cent. of the population to travel this distance, assuming the above diffusion coefficient to be accurate. Obviously individual snails would only travel a small part of this distance, but if the genotype does not influence the rate of movement the above figures would apply to 5 per cent. of the genotypes.

The measurements of speed of movement were made in vegetation, but when a snail finds itself on a bare patch of sand it will travel very much faster than in plant cover, and its movement will be more directional, thus the dispersal from one colony to another may be more rapid than indicated above. However, the figures do give some indication of the order of time involved and show that even the closest colonies are relatively isolated from one another.

Dobzhansky and Wright (1947), in their study of the speed of movement of a mutant, found that there was considerable kurtosis of the distribution curve, with values of Ku up to 13·0. This was due to heterogeneity of the dispersal movements of the flies. Bateman (1950) has also shown that different forms of gene dispersal tend to show leptokurtic distributions. The histograms of figs. 3 and 4 also show the same type of distribution, even though values of Ku are found to be not significantly different from 3.

The densities of *C. nemoralis* were found by Cain and Currey (1967) to average 0·6 snail/m.^{2} in grassland and 8 snails/m.^{2} in neighbouring nettle patches. Estimation of densities in sparsely populated and in thickly populated colonies of *T. pisana* give 6 snails/m.^{2} and 33 snails/m.^{2}. If it is assumed that the other colonies sampled had densities of snails intermediate between these values then table 7 shows that many colonies had 1000 or fewer individuals. Many colonies in the field were not sampled because the density of snails was so low that an adequate sample of snails could not be collected readily, and the total number of individuals in such colonies must

Plate I

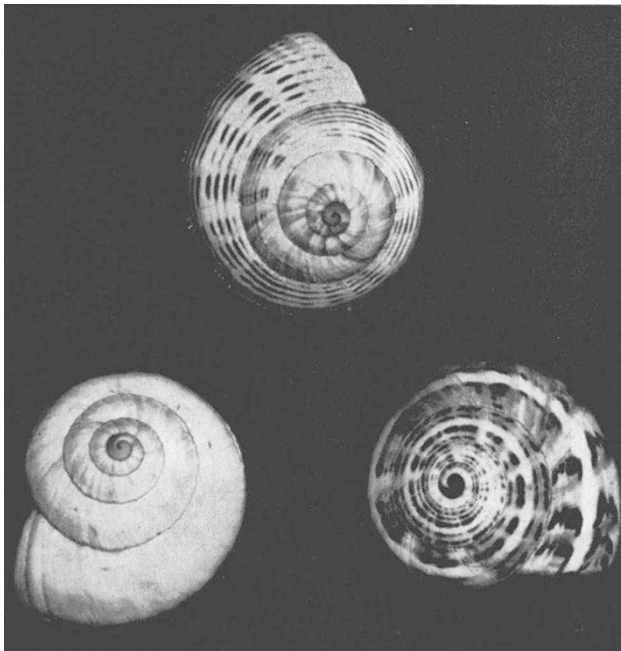*Plate Ia.*—Collecting site No. 10.   Most of the plant cover visible is *Tetragonia decumbens*.

Plate Ib.—Variation in shell striping. Left: " white "; top: " pale ";
right: " dark ".

Plate II

Specimens of *T. pisana* in situ on a twig of *T. decumbens*.

have been small. Probably a colony starts with a few founding members and then increases and decreases in size, corresponding with the success of the host plant and the waxing and waning of the size of the dune on which it is situated.

The small number of individuals in each colony, at least at some stages of colony history, and the relative isolation of these colonies, would seem to be features which are ideal for the demonstration of the change of populations by random sampling errors. This may either be a continuous process resulting in " Sewall Wright drift " or may be effected by the survival from time to time of " Founder stock ". As has been pointed out by Wright (1959), mathematically the latter is a particular case of the former and the effects would be virtually indistinguishable. The conclusion that random effects are responsible for the considerable diversity of frequencies of morphs of *Theba pisana* is strengthened by the facts that no differential predation can be demonstrated nor can any continuing selective effect of the environment be shown.

5. Summary

1. Populations of *Theba pisana* (Müller) found on sand dunes have been analysed according to the striping of the shell.

2. Significant differences have been found between many of the colonies for the frequencies of this character.

3. Predation by a rodent has been investigated and it has been shown that there is no differential predation for the striping character.

4. The snails were all taken from the same plant species, and the colonies were within a small homogeneous area so it is considered unlikely that environment is having an effect on morph frequencies.

5. No consistent overall change of frequencies of morphs is noted within the collecting area.

6. The " diffusion coefficient " within an area of vegetation was found to be approximately $0 \cdot 17$ m.^{2}/week, but this measurement is greatly influenced by the rainfall. This slow rate of movement indicates that the colonies are relatively isolated from each other.

7. The distribution curve of the movement of the snails within the vegetation follows fairly closely the theoretical normal curve, with some kurtosis evident.

8. The populations of two colonies have been found to contain 300 and 1800 individuals respectively. The densities of the snails in these colonies were 6 and 33 snails/m.^{2}. Using these figures, the populations of the colonies sampled were estimated to vary between approximately 200 and 5000 individuals.

9. In the absence of any evidence to show that the shell-striping character has been selected by a predator or by environment, and as the colonies are comparatively isolated and often contain quite low numbers, it is suggested that random sampling errors are the cause of the very different frequencies in the different populations.

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