Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Polymorphism and Selection in Cochlicella acuta

G. Lewis

Phil. Trans. R. Soc. Lond. B 1977 **276**, 399-451
doi: 10.1098/rstb.1977.0004

Email alerting service Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: **http://rstb.royalsocietypublishing.org/subscriptions**

This journal is © 1977 The Royal Society

Downloaded from rstb.royalsocietypublishing.org

POLYMORPHISM AND SELECTION IN *COCHLICELLA ACUTA*

By G. LEWIS
Department for External Studies, University of Oxford

(*Communicated by P. M. Sheppard, F.R.S. – Received* 19 *March* 1976)

[Plate 1]

CONTENTS

The Royal Society is collaborating with JSTOR to digitize, preserve, and extend access to *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences.*
www.jstor.org

Downloaded from rstb.royalsocietypublishing.org

Cochlicella acuta is a small, pointed sand-dune snail, which is polymorphic for shell banding, shell opacity and ground colour. From a survey of about eighty colonies between latitudes 58° N and 43° N in west and northwest Europe and a more extensive study of one of them, morph frequencies have been determined and corresponding habitats classified, according to their appearance. It has been shown previously that the principal alleles responsible for the shell characteristics of *C. acuta* behave as a supergene, that the known variations occur in certain preferred associations and that only a few morphs occur commonly. Now, the frequencies of certain morphs are shown to be associated with particular habitat types. Three such relationships are identified. Discontinuously opaque unbanded forms, which usually possess a buff/amber ground colour and are consequently of sandy appearance, predominate on backgrounds of exposed sand, where they are cryptic. Heavily-banded forms, which are dark in colour occur most commonly on dark coloured substrates while continuously opaque morphs with few bands which are of black and white appearance, occur principally and numerously in turfy habitats, where in contrast with the cryptic relationship of the other two associations, they are quite conspicuous. More-heavily-banded forms of the sympatric species *Helicella virgata* have also been found to occur most commonly where the substrate is dark. Predation by rooks, *Corvus frugilegus*, of both species is established. It is suggested that predation of this kind is likely to be selective and that, largely though not entirely, it determines the cryptic habitat/morph frequency relationships, such visual selection in turfy habitats being less influential.

By using Fisher's maximum likelihood method, the frequencies of the supergenes and genes that are responsible for the principal features of the shell polymorphism of *C. acuta* are computed from the sample data already recorded. An analysis of these frequencies in relation to habitat and to latitude shows certain supergenes and genes frequencies to be related to habitat, irrespective of latitude; others to latitude irrespective of habitat type. A third category is independent of both. These relationships are attributed to selection of at least three kinds, identified respectively by being related to habitat type, to latitude and to neither.

Visual predation, which consistently favours an absence of banding in sandy habitats, irrespective of latitude is probably the major influence of selection related to habitat. Latitude-related selection, which acts very strongly against the supergene *CO 00* in all types of habitat in northern latitudes, though progressively less in southern ones, is probably due to certain aspects of climate. These two kinds of selection appear to underlie most, but not all, of the supergene and gene frequency distributions within the range investigated. The exceptions are those determining the banded forms, which are discontinuously opaque. Gene interaction of sufficient strength to surpass the effects of other selective factors is suggested.

Downloaded from rstb.royalsocietypublishing.org

1. Introduction

Genetic polymorphism (Ford 1940, 1971; Clarke 1975) accounts for much natural variation in wild populations but what determines such variation and how it is controlled is by no means fully understood. Population genetic theory has explored the problems extensively but, as Lewontin (1974) has pointed out, they are more likely to be solved by the more practical approaches of ecological genetics (Ford 1971), which attempt to establish the selective forces involved. Studies of this sort have been comparatively few, however. One of the most extensive is that by Cain & Sheppard and their school of the land snail *Cepaea nemoralis*.

This paper presents the study of another species of land snail, *Cochlicella acuta*, which is considerably smaller than any of the species of *Cepaea* and has a more limited range of shell variation. In *C. acuta* this occurs mainly in the banding and in the extra-band opacity. Ground colour does vary but, unlike *Cepaea*, it is restricted to the range off-white through white to buff/amber. Experimental breeding (Lewis 1975) has established that the shell variation constitutes a genetic polymorphism, the main features of which do not appear to be much affected in their expression by the environment. The field work involved in this study has included a survey of colonies in west and northwest Europe within an area extending from the Outer Hebrides, which is the northern limit of the range of the species, to the Pyrenees and an intensive study of one colony in Cornwall.

Associations between habitat types and particular morphs are demonstrated and, by an analysis of supergene and gene frequencies in relation to habitat and to latitude, an attempt is made to identify and to distinguish between different kinds of selection.

2. Material

Cochlicella acuta is one of the smaller species of land snails. Descriptions are given by Ellis (1926) and Germain (1930). It occurs in maritime localities in Mediterranean regions and in west and northwest Europe, nearly always on substrates of salt-free blown sand. Since suitable habitats usually occur at irregular intervals the geographical distribution is discontinuous. Colonies vary greatly in size, large ones extending over sand dune systems many square miles in extent, small ones often being confined to the narrow strips of sandy soil at the top of the foreshore of small sandy beaches.

The shell of the snail is polymorphic, the variation occurring principally in the banding and in the extra-band opacity. There is variation in the ground colour also but, in the present analysis differences in shell ground colour have not been used. For the various patterns of banding, a nomenclature based upon a five-banded system similar to that proposed for *Cepaea* by von Martens (see Lamotte 1951) and subsequently adopted by Ellis (1926) and by Cain & Sheppard (1950, 1954) is used. The bands are numbered 1–5 depending on their positions on the shell, that nearest to the apex being band 1. In respect of the opacity, shells that are continuously opaque are distinguished from those that are partly transparent in the extra-band areas of the shell and the terms continuously opaque (abbreviated to CO) and discontinuously opaque (DO) are used to describe these characteristics of the morphs (Lewis 1975).

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

3. Visual selection

(*a*) *Survey: Outer Hebrides to Pyrenees*

(i) *Methods*

A. *Collecting*. Random samples of *Cochlicella acuta* were collected from colonies in Great Britain, excluding the Eastern side and France within a geographical area extending from the northern end of the Outer Hebrides to the Pyrenees. Morph frequencies for each sample were determined and these compared with the types of habitat from which the samples were obtained. I visited as many as possible of the coastal localities in that area that appeared to provide a suitable environment for *Cochlicella acuta* and, wherever the species was found, random population samples were collected, in all from about 80 colonies. The samples were collected in daylight. Frequently a number of samples were obtained from one colony by walking across the ground it occupied and stopping at irregular intervals to take samples. Undoubtedly, many individuals were overlooked, although care was taken to collect as thoroughly as possible. I consider it unlikely, however, that many snails were missed because they were buried in the substrate, since *Cochlicella acuta*, unlike a number of other species of land snails as far as I know, does not pull itself down into the substrate. I have failed to find any records of reports that it does and I have never observed specimens kept and bred in transparent boxes in the laboratory

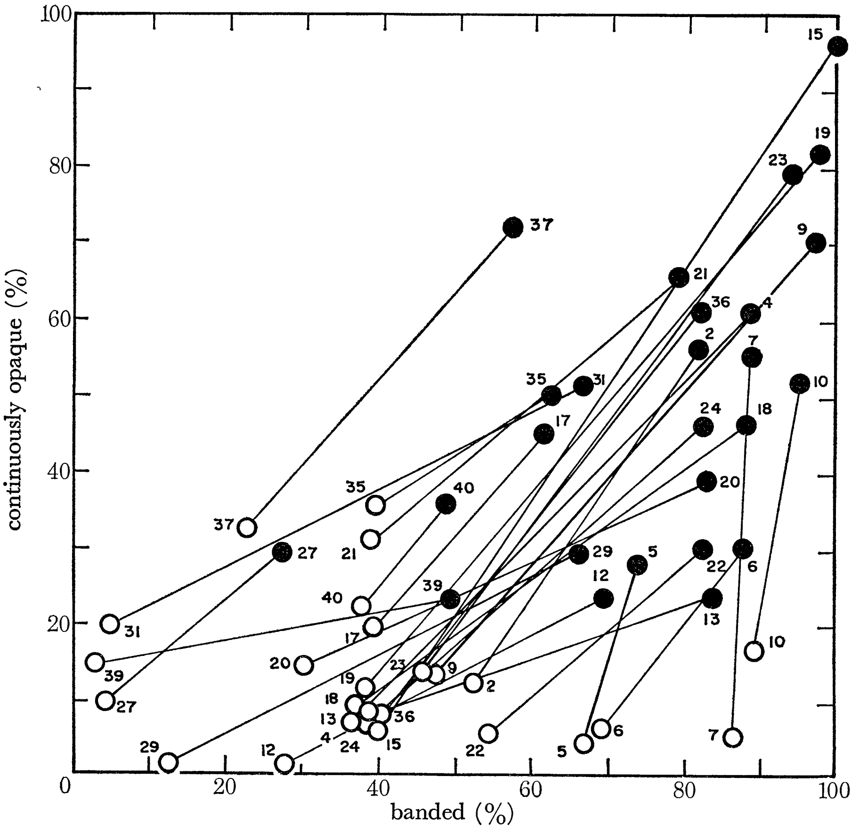


Figure 1. A dipole diagram showing the relation between percentage of banded shells, of continuously opaque shells and the nature of the habitat. Each dipole represents a different colony and its two ends the composition of samples from the contrasting habitat types within it. Colony reference numbers accompany each dipole (see table 1 and figure 4). ○, Exposed sand; ●, close turf.

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

to do so not even during egg-laying. At the time of collection, the location within the colony and details of the nature of the habitat were included in the data recorded for each sample.

B. *Scoring of habitats*. Although colonies of *Cochlicella acuta* are confined almost entirely to areas covered by blown calcareous sand from nearby sandy foreshores, the habitats in which they live are not all alike. Two principal habitat types predominate and, in the majority of the bigger colonies, both are to be found. One consists largely of loose sand with a minimum coverage of vegetation; the other is of turf, in which the closely-growing plants almost completely hide the sandy substrate and give a very different appearance to the background. In addition to these two principal types, two others have been distinguished, namely those in which the vegetation cover is intermediate in extent and those in which the background is very dark, for example where peat lies beneath a light dusting of blown calcareous sand or in small hollows in dune slacks, where humus blackens the surface of the substrate.

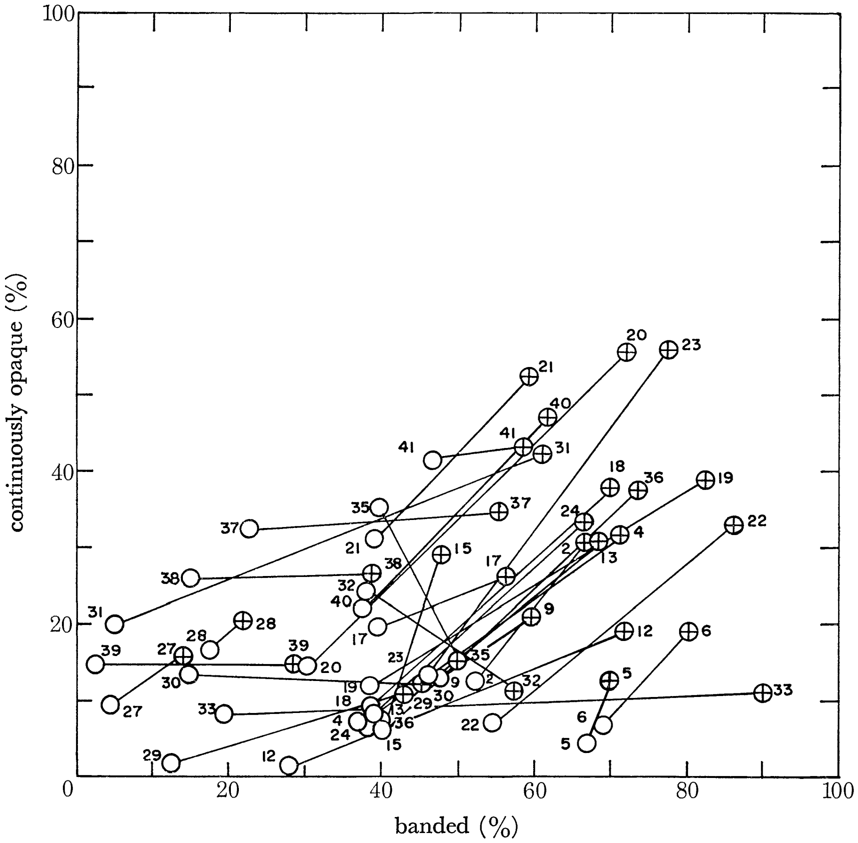


FIGURE 2. A dipole diagram showing the relation between percentage of banded shells, of continuously opaque shells and the nature of the habitat. Each dipole represents a different colony and its two ends the composition of samples from the contrasting habitat types within it. Colony reference numbers accompany each dipole (see table 1 and figure 4). ⊕, Mixed vegetation; ○, exposed sand.

Accordingly, I have classified the *Cochlicella acuta* habitats into four types, defined as follows:

(1) *Exposed sand*: characterized by Marram (*Ammophila arenaria* L.) tussocks or sparse grass with considerable exposure of the sandy substrate.

(2) *Close turf*: in which the dense turf or thick grass completely covers and so obscures the surface of the substrate.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(3) *Mixed vegetation*: comprising all habitats, having a coverage of vegetation varying in species composition and density intermediate between 1 and 2.

(4) *Dark substrates*: where the background against which the snails live is particularly dark.

The first three habitat types occur over a wide geographical range (see figure 4) and vary little between colonies. The fourth, dark substrates, is much more local and has been found in comparatively few colonies.

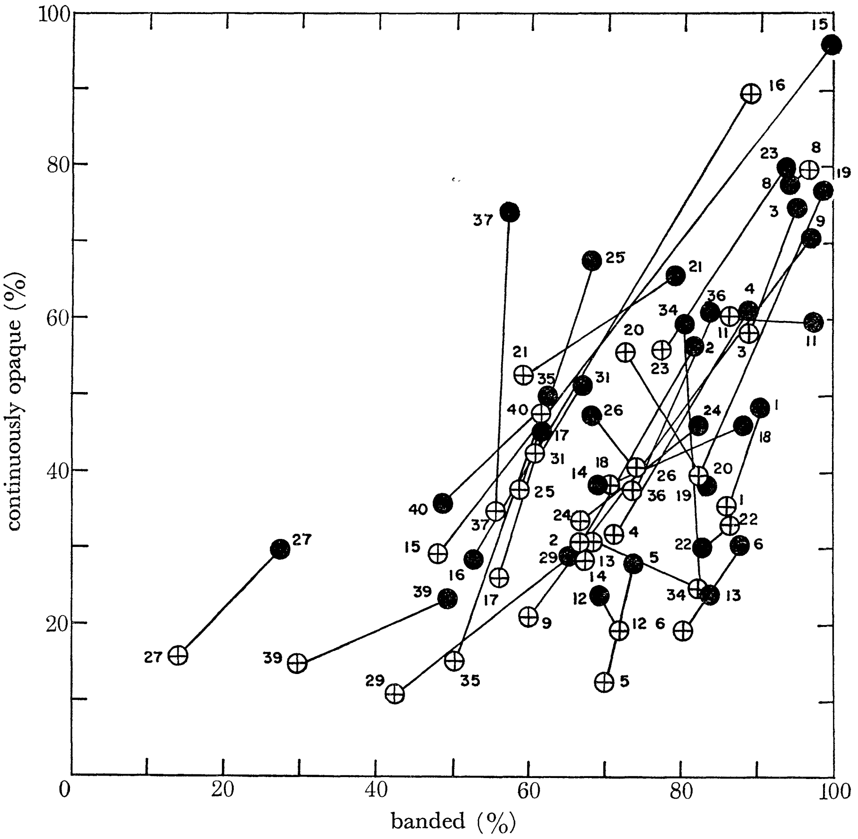


FIGURE 3. A dipole diagram similar to figures 1 and 2 showing the relation between percentage of banded shells, of continuously opaque shells and the habitat types close turf and mixed vegetation. ●, Close turf; ⊕, mixed.

C. *Scoring of samples*. After being cleaned and dried, shells were classified into the following categories: in respect of opacity, continuously opaque (CO) and discontinuously opaque (DO) and, in respect of banding, unbanded, one-banded and more-than-one-banded. Samples were classified according to the type of habitat from which they had come. Where more than one sample from the same type of habitat had been obtained within one colony, the mean colonial values for each phenotype were calculated.

(ii) *Relationships between habitat and shell polymorphism*

A. *Habitat: types exposed sand, close turf and mixed vegetation*. Table 1 gives the observed data for the composition of the samples arranged in three groups according to habitat types 1, 2 and 3. Figures 1, 2, 3, 5 and 6 show the relations between the appearance of the shell, in respect of its opacity and banding, and the habitat type. The dipole diagrams, figures 1, 2 and 3, are for colonies having habitats of more than one type. For each colony, the percentages of banded

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

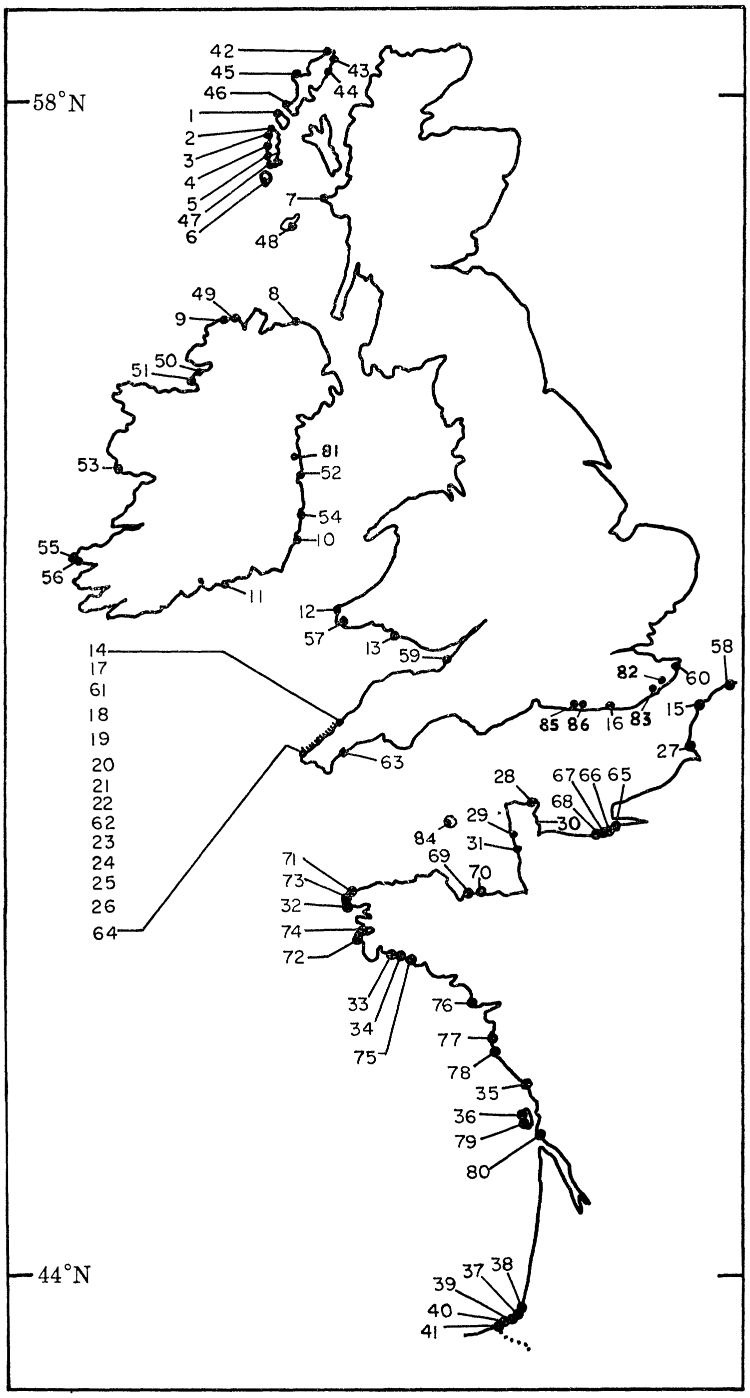


Figure 4. The geographical locations of the colonies from which samples have been collected. Place names are given against the corresponding colony reference numbers in table 7.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

shells and of continuously opaque shells are plotted for pairs of contrasting habitat types, the two points representing the two habitat types of a particular colony being joined by a straight line to form the dipole. Each dipole is identified by a colony reference number. The locations of all the colonies are shown on the map, figure 4.

With few exceptions in all three diagrams, the dipoles lie in a preferred direction. In figure 1, for example, without any exceptions, the open circles, representing populations living on a substrate of exposed sand lie to the left and below the corresponding closed circles which represent close turf populations in the same colonies. This shows that populations of *Cochlicella acuta* that live on backgrounds of exposed sand are less banded and have shells that are less continuously opaque and so more closely resemble their sandy background than those that live on turf. Although there is variation in degree in the relationship this holds for every one of the colonies studied, in which these two extreme habitat types occur.

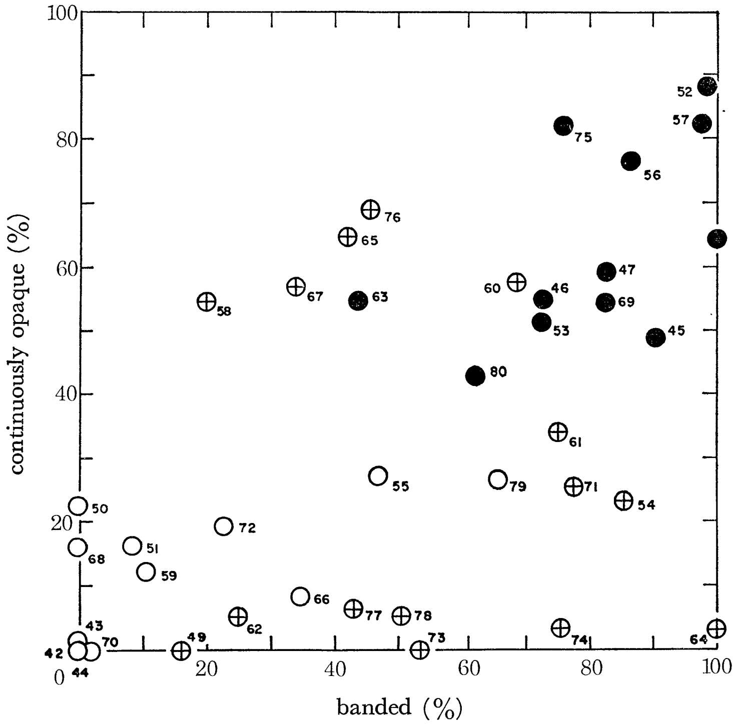


Figure 5. A scatter diagram showing the composition of the samples from single habitat type colonies. The symbols used to indicate the nature of the habitat are the same as those used in figures 1, 2 and 3. Colony reference numbers accompany each plot (see table 1 and figure 4). ●, Close turf; ⊕, mixed vegetation; ○, exposed sand.

In twenty-four of the colonies surveyed, all three habitat types do occur and in 18 of these the dipoles representing mixed vegetation and close turf (figure 3) continue in a similar direction to those representing exposed sand and mixed vegetation (figure 2) for the same colonies. Only in colonies nos. 12, 13, 20, 22, 35 and 40 is this not so. These two diagrams illustrate a relationship similar to that shown in figure 1 though less distinctly. This is to be expected, since the contrast between the pairs of habitat types represented in figures 2 and 3 is not so great as that between the extreme types, in figure 1. Moreover, as figures 2 and 3 both include plots representing samples from mixed vegetation type habitats, which by definition include a greater

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

range of habitat variation than the other types do, the plots may be expected to be scattered more widely than are those for either close turf or exposed sand. Even so, the diagrams do show that the populations inhabiting close turf are more continuously opaque and more banded than are those for mixed vegetation and that those populations in turn have a greater proportion of individuals that are C.O. and banded than do the exposed-sand type ones.

During the course of the survey, *Cochlicella acuta* was found and random samples of it obtained from a number of colonies that did not extend over more than one habitat type. Many such colonies were quite small. The samples obtained from these single habitat type colonies (table 1, nos. 42–80) have been scored in the same way as the others. Using the same symbols to indicate the habitat types, their compositions are shown as a scatter diagram in figure 5. The plots are quite evidently not randomly distributed. Those from like habitats tend to lie together, indicating that the compositions of these populations are related to the type of habitat in which they live, the relationships being the same as those shown in the dipole diagrams (figures 1, 2 and 3).

B. *Habitat type: dark substrate.* In thirteen colonies, samples were collected from habitats classified as dark substrate type. In most of these colonies, samples were obtained from other habitat types as well; in some, from all four types. The composition of all the samples obtained from these colonies is given, in respect of banding only in table 2, the data being arranged according to habitat type and, as before, mean colonial values being used where these are appropriate.

Using triangular coordinates, in order to include the banding category more-than-one-banded, the composition of the samples obtained from these thirteen colonies is shown in figure 6. In this diagram, the segregation of the plots representing different habitat types is clear. More than half of the samples from populations inhabiting dark substrates lie above the line representing 49% more-than-one-banded, whereas none at all for those for the other habitat types do. This separation shows that there is a further relationship between habitat and the frequency of occurrence of particular morphs, namely between dark substrates and morphs that are heavily banded, which, for that reason, are darker in appearance than less heavily-banded forms.

(*b*) *Study of one colony: at Godrevy, Cornwall*

(i) *Description of site*

The colony, which covers an area of about 0.5 square miles, lies on the north Cornish coast at the northeasterly end of St Ives Bay about 1 mile (0.6 km) due north of the village of Gwithian (map reference SW/59 1423). It includes a sand-covered hill, known locally as Godrevy Towans and is bounded to the south by the Gwithian to Portreath road (B 3301). The area was formerly a shallow bay bordered, on the north side, by a cliff. Now it is a flattish, gently sloping field with the steep hillside to the north rising from it. The aerial photograph (figure 7, plate 1) shows the principal features of the area, particularly the contrasting nature of the present land surface in different parts of it. In the field there is turf; on the hillside loose well-exposed sand. Between the two there is a sharp transition lying very nearly in a straight line west to east and roughly at right-angles to the present shoreline. This transition follows approximately the 23 m (75 ft) contour (see figure 8). The lowest-lying part of the area is at the western (seaward) end of the field. Running through it there is a low ridge represented in figure 8 by two lines of small crosses. Eastwards, the ridge diminishes in height and finally disappears but at the western end it forms the southern boundary of a depression, which lies between it and the foot of the hillside.

Downloaded from rstb.royalsocietypublishing.org

colony ref. no.	colony	exposed sand										mixed vegetation										close turf									
			CO			DO							CO			DO							CO			DO					
		sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO	sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO	sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO
1	Veilish											1a	0	2	9	3	12	2	28	89.3	39.3	1c	0	13	33	9	38	2	95	90.5	48.4
												b	0	5	9	8	20	3	45	82.2	31.1										
	mean																			85.8	35.2									90.5	48.4
2	Nunton	2a	0	3	3	43	30	2	81	46.9	7.4	2c	0	13	23	38	35	0	109	65.1	33.0	2f	0	28	20	9	13	0	70	87.1	68.6
		b	0	4	12	39	36	1	92	57.6	17.4	d	0	13	18	44	34	0	109	59.6	28.4	g	0	15	18	21	26	0	80	73.8	41.2
												e	0	4	10	11	20	0	45	75.6	31.1	h	0	15	12	7	10	2	46	84.8	58.7
	mean									52.3	12.4									66.8	30.8									81.9	56.2
3	South Nunton											3a	0	1	5	1	2	1	10	90.0	60.0	3j	0	23	3	1	8	1	36	97.2	72.2
												b	0	11	44	12	29	0	96	87.5	57.3	k	0	27	63	3	29	2	124	97.6	72.6
												c	0	27	28	4	28	0	87	95.4	63.2	l	0	8	47	3	8	0	66	95.5	83.3
												d	0	11	20	3	7	1	42	92.9	73.8	m	0	28	47	11	20	0	106	89.6	70.8
												e	0	14	52	16	36	1	119	86.6	55.5										
												f	0	12	24	7	29	1	73	90.4	49.3										
												g	0	7	20	9	12	0	48	81.2	56.2										
												h	0	18	43	11	43	0	115	90.4	53.0										
												i	0	18	37	13	30	2	100	87.0	55.0										
	mean																			89.0	58.2									95.0	74.7
4	Stonybridge	4a	0	8	0	50	29	0	87	42.5	9.2	4c	0	28	35	14	39	0	116	87.9	54.3	4e	0	46	29	3	22	3	103	97.1	72.8
		b	0	2	3	57	21	0	83	31.3	6.0	d	0	0	1	5	5	0	11	54.5	9.1	f	0	14	21	14	21	1	71	80.3	49.3
	mean									36.9	7.6									71.2	31.7									88.7	61.0
5	Kilpheder	5a	0	2	0	17	31	0	50	66.0	4.0	5c	0	10	0	25	52	0	87	71.3	11.5	5e	0	22	9	20	49	2	111	73.9	27.9
		b	0	2	0	13	26	0	41	68.3	4.9	d	0	12	0	28	49	0	89	68.5	13.5										
	mean									67.1	4.5									69.9	12.5									73.9	27.9
6	Barra	6a	0	1	0	10	29	0	40	75.0	2.5	6c	0	4	0	3	12	0	19	84.2	24.1	6f	0	23	0	11	49	0	83	86.7	27.7
		b	0	8	0	27	38	0	73	63.0	11.0	d	0	14	0	16	56	0	86	81.4	16.3	g	0	29	0	12	57	0	98	87.0	29.6
												e	0	12	0	15	33	0	60	75.0	20.0	h	0	27	0	17	60	0	104	83.7	26.0
																						i	0	29	0	12	60	0	101	88.1	28.7
																						j	0	30	0	15	64	0	109	86.2	27.5
																						k	0	38	0	10	54	0	102	90.2	37.3
																						l	0	32	1	7	56	0	96	92.7	34.4
	mean									69.0	6.8									80.2	19.1									87.9	30.2
7	Sanna	7a	0	2	0	5	30	7	37	86.5	5.4											7b	0	26	0	1	10	0	37	97.3	70.3
																						c	0	18	0	9	18	0	45	80.0	40.0
	mean									86.5	5.4																			88.7	55.2
8	Portstewart											8a[1]	1	46	42	3	20	0	112	96.4	79.5	8b	0	31	196	17	41	7	292	94.2	77.7
9	Tramore	9a	0	5	0	14	25	0	44	68.2	11.4	9c	4	29	1	59	55	0	148	57.4	23.0	9e	0	24	0	1	9	0	34	97.1	70.6
		b	0	5	0	25	4	0	34	26.5	14.7	d	1	22	0	45	53	0	121	62.0	19.0										
	mean									47.4	13.1									59.7	21.0									97.1	70.6

Downloaded from rstb.royalsocietypublishing.org

																						c[2]	2	2	22	18	61	8	113	82.3	23.0
	mean									89.2	16.7																			95.5	52.0
11	Youghal											11a	0	16	1	5	7	0	29	82.8	58.6	11c	0	18	4	1	13	1	37	97.3	59.5
												b	4	138	1	19	69	0	231	90.0	61.9										
	mean																			86.4	60.3									97.3	59.5
12	South Angle	12a	0	1	0	49	18	0	68	27.9	1.5	12b	0	23	0	34	62	2	121	71.9	19.0	12c	0	22	0	23	32	4	81	71.6	27.2
																						d	0	16	0	26	38	0	80	67.5	20.0
	mean									27.9	1.5									71.9	19.0									69.6	23.6
13	Port Eynon	13a	0	26	0	153	62	0	241	36.5	10.8	13c[6]	3	13	0	41	25	0	82	46.3	19.5	13g[6]	0	6	0	4	15	0	25	84.0	24.0
		b	0	7	0	64	38	0	109	41.3	6.4	d	0	58	0	13	42	0	113	88.5	51.3										
												e[5]	0	47	1	10	37	0	95	89.5	50.5										
												f	0	1	0	21	19	0	41	48.8	2.4										
	mean									38.9	8.6									68.3	30.9									84.0	24.0
14	Polzeath											14a	3	27	3	35	46	2	116	67.2	28.4	14b	4	37	0	29	33	4	107	69.2	38.3
15	Ambleteuse	15a	0	2	4	57	17	15	95	40.0	6.3	15b	5	20	6	50	14	11	106	48.1	29.2	15c	0	0	48	0	1	1	50	100.0	96.0
16	Seaford											16a	2	38	4	3	2	0	49	89.8	89.8	16b	7	16	0	31	27	0	81	53.1	28.4
17	Mawgan	17a	1	4	0	18	9	9	41	53.7	12.2	17g	3	15	12	17	21	7	75	73.3	40.0	17n	25	26	7	42	15	24	139	51.8	41.7
		b	6	9	3	30	12	9	69	47.8	26.1	h	2	12	1	14	9	6	44	63.6	34.1	o[10]	14	49	11	30	16	22	142	69.0	52.1
		c	5	15	14	60	43	8	145	55.2	23.4	i	2	8	2	51	11	14	88	39.8	13.6	p	9	12	0	26	3	1	51	31.4	41.2
		d	4	22	0	64	20	0	110	38.2	23.6	j	12	17	4	68	17	8	126	36.5	26.2	q[11]	4	14	2	11	14	8	53	71.7	37.7
		e	8	5	0	59	14	3	89	24.7	14.6	k	8	4	8	30	23	16	89	57.3	22.5	r	11	54	7	15	9	22	118	78.0	61.0
		f	8	4	1	52	4	3	72	16.7	18.1	l	4	8	4	18	8	14	56	60.7	28.6	s	7	28	7	19	14	16	91	71.4	46.2
												m	6	6	7	33	38	11	101	61.4	18.8	t	14	18	5	29	20	19	105	59.0	35.2
	mean									39.4	19.7									56.1	26.3									61.8	45.0
18	Holywell	18a	0	7	3	58	36	5	109	46.8	9.2	18c[2, 8]	5	37	14	27	32	6	121	73.6	46.3	18f	1	45	29	2	25	9	111	97.3	67.6
		b	2	6	0	58	11	7	84	28.6	9.5	d[2]	6	28	15	20	30	6	105	75.2	46.7	g	4	21	15	20	22	2	84	71.4	47.6
												e	1	6	6	23	13	13	62	61.3	21.0	h[18]	1	4	16	11	27	10	69	82.6	30.4
																						i	0	9	12	14	36	27	98	85.7	21.4
																						j	0	9	24	5	27	25	90	94.4	36.7
																						k[9, 16, 17]	1	45	26	1	19	5	97	97.7	74.2
	mean									37.7	9.4									70.0	38.0									88.2	46.3
19	Penhale	19a	0	3	1	21	9	0	34	38.2	11.8	19b	0	25	15	18	32	12	102	82.4	39.2	19c[11]	1	28	37	1	13	6	86	97.7	76.7
20	Perran	20a	4	11	4	48	16	4	87	40.2	21.8	20c	0	4	6	6	3	2	21	71.4	47.6	20e	0	5	22	16	29	25	97	83.5	27.8
		b	0	2	2	38	12	1	55	30.9	7.3	d	5	31	35	24	12	4	111	73.9	64.0	f	1	8	33	26	54	29	151	83.1	27.8
																						g	1	13	41	14	25	30	124	87.9	44.4
																						h	1	18	29	22	22	14	116	80.2	50.0
																						i	3	4	42	20	13	40	122	81.1	40.2
																						j	2	4	18	7	19	6	56	83.9	42.9
	mean									36.6	14.6									72.7	55.8									83.1	38.9
21	Perranporth	21a	3	14	22	60	22	4	125	49.6	31.2	21i	0	1	32	0	1	4	38	100.0	86.8	21q	8	23	20	11	6	9	77	75.3	66.2
		b	2	8	19	77	19	14	139	43.2	20.9	j	0	2	63	0	1	10	76	100.0	85.5	r	4	14	153	3	4	15	193	96.4	88.6
		c	4	3	5	20	1	4	37	35.1	32.4	k	17	11	47	29	6	6	116	60.3	64.7	s	4	5	48	10	6	21	94	85.1	60.6
		d	16	8	7	24	4	4	63	36.5	49.2	l	6	6	34	45	17	3	111	54.1	41.4	t	1	0	55	7	1	8	72	88.9	77.8
		e	5	12	19	56	8	17	117	47.9	30.8	m	14	21	43	87	13	23	201	49.8	38.8	u	1	4	18	9	4	5	41	75.6	56.1
		f	10	3	15	57	4	5	94	28.7	29.8	n	14	15	9	43	12	1	94	39.4	40.4	v	4	12	47	24	10	29	126	77.8	50.0

Downloaded from rstb.royalsocietypublishing.org

		exposed sand										mixed vegetation										close turf									
			CO			DO							CO			DO							CO			DO					
colony ref. no.	colony	sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO	sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO	sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO
	Perranporth (*cont.*)	21g	8	0	17	56	2	19	102	37.3	24.5	21o	15	15	5	64	7	3	109	27.5	32.1	21w	1	12	64	9	7	26	119	91.6	64.7
		h	11	6	13	52	8	8	98	35.7	30.6	p	5	15	8	47	7	9	91	42.9	30.8	x	11	9	40	28	13	7	108	63.9	55.6
																						y	4	9	37	13	2	8	73	76.7	68.5
																						z	5	16	27	13	1	4	66	72.7	72.7
																						aa	15	23	31	21	15	7	112	67.9	61.6
	mean									39.2	31.2									59.3	52.6									79.3	65.7
22	Porth towan	22a	0	3	6	65	21	9	104	37.5	8.7	22c[19]	1	27	22	20	60	21	151	86.1	33.1	22d	0	22	23	26	54	25	150	82.7	30.0
		b	0	1	2	27	53	12	95	71.6	3.2																				
	mean									54.6	6.0									86.1	33.1									82.7	30.0
23	Godrevy	23a	1	24	3	97	53	1	179	45.3	15.6	23f	5	68	9	17	21	1	121	81.8	67.8	23j	1	93	13	2	12	3	124	97.6	86.3
		b	1	7	2	64	28	1	103	36.9	9.7	g	3	52	14	16	14	2	101	81.2	68.3	k	2	40	4	2	12	2	62	93.5	74.2
		c	4	16	2	55	43	0	120	50.8	18.3	h	4	39	6	22	41	0	112	76.8	43.8	l	1	17	6	14	30	2	70	78.6	34.3
		d	0	13	1	69	45	1	129	46.5	10.9	i[11]	9	36	27	39	48	3	162	70.4	44.4	m	0	82	4	2	18	3	109	98.2	78.9
		e	3	12	1	59	50	0	125	50.4	12.8											n	0	19	14	9	33	3	78	88.5	42.3
																						o	0	21	13	17	16	2	69	75.4	49.3
																						p	0	54	5	1	7	0	67	98.5	88.1
																						q	0	59	7	1	8	0	75	98.7	88.0
																						r[20]	1	110	8	0	9	0	128	99.2	93.0
																						s[2]	3	55	3	20	32	1	114	79.8	53.5
																						t	0	71	11	1	4	0	87	98.9	94.3
																						u	0	78	13	1	9	5	106	99.1	95.8
																						v	1	65	6	3	6	3	84	95.2	85.7
																						w	0	47	5	1	10	0	63	98.4	82.5
																						x	2	76	10	1	3	2	94	96.8	93.6
																						y[1]	1	83	21	0	10	2	117	99.1	89.7
																						z	1	56	23	2	12	0	94	96.8	85.1
																						aa	1	37	31	1	3	2	75	97.3	92.0
																						ab	3	79	7	2	7	3	101	95.0	88.1
																						ac[6, 15]	0	54	6	0	6	2	68	100.0	88.2
																						ad	2	111	8	4	6	4	135	95.6	89.6
																						ae	1	77	16	1	9	4	108	98.1	87.0
																						af	1	54	17	2	8	1	83	96.4	86.7
																						ag	1	78	10	1	7	3	100	98.0	87.0
																						ah	2	54	9	23	36	0	124	79.8	52.4
	mean									46.0	13.5									77.6	56.1									94.1	79.1
24	Gwithian	24a	0	1	0	8	4	0	13	38.5	7.7	24b	7	31	4	77	66	14	199	57.8	21.1	24h	3	45	0	40	42	0	130	66.9	36.9
												c	32	23	0	60	36	0	151	39.1	36.4	i	4	68	1	31	48	7	159	78.0	45.9
												d	3	17	2	20	43	7	92	75.0	23.9	j	0	78	2	28	71	3	182	84.6	44.0
												e	6	40	3	48	41	17	155	65.2	31.6	k	0	43	19	0	39	7	108	100.0	57.4
												f	6	36	0	44	40	4	130	61.5	32.3										
												g	0	13	0	0	10	0	23	100.0	56.5										
	mean									38.5	7.7									66.4	33.6									82.4	46.1

Downloaded from rstb.royalsocietypublishing.org

25	Upton											25a	2	18	1	30	32	15	98	67.3	21.4	25e	18	48	8	30	24	6	134	64	
												b	0	19	3	19	27	2	70	72.9	31.4	f	20	68	0	18	14	0	120	68.[illegible]	73.3
												c	4	21	1	34	14	0	74	48.6	35.1	g	6	32	0	8	2	3	51	72.5	74.5
												d	33	27	4	21	13	3	101	46.5	63.4										
	mean																			58.8	37.8									68.3	67.7
26	Phillack											26a	1	19	5	27	58	3	113	75.2	22.1	26h	11	35	8	12	19	3	88	73.9	61.4
												b	0	30	3	25	52	7	117	78.6	28.2	i	7	33	2	33	43	0	118	66.1	35.6
												c	3	19	0	10	22	2	56	76.8	39.3	j	3	28	1	22	15	2	71	64.8	45.1
												d	8	32	3	42	46	2	133	62.4	32.3										
												e	8	30	8	16	30	8	100	76.0	46.0										
												f	4	18	3	3	10	0	38	81.6	65.8										
												g	12	39	2	23	30	2	108	67.6	49.1										
	mean																			74.0	40.4									68.3	47.4
27	Fort Mahon	27a	11	1	0	67	4	0	83	6.0	14.5	27c	9	10	0	80	11	1	111	19.8	17.1	27h	17	12	2	59	15	0	105	27.6	29.5
		b	2	1	0	58	1	0	62	3.2	4.8	d	0	2	0	34	1	0	37	8.1	5.4										
												e	13	7	1	73	13	2	109	21.1	19.3										
												f	7	1	0	33	3	2	46	13.0	17.4										
												g	12	5	0	67	2	0	86	8.1	19.8										
	mean									4.6	9.7									14.0	15.8									27.6	29.5
28	Jonville	28a	16	6	0	54	0	8	84	16.7	26.2	28d	7	8	1	61	15	0	92	26.1	17.4										
		b	3	3	0	43	6	0	55	16.4	10.9	e	10	3	0	48	10	0	71	18.3	18.3										
		c	7	5	0	66	13	0	91	19.8	13.2	f	24	16	0	105	20	0	165	21.8	24.2										
	mean									17.6	16.7									22.1	20.3										
29	La Renaudière	29a	1	1	0	98	13	0	113	12.4	1.8	29b	0	4	0	67	29	0	100	33.0	4.0	29e	1	19	0	22	26	0	68	66.2	29.4
												c	0	15	0	62	39	0	116	46.6	12.9										
												d	0	6	0	19	12	0	37	48.6	16.2										
	mean									12.4	1.8									42.7	11.0									66.2	29.4
30	Utah Beach	30a	4	1	1	56	13	0	75	20.8	8.0	30d	0	2	0	48	46	0	96	50.0	2.1										
		b	9	1	4	59	11	1	85	20.0	16.5	e	1	5	0	29	57	0	92	67.4	6.5										
		c	10	1	0	56	1	1	69	4.3	15.9	f	5	2	9	57	12	5	90	31.1	17.8										
												g	7	6	9	57	13	2	94	31.9	23.4										
	mean									14.8	13.5									45.1	12.5										
31	La Barbarie	31a	11	1	0	46	2	0	60	5.0	20.0	31b	4	24	0	22	25	0	75	65.3	37.3	31e	22	84	2	47	52	3	210	67.1	51.4
												c	7	17	3	11	4	0	42	57.1	64.3										
												d	3	22	0	36	34	4	99	60.6	25.3										
	mean									5.0	20.0									61.0	42.3									67.1	51.4
32	Le Conquet	$32a^1$	9	17	1	59	24	0	110	38.2	24.5	32b	0	1	2	6	8	8	25	76.0	12.0										
												c	31	21	0	90	31	3	177	31.6	29.9										
												d	0	3	6	27	38	19	93	71.0	9.7										
												e	0	0	0	10	9	2	21	52.4	0										
												f	1	2	0	28	34	0	65	55.4	4.6										
	mean									38.2	24.5									57.3	11.2										
33	Pte de Trévignon	33a	1	2	0	28	5	0	36	19.4	8.3	33b	0	9	4	12	31	62	118	89.8	11.0										
34	Kerfany											34a	0	26	1	19	62	1	109	82.6	24.8	$34b^{11}$	0	33	1	11	12	0	57	80.7	59.6

Downloaded from rstb.royalsocietypublishing.org

		exposed sand										mixed vegetation										close turf									
	colony		CO			DO							CO			DO							CO			DO					
colony ref. no.		sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO	sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO	sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO
35	La Faute	35a[2, 15]	16	17	0	44	21	1	99	39.4	33.3	35c	3	2	0	41	41	0	87	49.4	5.7	35f[3, 26]	14	25	0	15	20	4	78	62.8	50.0
		b[2, 16]	19	15	2	38	20	1	95	40.0	37.9	d	6	15	0	50	45	1	117	52.1	17.9										
												e[2, 15]	10	9	0	35	32	2	88	48.9	21.6										
	mean									39.7	35.6									50.1	15.1									62.8	50.0
36	Le Colombier	36a	0	0	0	46	8	0	54	14.8	0	36c	1	24	7	21	33	1	87	74.7	36.8	36e	5	51	4	7	9	1	77	84.4	77.9
		b	3	21	3	54	77	0	158	63.9	17.1	d	1	29	4	23	29	2	88	72.7	38.6	f	2	17	3	6	22	0	50	84.0	44.0
	mean									39.4	8.6									73.7	37.7									84.2	61.0
37	Biarritz	37a	11	7	0	64	9	0	91	17.6	19.8	37c	12	14	2	30	39	0	97	56.7	28.9	37j	23	53	1	18	15	0	110	62.7	70.0
		b	23	11	0	31	10	0	75	28.0	45.3	d	11	25	0	49	20	2	107	43.9	33.6	k	44	60	0	17	9	0	130	53.1	80.0
												e	8	22	4	29	39	2	104	64.4	32.7	l	47	74	0	26	21	0	168	56.5	72.0
												f	12	32	3	33	27	1	108	58.3	43.5										
												g	10	36	1	36	23	0	106	56.6	43.3										
												h	7	26	0	40	36	0	109	56.9	30.3										
												i	3	18	2	33	15	4	75	52.0	30.7										
	mean									22.8	32.6									55.5	34.9									57.4	74.0
38	La Barre	38a	14	5	0	48	6	0	73	15.1	26.0	38b	6	13	0	38	15	0	72	38.9	26.4										
39	Ilbarritt	39a	0	1	0	82	1	0	93	2.2	10.8	39c	6	20	0	85	20	0	131	30.5	19.8	39f	15	3	0	24	35	0	77	49.4	23.4
		b	17	1	0	75	2	0	95	3.2	18.9	d	5	3	0	49	20	0	77	29.9	10.4										
												e	9	6	0	66	25	0	106	29.2	14.2										
	mean									2.7	14.9									29.9	14.8									49.4	23.4
40	Bidart	40a	10	10	0	46	24	0	90	37.8	22.2	40b	10	21	0	23	15	0	69	52.2	44.9	40d	9	19	0	31	19	0	78	48.7	35.9
												c	2	34	0	19	18	0	73	71.2	49.3	e	12	21	0	18	14	0	65	53.8	50.8
	mean									37.8	22.2									61.7	47.1									51.3	43.4
41	Hendaye	41a	17	28	0	35	18	0	98	46.9	45.9	41d	9	30	0	34	34	0	107	59.8	36.4										
		b	8	24	6	42	17	0	97	48.5	39.2	e	9	38	4	34	17	0	102	57.8	50.0										
		c	12	22	0	34	16	0	84	45.2	40.5																				
	mean									46.9	41.9									58.8	43.2										
42	Cunndal	42a	0	0	0	90	0	0	90	0	0																				
43	Gress	43a[21]	1	0	0	77	0	0	78	0	1.3																				
44	Coll	44a	0	0	0	35	0	0	35	0	0																				
45	Valtos																					45a	0	1	24	5	14	7	51	90.2	49.0
46	Starasta																					46a	0	0	42	14	4	4	64	78.1	65.6
																						b	0	4	31	26	18	0	79	67.1	44.3
	mean																													72.	

Downloaded from rstb.royalsocietypublishing.org

47	ollachar																						47a	0	31	29	18	23	0	101	82.2	59.4
48	Scarinish																						48a	0	35	29	0	24	11	99	100.0	64.6
49	Sheeps Haven											49a	0	0	0	21	4	0	25	16.0	0									
50	Streedagh	50a[22]	39	0	0	156	0	0	195	0	20.0																			
		b[22]	31	0	0	89	0	0	120	0	25.8																			
	mean									0	22.7																			
51	Mullaghmore	51a	3	1	2	31	0	0	37	8.1	16.2																			
52	Corballis																						52a[6, 15]	1	167	28	3	21	2	222	98.2	88.3
53	Dogs Bay																						53a[13]	16	28	0	8	15	19	86	72.1	51.2
54	Brittas Bay											54a	0	42	1	27	111	2	183	85.2	23.5									
55	Ferriter's Cove	55a	5	30	0	63	30	0	128	46.9	27.3																			
56	Ventry																						56a	5	52	16	8	14	0	95	86.3	76.8
57	Marloes																						57a	0	160	0	5	29	0	194	97.4	82.5
58	Sangatte											58a[12]	42	0	17	39	0	0	98	17.3	60.2									
												b	12	1	11	34	0	1	59	22.0	40.7									
												c	29	9	5	25	0	0	68	20.6	63.2									
	mean																			20.0	54.7									
59	Berrow	59a	4	3	0	47	3	0	57	10.5	12.3																			
60	Richborough											60a	8	45	14	18	15	4	104	75.0	64.4									
												b	4	16	4	14	9	0	47	61.7	51.1									
	mean																			68.4	57.8									
61	Fistral											61a	0	13	5	13	18	4	53	75.5	34.0									
62	Portreath											62a	0	7	0	98	27	0	132	25.8	5.3									
63	Porth Farm																						63a[14]	15	43	0	45	3	0	106	43.4	54.7
64	White Sand Bay											64a	0	2	4	0	52	25	83	100.0	7.2									
												b	0	0	0	0	26	21	47	100.0	0									
	mean																			100.0	3.6									
65	Blonville											65a[2]	18	13	0	25	2	0	58	25.9	53.4									
												b	22	35	1	9	9	0	76	59.2	76.3									
	mean																			42.6	64.9									
66	Deauville	66a	1	11	0	93	38	1	144	34.7	8.3																			
67	Villiers											67a	18	17	0	30	4	0	69	30.4	50.7									
68	Merville	68a	13	0	0	67	0	0	80	0	16.2																			
69	St Pabu																						69a	0	86	1	30	73	14	204	85.3	42.6
																							b	4	38	0	9	9	3	63	79.4	66.7
	mean																														82.4	54.7
70	Sables d'or	70a	0	0	0	98	4	0	102	3.9	0																			
		b	0	0	0	70	0	0	70	0	0																			
	mean									2.0	0																			

Downloaded from rstb.royalsocietypublishing.org

TABLE 1 (*cont.*)

		exposed sand										mixed vegetation										close turf									
	colony		CO			DO							CO			DO							CO			DO					
colony ref. no.		sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO	sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO	sample ref. no.	unbanded	one-banded	more-than-one-banded	unbanded	one-banded	more-than-one-banded	total	% banded	% CO
71	Kerhornous											71a	2	6	0	5	18	0	31	77.4	25.8										
72	Dournenez	72a	7	12	0	68	10	0	97	22.7	19.6																				
73	Trèxen											73a	0	0	0	27	30	1	58	53.4	0										
74	Kervel											74a	0	1	0	13	35	0	49	73.5	2.0										
												b	0	2	0	9	28	0	39	76.9	5.1										
	mean																			75.2	3.6										
75	Le Poldu																					75a	18	81	2	7	10	1	119	79.0	84.9
																						b	22	43	2	8	7	1	83	63.9	80.7
																						c[11,15]	10	59	1	3	14	0	87	85.1	80.5
	mean																													76.0	82.0
76	Batz											76a	42	9	0	16	0	0	67	13.4	76.1										
												b[1]	7	34	0	8	17	0	66	77.3	62.1										
	mean																			45.4	69.1										
77	La Parée											77a	1	4	0	44	30	0	79	43.0	6.3										
78	Bourgenez											78a	0	5	0	47	43	0	95	50.5	5.3										
79	Ile D'Olèron	79a	2	16	14	39	41	7	119	65.5	26.9																				
80	Pte Espagnole																					80a	7	16	11	23	22	0	79	62.0	43.0

[1] One: 00005.
[2] One: 00300.
[3] Two: 00300.
[4] Five: 00300.
[5] One: 02040.
[6] Some CO: 00040 not white but pale coffee coloured.
[7] One: pigment banding (123)40 with structural banding 00040.
[8] Two: pigment banding (123)40 with structural banding 00040.
[9] Three: pigment banding (123)40 with structural banding 00040.
[10] Five: pigment banding (123)40 with structural banding 00040.
[11] One: 00040 hz.
[12] Two: 00040 hz.
[13] Three: 00040 hz.
[14] Five: 00040 hz.
[15] One: pigment banding 00340 with structural banding 00040.
[16] Two: pigment banding 00340 with structural banding 00040.
[17] Two: pigment banding (123)(45) with structural banding 00040.
[18] Two: DO 00040 quite colourless ('albino').
[19] Several 00000, 00040 and 00(345) not opaque at all and with deep ginger ground colour.
[20] One: pigment banding 00040 with structural banding 00000 (i.e. all CO).
[21] One: CO unbanded and lacking ground colour.
[22] All DO unbandeds lack ground colour.

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The depression differs from other parts of the field in a number of respects, of which the most evident are that it is wet and that the surface layer of the sand is very dark in colour. Although the sand there is several feet deep, the water table, even in August, remains at less than three feet below the surface. Another characteristic feature of the middle part of the depression is the abundant growth of *Agrostis stolonifera* L., and a paucity of other plant species so that the sandy substrate which is very dark in colour is quite visible. The top of the hillside gradually merges into a plateau. At the seaward (western) end its uneven surface is of exposed sand with coarse tussocks of Marram grass. In an easterly direction, it becomes progressively more densely covered by Marram and other grasses.

Table 2

		exposed sand			mixed vegetation		
colony ref. no.	colony	unbanded (%)	one-banded (%)	more-than-one-banded (%)	unbanded (%)	one-banded (%)	more-than-one-banded (%)
1	Veilish	—	—	—	14.2	52.8	33.0
2	Nunton	47.7	42.1	10.2	33.2	46.8	20.0
3	South Nunton	—	—	—	12.2	45.4	42.4
16	Kilmichael	10.8	68.6	20.6	—	—	—
17	Mawgan	60.6	28.8	10.6	44.1	36.1	19.8
18	Holywell	62.3	29.8	7.9	30.0	47.7	22.3
20	Perran	69.4	28.2	2.4	27.3	36.0	36.7
21	Perranporth	60.8	14.9	24.3	54.4	20.9	24.7
22	Porth Towan	45.4	40.0	14.6	13.9	57.6	28.5
23	Godrevy	54.0	42.1	3.9	20.1	70.1	9.8
33	Pte de Trévignon	80.6	19.4	0	—	—	—
46	Starasta	—	—	—	—	—	—
48	Scarinish	—	—	—	—	—	—

		close turf			dark substrate		
colony ref. no.	colony	unbanded (%)	one-banded (%)	more-than-one-banded (%)	unbanded (%)	one-banded (%)	more-than-one-banded (%)
1	Veilish	—	—	—	9.5	53.7	36.8
2	Nunton	19.5	54.9	25.6	15.2	54.3	30.5
3	South Nunton	6.6	65.7	27.7	7.4	43.2	49.4
16	Kilmichael	17.7	55.8	26.5	1.3	2.5	96.2
17	Mawgan	40.9	40.7	18.4	35.2	39.9	24.9
18	Holywell	13.0	54.6	32.4	5.6	40.0	54.4
20	Perran	16.5	36.5	47.0	18.9	14.0	67.1
21	Perranporth	27.8	25.8	46.4	8.8	8.9	82.3
22	Porth Towan	—	—	—	17.3	50.7	32.0
23	Godrevy	5.9	80.1	14.0	29.6	51.8	18.6
33	Pte de Trévignon	—	—	—	10.2	33.9	55.9
46	Starasta	32.9	27.9	39.2	21.9	6.2	71.9
48	Scarinish	—	—	—	0	59.6	40.4

(ii) *Survey: Godrevy*

Although a number of population samples had already been obtained from Godrevy in the course of the major survey, there were areas of the colony that had not been sampled. From

Downloaded from rstb.royalsocietypublishing.org

such areas further samples were collected. The composition of each was determined as before, according to phenotypes:

unbanded and continuously opaque (CO)
one-banded and CO
more-than-one-banded and CO
unbanded and discontinuously opaque (DO)
one-banded and DO
more-than-one-banded and DO

The results for all the Godrevy samples are recorded in table 3, and shown on the map, figure 8. On the map, each disk represents a single sample. The extent of the sectoring shows its composition and its position (on the map) the place of origin in the colony.

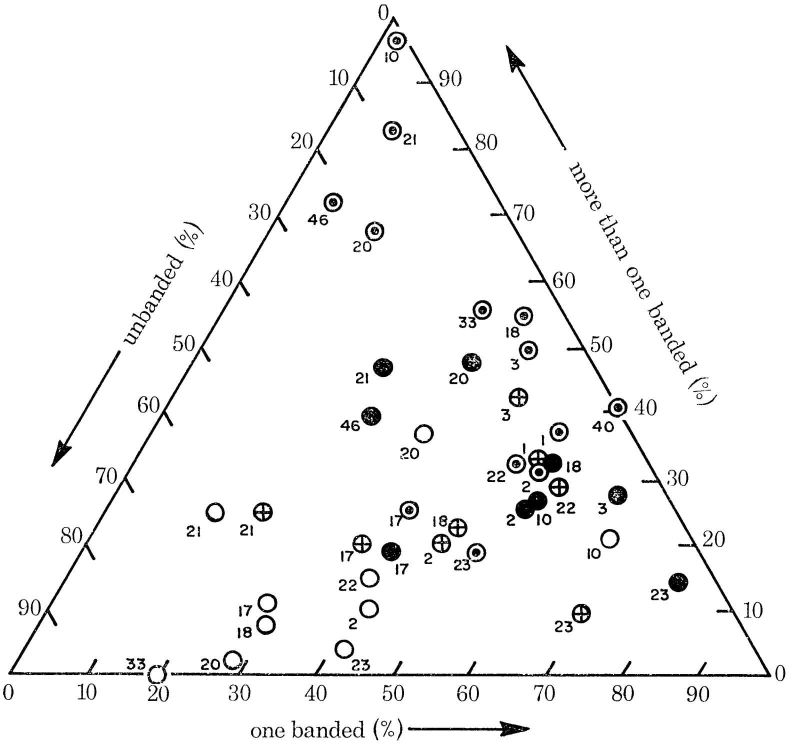


Figure 6. A scatter diagram showing the composition of populations in different types of habitat for those colonies in which dark substrates occur. In six of the colonies (nos. 2, 17, 18, 20, 21 and 23) the other three habitat types also occur and each of these colonies is therefore represented by four plots, one for each habitat type. No type besides the dark substrate type occurs in no. 48 and consequently there is only one plot representing that colony. The four habitat types are denoted by different symbols, three of which are the same as those used in figure 5. Population composition is shown in terms of banding only. Colony reference numbers accompany each plot (see table 1 and figure 4). ⊙, Dark substrate; ⊕, mixed vegetation; ●, close turf; ○, exposed sand.

The relationships that have been demonstrated in the major survey between habitat type and the frequencies of certain morphs can be seen to apply throughout the colony. Populations that are less banded and more discontinuously opaque occur in areas where there is more exposed sand, as is well shown by the populations of *Cochlicella actua* (represented by the samples a, b, c, d, e, f, g, h, s, v and u) taken from the seaward end of the hill and the steeply-sloping hillside where the sandy substrate is much exposed.

Downloaded from rstb.royalsocietypublishing.org

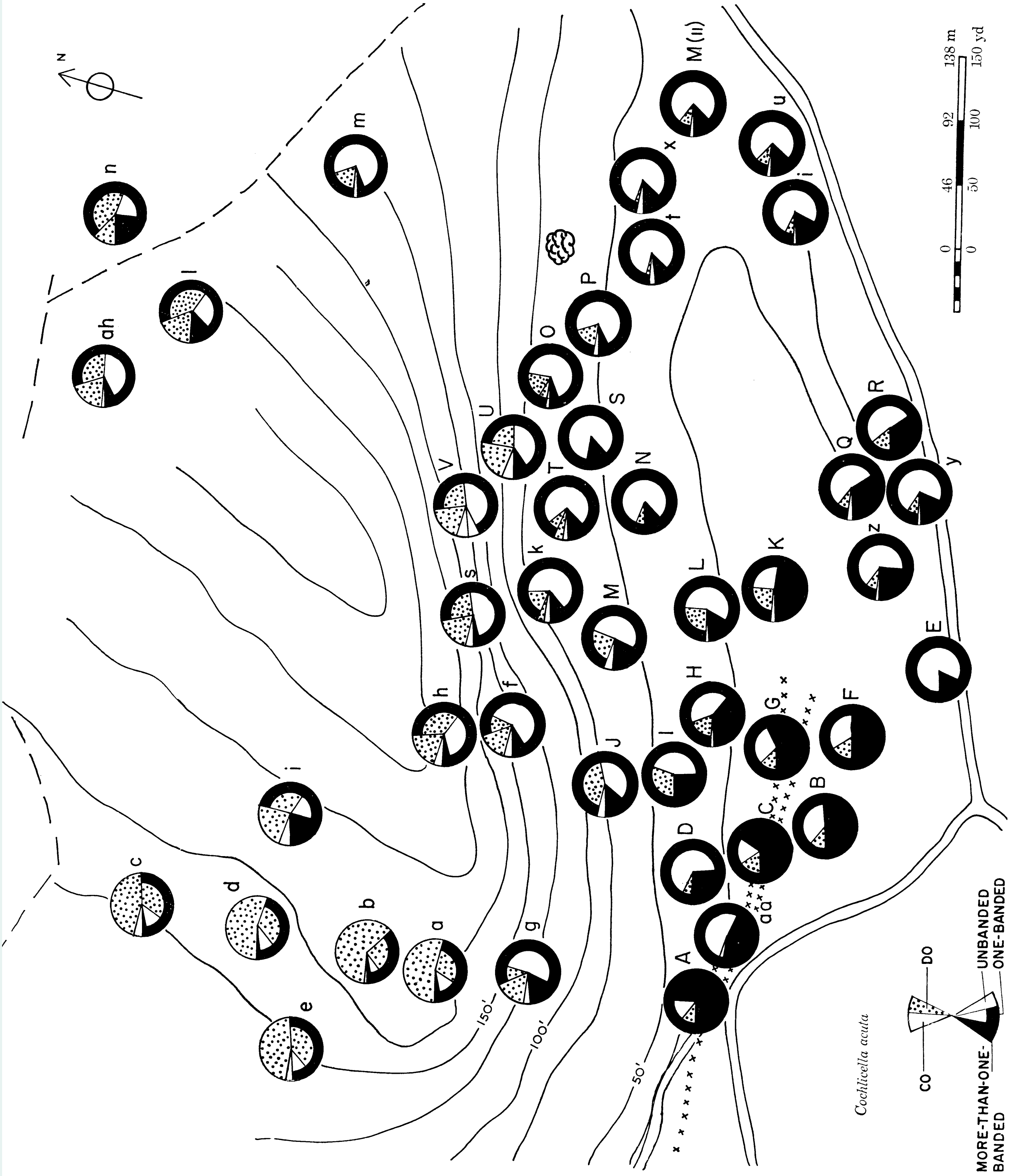
FIGURE 7. An aerial photograph of the site at Godrevy showing the principal features of the area. The line drawn on the photograph represents the transect (see figure 9).

Downloaded from rstb.royalsocietypublishing.org

TABLE 3. COLONY: GODREVY

sample ref.	unbanded (%)			one-banded (%)			more-than-one-banded (%)	total size of sample
	CO	DO	total	CO	DO	total		
a	1	54	55	13	30	43	2	179
b	1	62	63	7	27	34	3	103
c	3	46	49	13	36	49	2	120
d	0	53	53	10	35	45	2	129
e	2	47	49	10	40	50	1	125
f	4	14	18	57	17	74	8	121
g	3	6	9	51	14	65	16	101
h	4	20	24	35	36	71	5	112
i	6	24	30	22	30	52	18	162
j	1	2	3	74	10	84	13	124
k	3	3	6	65	19	84	10	62
l	1	20	21	24	43	67	12	70
m	0	2	2	75	17	92	6	109
n	0	12	12	24	42	66	22	78
s	3	18	21	48	27	75	4	114
t	0	1	1	82	4	86	13	87
u	0	1	1	74	8	82	17	106
x	2	1	3	81	3	84	13	94
y	1	0	1	71	9	80	19	117
z	1	2	3	60	13	73	24	94
aa	1	1	2	50	4	54	44	75
A	0	0	0	14	12	26	74	85
B	0	0	0	35	12	47	53	107
C	0	0	0	17	16	33	67	84
D	0	1	1	66	7	73	26	106
E	0	0	0	83	0	83	17	12
F	0	0	0	33	17	50	50	52
G	1	0	1	27	14	41	58	113
H	0	1	1	40	18	58	41	113
I	0	0	0	45	30	75	25	112
J	0	4	4	40	42	82	14	97
K	1	1	2	26	24	50	48	137
L	0	1	1	58	25	83	16	119
M	1	5	6	53	24	77	17	110
N	0	0	0	82	6	88	12	133
O	1	2	3	87	5	92	5	148
P	0	3	3	72	17	89	8	138
Q	0	2	2	57	8	65	33	102
R	0	0	0	53	13	66	34	95
S	0	1	1	90	2	92	7	104
T	2	4	6	74	8	82	12	96
U	6	22	28	43	21	64	8	122
V	6	17	23	46	24	70	7	102
ah	2	18	20	44	29	73	7	124
ab	3	2	5	78	7	85	10	101
ac	0	0	0	79	9	88	12	68
ad	1	3	4	83	4	87	9	135
ae	1	1	2	71	8	79	19	108
af	1	2	3	65	10	75	22	83
ag	1	1	2	78	7	85	13	100
p	0	1	1	81	11	92	7	67
q	0	1	1	79	11	90	9	75
r	1	0	1	86	7	93	6	128
v	1	4	5	77	7	84	11	84
w	0	1	1	75	16	91	8	63
M(11)	1	1	2	77	9	86	12	1012

Downloaded from rstb.royalsocietypublishing.org



PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

In contrast, on the turf in the field, the populations are far less discontinuously opaque and much more banded, those at the eastern end where the turf is denser being predominantly one-banded while those in the lower-lying more westerly end, where the sandy substrate is blacker and more visible being more heavily banded. There are six samples (A, B, C, F, G and K) from that part of the colony in which the percentage of individuals possessing a greater degree of banding than 00040 exceeds 45 %.

Since the total number of samples obtained from habitats classified as dark-substrate type is comparatively very small and the method of habitat classification wholly subjective, the tenuous dark-substrate/heavily-banded morph relationship was investigated further along a transect indicated by the straight line drawn on figure 7.

TABLE 4. SHELLS OF *COCHLICELLA ACUTA*

sample ref. number	unbanded (%)		one-banded (%)		more-than-one-banded (%)	total – size of sample	sand substrate relative reflectivity	
	CO	DO	CO	DO			dry	wet
TR1	15	46	19	12	8	26	21.0 ± 0.6	10.2 ± 0.5
TR2	5	36	29	25	5	44	30.3 ± 0.5	13.8 ± 1.0
TR3	3	16	50	13	18	38	28.5 ± 1.2	13.8 ± 0.7
TR4	0	7	21	25	47	28	19.7 ± 0.8	10.2 ± 0.7
TR5	3	0	21	21	55	29	21.6 ± 0.5	10.6 ± 0.6
TR6	0	0	30	13	57	23	15.8 ± 0.4	5.3 ± 0.1
TR7	0	0	15	23	62	13	16.4 ± 0.5	5.6 ± 0.6
TR8	0	0	35	12	53	34	21.6 ± 0.8	11.9 ± 0.6
TR9	0	0	23	36	41	22	18.0 ± 1.2	8.8 ± 0.9
TR10	0	0	43	22	35	23	14.1 ± 0.7	5.2 ± 1.0
TR11	0	0	24	27	49	33	17.8 ± 0.8	6.3 ± 0.9
TR12	0	0	18	15	67	34	10.1 ± 0.6	4.6 ± 0.5
TR13	0	0	25	25	50	4	19.9 ± 0.5	11.1 ± 0.5
TR14	0	0	34	22	44	18	13.7 ± 0.1	6.9 ± 0.1
TR15	0	0	20	0	80	15	13.7 ± 1.1	6.5 ± 0.1

(iii) *The dark-substrate/heavily-banded morph relationship*

A. *Quantitative comparison of lightness of substrate and morph frequency.* A number of random samples of *Cochlicella acuta* and of the corresponding substrates were collected along a transect, which started at the level of the 60 m (200 ft) contour of the hillside, ran southwards down to the foot, continued across the depression and ended at the south side of the ridge. The intervals between samples were 36 m (40 yd) on the sloping hillside and 9 m (10 yd) along the rest of the transect. The area from which each sample was taken was restricted to a circle of about 1.5 m (5 ft) in diameter and sample sizes of the snails tended to be rather small. The sand samples, each of about 200 ml, were obtained by scooping up about 50 ml of the surface layer of the substrate from several places randomly chosen within the area from which each snail sample had been collected.

In the laboratory, the snails were killed, cleaned and scored for shell banding and opacity as before and quantitative measurements were made of the visible lightness of each substrate sample by determining its relative reflectivity.

FIGURE 8. The compositions of the samples taken from the colony at Godrevy. Each sectored disc represents one sample and its position on the map its location within the colony. The nature of the habitat can be seen by reference to the aerial photograph (figure 7). The scales of the photograph and the map correspond.

Downloaded from rstb.royalsocietypublishing.org

Relative reflectivity measurements were made photoelectrically using a Zeiss Stereo II microscope fitted with a photocell the output of which was measured by a moving-coil microammeter. Values of surface reflectivity relative to a standard white reference surface were obtained respectively for wet and dry conditions of each of the substrate specimens.

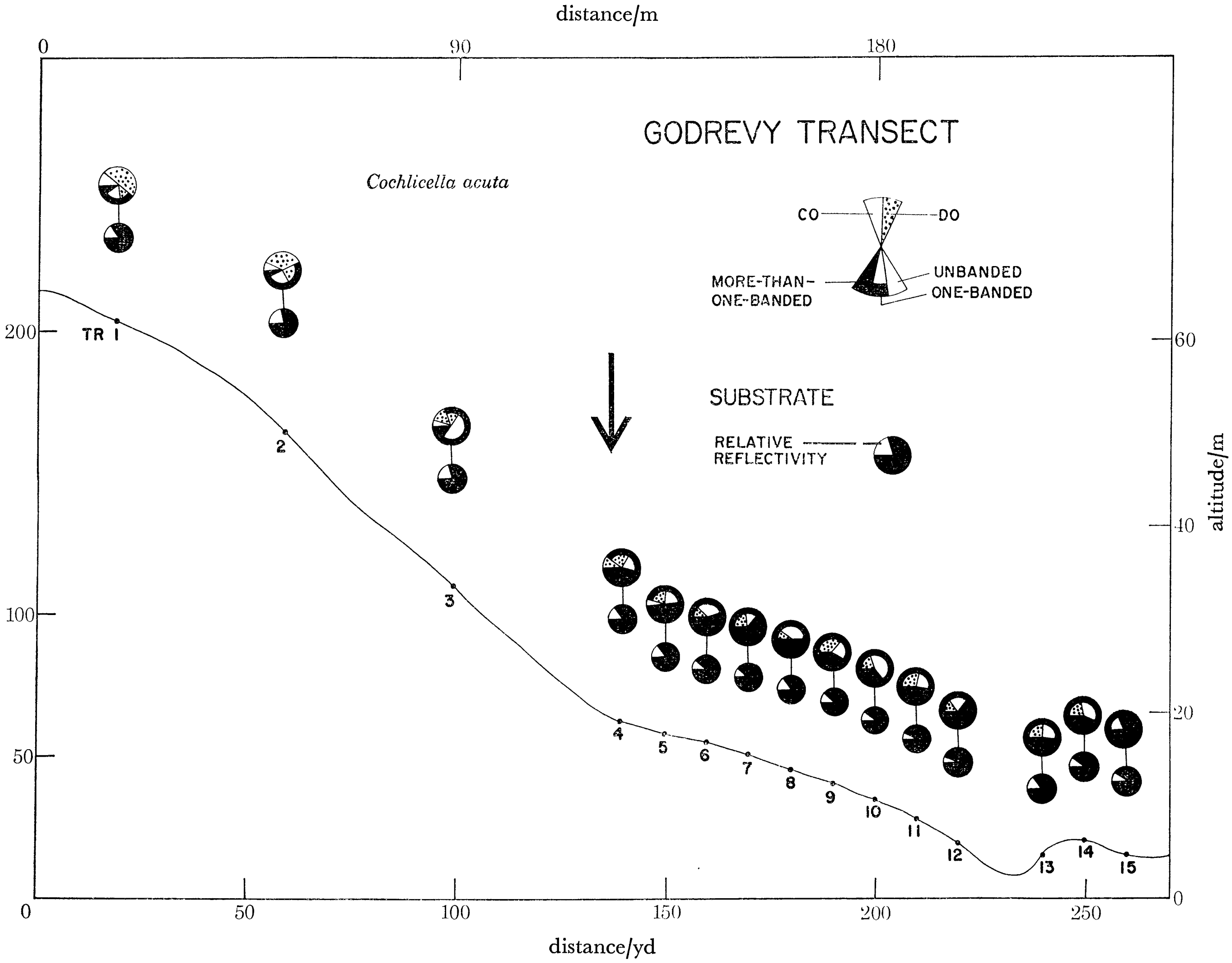


FIGURE 9. Compositions of the snail samples and relative reflectivities of the corresponding sand samples along the transect at Godrevy. The line of the transect is shown in the aerial photograph (figure 7).

The results for the substrate samples and the corresponding snail samples taken along the transect are shown in table 4. Figure 9 shows these diagrammatically. Regressions of substrate relative reflectivity on percentage more-than-one-banded were calculated for the two series. For substrates dry the regression coefficient has the value of -0.185 ± 0.025 and for substrates wet -0.093 ± 0.013. Both of these estimates depart from zero by more than 7 times the standard error, showing that a significant relation exists between the frequency of more-than-one-bandeds and the darkness of the substrate on which they live.

The scatter diagrams for wet and dry conditions respectively are shown in figure 10. In this diagram, percentage more-than-one-banded is plotted against the mean substrate relative

Downloaded from rstb.royalsocietypublishing.org

reflectivity of the corresponding sand sample. Lines indicating standard deviations of the relative reflectivity values and the linear regression lines have also been drawn in.

In reality in the field, the differences between the relative reflectivity of pale and dark sand substrates would be even greater than the results obtained in the laboratory have shown them to be. The principal reason for this is that the dark sand samples used in the laboratory were homogeneous specimens of samples of surface sand taken at Godrevy. In these specimens, the fine particles of humus that give the sand its dark appearance were dispersed throughout the sand in the laboratory but, in the field, it is not usually so dispersed. Heavy rain causes humus to float out from the top few millimetres of the sand and, when drying out subsequently incurs, this blackish scum tends to be left as a fine deposit on the surface of the sand. The actual surface tends to be darker for this reason than it would be if the humus were uniformly distributed in the top layer. This effect can be very easily demonstrated in the laboratory. Another reason is that in reality the substrate samples that were taken from the low-lying places along the transect, that is the darker ones tend to remain wetter than the less dark ones from the hillside, where drying out will be more rapid. *In situ*, the sand in the two places will not very often be equally wet. Except when it is, the differences between their relative reflectivities will be even greater than indicated by the laboratory measurements, which were obtained for equally wet and equally dry conditions respectively.

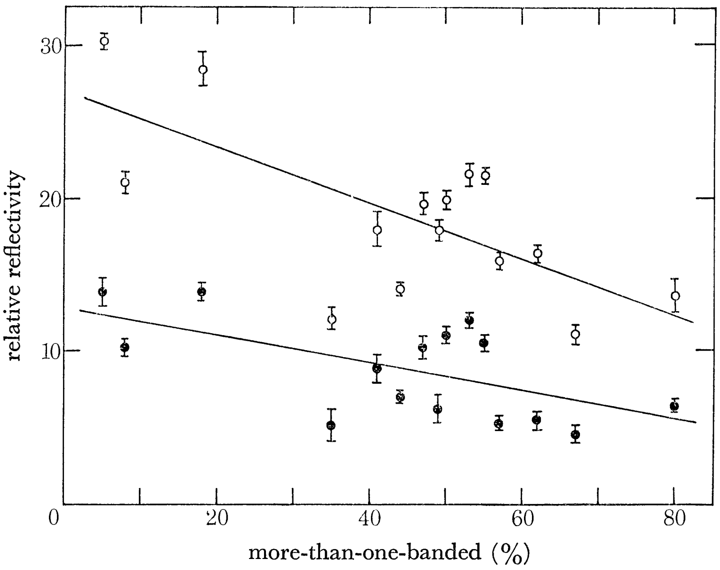


FIGURE 10. Scatter diagrams showing percentage more-than-one-bandeds in the samples in relation to the relative reflectivity of corresponding samples of the substrate, when wet and when dry. Lines indicating the standard deviations and the calculated linear regressions are shown. ○, Sand dry; ●, sand wet.

B. *Heavily-banded morphs in the sympatric species* Cochlicella acuta *and* Helicella virgata. *Helicella virgata* is one of the other species of polymorphic snails that inhabits many of the sand dunes and slacks where *Cochlicella acuta* is found. At Godrevy, it occurs throughout the field areas but most frequently in the low-lying and wetter parts. At the western end of the field, where the higher frequencies of the more-than-one-banded morphs of *Cochlicella acuta* occur most commonly (see figures 7 and 8) the populations of *Helicella virgata* appeared to me to be more heavily banded too. I have demonstrated this correspondence more quantitatively by

Downloaded from rstb.royalsocietypublishing.org

comparing the frequencies of more-than-one-banded forms in the two species in pairs of samples which ecologically correspond exactly in that they were collected together, from the same small area and at the same time. There are 15 such pairs of samples.

TABLE 5

sample reference number	*Cochlicella acuta* more-than-one-banded (%)	*Cochlicella acuta* total	*Helicella virgata* more-than-one-banded (%)	*Helicella virgata* total
aa	44	75	18	34
A	74	85	34	59
B	53	107	13	86
C	67	84	20	30
D	26	106	10	29
F	50	52	17	78
G	58	113	22	79
H	41	113	14	59
L	16	119	6	75
M (11)	12	1012	16	236
N	12	133	0	20
O	5	148	0	3
P	8	138	0	4
Q	34	95	11	35
R	33	102	11	80

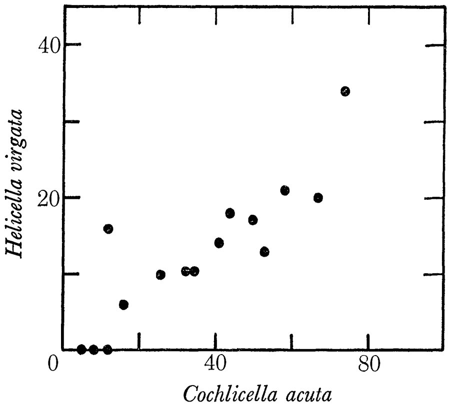


FIGURE 11. A scatter diagram showing the percentages of 'more-than-one-bandeds' in the two sympatric species *Cochlicella acuta* and *Helicella virgata*. Each plot represents a pair of samples collected together from the same area of the site.

As there is no established banding nomenclature for *Helicella virgata*, I classified the shells into two groups, simply distinguishing those that possessed band pigment above the mid-band (that is, towards the apex), from all other states of banding, including mid-banded, since it is only the banding of the upper parts of the shell whorls that contributes significantly to the darker appearance. This procedure was similar to that adopted by Cain & Sheppard (1950), and used by many workers subsequently for distinguishing banded from 'effectively unbanded' shells in *Cepaea*, my more-than-one-banded class corresponding with their banded class.

Table 5 gives the percentages of more-than-one-banded in each species, respectively, and these values are shown plotted against each other in figure 11. It is evident from this diagram, that there is a linear relation between the frequencies of more heavily banded morphs in the

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

two species. The relation associated with a dark substrate that I have established is thus shown to exist not only in respect of *Cochlicella acuta* but of *Helicella virgata* as well. I have insufficient quantitative data to show that this is true elsewhere but observations in other colonies lead me to believe that it is.

(iv) *Visual predation of* Cochlicella acuta *and* Helicella virgata

The visual nature of the relationships that have been shown to exist between certain habitats and the associated snail populations suggests that some predator which hunts by sight is likely to be responsible, such as a bird. Observations made at Godrevy showed that a number of bird species were frequently to be seen in all parts of the colony there. The only ones that were seen regularly to feed on dunes were rooks, *Corvus frugilegus*, and jackdaws, *Corvus monedula*, usually in mixed flocks. At Godrevy, I shot and dissected one jackdaw and two rooks, a young one and a mature one. They were shot when they came sufficiently close to my hide, after they had walked across a piece of the eastern end of the hillside feeding as they came. I found in the gizzards of both rooks but not in that of the jackdaw a number of partly digested snails. They had been taking both *Cochlicella acuta* and *Helicella virgata*, and this provides conclusive evidence of visual predation.

(*c*) *Morph frequencies and selection*

(i) *Cryptic habitat/morph frequency relationships*

In two of the habitat/morph frequency relationships that I have demonstrated, the morphs are very inconspicuous when seen against the substrates on which they live. On sandy substrates the predominating morph being of sandy appearance (see Lewis 1975) blends well with the background while on dark substrates the heavily banded morphs which are very dark in appearance on account of their banding similarly match their backgrounds.

Shell variation in land snails is common but in only a few species has the frequency of different morphs been shown to vary in any discernible way from place to place, *Partula* (Crampton 1916, 1932; Clarke & Murray 1969), *Euparypha* (Porpora & Sacchi 1958), *Pseudotachea splendida* (Sacchi 1956, 1962), *Cepaea nemoralis* (Cain & Sheppard 1954; Cain & Currey 1963; Arnold 1968), *Cepaea vindobonensis* (Jones 1973, 1974), *Hygromia striolata* (Jones *et al.* 1974). There are even fewer instances amongst snails where morph frequencies have been shown to be related to some visibly recognizable property of the habitat, although such relationships have been demonstrated in other kinds of animals (see Mayr 1963 for review). Cain & Sheppard (1950, 1954) and Currey, Arnold & Carter (1964) have shown such a visible relationship in *Cepaea nemoralis*. So has Clarke (1960) in *Cepaea hortensis*. In *Cepaea*, although a visible relationship with habitat has been demonstrated, not all populations of the species exhibit it (Cain & Currey 1964) but, in those that do, the association between colour and banding morphs and the appearance of the habitat is a cryptic one which Cain & Sheppard and their co-workers attribute primarily to visual selection. Experiments designed to test the selective nature of the visual predation of *Cepaea* by thrushes on different background have produced positive results. (Sheppard 1951; Carter 1968). Although visual predation of *Cochlicella acuta* by birds has been proved to occur, it does not follow that such predation is selective. The cryptic nature of the habitat/morph frequency relationships however strongly suggests that it is. Furthermore, the correspondence between the frequencies of the more-heavily-banded morphs of the sympatric species *Helicella virgata* and *C. acuta* seems much more likely to be determined by selective

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

predation than by chance. That this correspondence occurs where the substrate is dark suggests very strongly that the selection responsible is visual.

However closely related the visible features of environments and those of associated morphs may be, the possibility that non-visual factors, which may also be selective, could be operating cannot be excluded. But, in the instances just discussed, the evidence seems to point clearly to visual selection being the principal factor in producing the relationships.

That non-visual factors do operate and, in certain cases, with sufficient strength to over-ride the effects of visual selection is suggested by the quite considerable variation that occurs in the compositions of populations inhabiting habitats of similar appearance in different colonies. The extent of such variation is indicated by the wide scatter of points in figures 1 and 5, for example. Clearly, some of this scatter must be attributed to sampling errors but, as far less variation occurs between samples respectively taken in successive years from the same places, it seems likely that much of it is due to environmental influences that are non-visual and which vary from colony to colony. Visual selection and such non-visual influences cannot be independent. Since the polymorphic shell characteristics upon which visual selection acts do not become evident until the snails are nearly half-grown, visual selection can act only upon populations that have survived the early period in the life cycle during which non-visual factors alone are influential. That both non-visual and visual selective factors are operating is also indicated from considerations of the frequencies of the morphs CO 00000 and CO 00040.

TABLE 6

	colonies between						
	latitude 43° N and 50½° N			latitude 50½° N and 58° N			
	exposed sand	mixed vegetation	close turf	exposed sand	mixed vegetation	close turf	total
number of samples lacking CO unbanded morphs when constituent genes present	7	18	15	16	27	33	116
total number of samples	58	103	87	24	41	40	353
percentage lacking CO unbandeds	12	17.5	17	67	66	82	33

(ii) *Frequency of the morph* CO 00000

In many colonies where it would be expected to occur quite frequently since the constituent genes are present in the population, CO unbandeds are at low frequency or lacking altogether (see table 1). The colonies in the Outer Hebrides provide good examples of this. From the thirteen different colonies in these islands 4308 snails have been collected. Among them only one was CO 00000. A deficiency of this morph in populations in which the constituent genes are present is not confined to colonies in the Outer Hebrides but it does appear to occur much more frequently in the populations in the northern parts of the species' range than further south. Table 6 shows the frequency of occurrence of this disequilibrium for the three habitat types in the geographical areas respectively north and south of latitude 50½° N. There is a marked difference between the two areas but in neither is there any significant difference between habitat types. For the southern area $P \approx 0.7$ and for the northern one $P \approx 0.6$. Visually, the

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

morph CO 00000 closely resembles CO 00040 because the two are alike except for the single band, that being visible only in the last shell-whorl (Lewis 1975). Usually, CO 00040 is found quite commonly in populations in which the CO 00000 morph-frequency is below expectation. This suggests that some non-visual influence is involved, such as some disadvantageous consequence of interaction between the genes determining the shell characteristics CO and unbanded. Since the magnitude of selection against the morph CO 00000 appears to be less in southern colonies than in northern ones, some factor that changes with latitude, some climatic factor, for example, seems likely to be responsible.

(iii) *Frequency of the morph* CO 00040

Selective visual predation may provide a satisfactory explanation for two of the habitat/morph frequency relationships that have been demonstrated, namely, those between dark substrates and heavily-banded morphs and sandy substrates and morphs of sandy appearance, respectively. It does not, however, explain the very high frequencies of the one-banded black and white morph CO 00040 that predominates in turfy habitats. This non-cryptic morph/habitat association is a very constant one in colonies over a considerable geographic range in northwest Europe. Moreover, in those places where the substrate is dark in colour and where the highest frequencies of more-than-one-banded snails occur, the frequency of CO 00040 does not become insignificantly low. The mean frequency of that morph for all the dark-substrate samples of the major survey is nearly 0.2 while the mean for those along the transect at Godrevy, excluding TR1, 2 and 3, is even slightly higher. Unless the morph CO 00040 is maintained in some way in populations living on dark substrates, the effect of selective visual predation would be to eliminate it and bring the morphs of dark appearance to fixation.

The CO 00040 morph could be maintained in areas where the substrate is dark by dispersal from surrounding turfy areas where it is usually at high frequency and nearly always numerous. This does not seem to be a very likely explanation however since the distances that these snails would have to move would be of the order of tens of yards, and, although I know of no evidence that *Cochlicella acuta* does not move this far, it does seem very unlikely that enough individuals would do so to maintain the numbers found on dark substrates. Moreover, unless the mobilities of the one-banded and more-than-one-banded morphs were significantly different, one would expect considerable numbers of heavily-banded morphs to have spread in the reverse direction into turfy areas, which they have not done.

Seasonal changes in the environment may influence the frequency of occurrence of the CO 00040 morph. At different times of the year depending on the state of growth of the vegetation, particularly if the flora includes broad-leaved plants, the extent to which a dark substrate would be visible will alter and, as Sheppard (1951) demonstrated for *Cepaea nemoralis*, such changes in the background can influence selection by visual predation. Since the black and white morph CO 00040 of *C. acuta* is distinctly conspicuous rather than cryptic when seen against *either* a background of green vegetation *or* the underlying dark substrate, the effect of any seasonal changes in vegetational cover is likely to be minimal. It thus seems most unlikely that the principal kind of selection favouring the black and white morph CO 00040 can be visual.

According to Cain & Currey (1963), strong associations observable between the frequency of a particular morph in various populations and some variable in the environment, such as that between the morph CO 00040 and the uniform and green background of the close-turf type

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

habitat, must be attributed to the action of selection of some kind. It must be recognized, however, as Cain & Currey have firmly pointed out in asserting as a general principle that such associations as these may be taken to be demonstrative of selection, that the observed environmental variables are not necessarily the active selective agents; they may be only concomitants. What is probably equally true is that the character by which the given morph is recognized is not necessarily that by which it is selected. Pleiotropy may be involved. In that case, this could mean that the appearance of the shell would not necessarily have any particular selective significance itself but that the selective advantage of the morph would be due to certain non-visible pleiotropic effects of one, or perhaps more, of the genes which also determine the visible shell characteristics.

If such effects do occur, their relationships may be explored further by estimating, first of all, the frequencies of the supergenes and genes, which determine the polymorphic features of the shell and then by proceeding to examine the relationships that these may have with various environmental factors that could have a selective influence upon them. Such an analysis may also provide information concerning interaction between visual and non-visual selective factors and may, for example, supply an explanation for the deficiency of the universal recessive CO 00000.

4. NON-VISUAL SELECTION

(a) *Supergene and gene frequencies in relation to habitat and latitude*

(i) *Methods*

Supergene and gene frequencies were estimated for each of the samples obtained in the course of the surveys reported above (see §§3(*a*), 3(*b*) (ii)). The geographical locations of the colonies sampled are shown on the map, figure 4. The data obtained from experimental breeding (see Lewis 1975) of the species and Fisher's maximum likelihood method (Fisher 1946, 1947; Boyd 1954*a*, *b*, 1955), were used in the computation of values for the frequencies of the six supergenes:

continuously opaque and unbanded	*CO 00*
continuously opaque and one-banded	*CO 04*
continuously opaque and more-than-one-banded	*CO* + +
discontinuously opaque and unbanded	*DO 00*
discontinuously opaque and one-banded	*DO 04*
discontinuously opaque and more-than-one-banded	*DO* + +

and the five genes:

continuously opaque	CO
discontinuously opaque	DO
unbanded	00
one-banded	04
more-than-one-banded	+ +

Mean colonial values were calculated when more than one sample had been obtained from the same type of habitat in any colony. By using these mean colonial values for each frequency as the basic data in the manner described by Bailey (1959), regression parameters for the thirty-three linear regressions of the six supergene and five gene frequencies, respectively, on latitude for each of the three habitat types close turf (t.), mixed vegetation (m.v.) and exposed sand (s.) were calculated.

Downloaded from rstb.royalsocietypublishing.org

(ii) *Results*

Table 7 shows the latitude of each colony, with intervals of one-half of one degree, the supergene and gene frequencies for each sample and, where appropriate, the mean colonial values. Figures 12–16 show the colonial supergene and gene frequencies for each habitat type, plotted against latitude. A figure showing the number of times the standard error by which the regression coefficient departs from zero is included in each diagram. Table 8 shows the regression parameters.

A. *Linear regressions of frequency on latitude, nos.* 1–16. These involve the alleles CO and DO unbanded (00) and one-banded (04) in the contrasting habitat types close turf (t.) and exposed sand (s.).

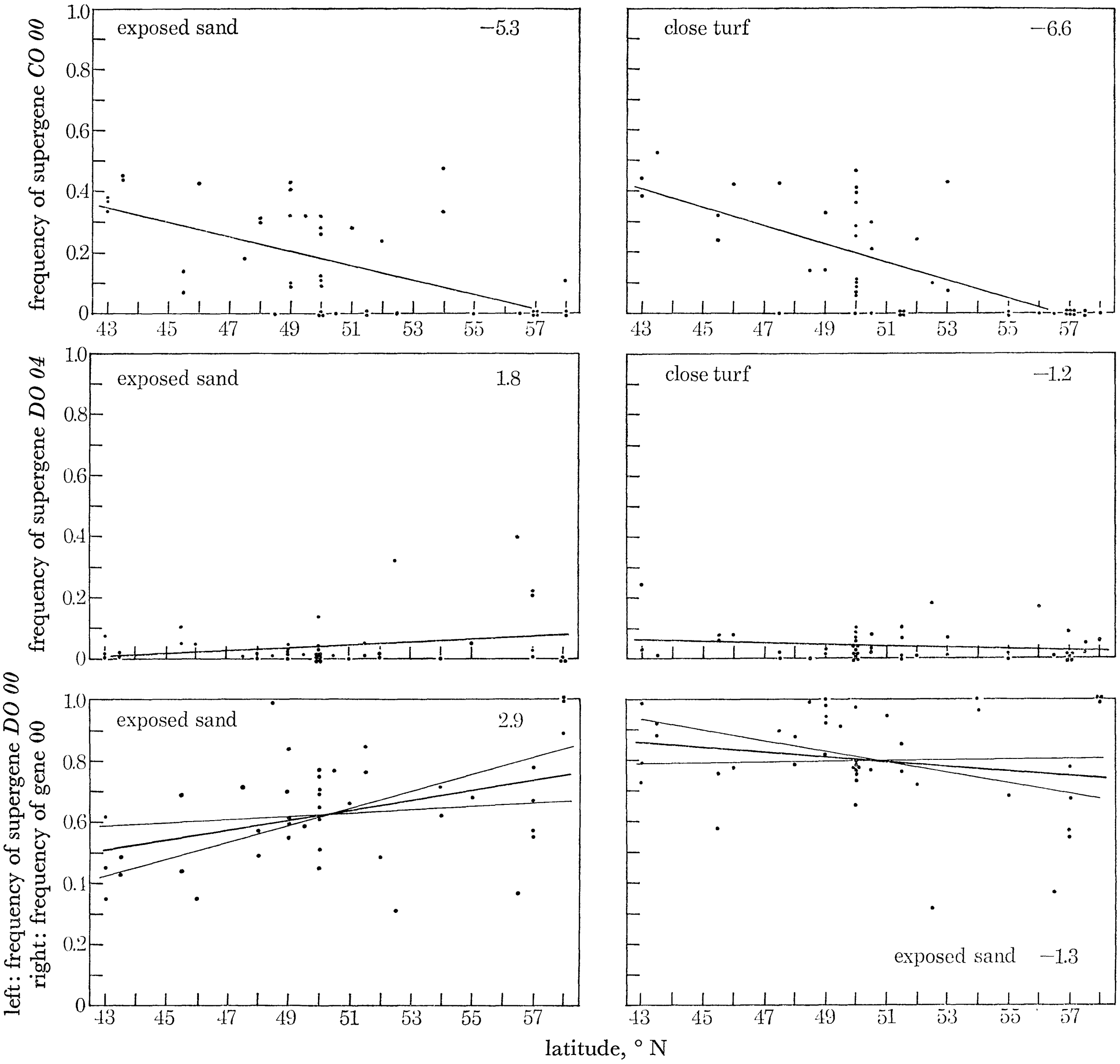


FIGURE 12. Relationships between colonial supergene and gene frequencies and latitude. In each diagram the type of habitat is shown and also a figure showing the number of times the standard error by which the regression coefficient departs from zero, a value of ± 1.96 being significant at the 5% level. The 5% confidence limits are drawn in on either side of the fitted line of linear regression in two of the diagrams but in the others only the regression line is shown.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

TABLE 7

colony ref. no.	colony	latitude ° N	sample ref.	supergene frequency *CO 00*	supergene frequency *CO 04*	supergene frequency *CO + +*	supergene frequency *DO 00*	supergene frequency *DO 04*	supergene frequency *DO + +*	gene frequency 00	gene frequency 04	gene frequency + +	gene frequency CO	gene frequency DO	size of sample	colony total
							exposed sand									
2	Nunton	57	a	0	0.211	0.032	0.710	0.038	0	0.719	0.249	0.032	0.243	0.757	81	
			b	0	0.283	0.079	0.619	0.020	0	0.619	0.303	0.079	0.362	0.638	92	
	mean			0	0.247	0.056	0.669	0.029	0	0.669	0.277	0.056	0.303	0.698		173
4	Stoneybridge	57	a	0	0.256	0	0.740	0.004	0	0.740	0.260	0	0.256	0.744	87	
			b	0	0.162	0.019	0.812	0.007	0	0.812	0.169	0.019	0.181	0.819	83	
	mean			0	0.209	0.010	0.776	0.006	0	0.776	0.215	0.010	0.219	0.782		170
5	Kilpheder	57	a	0	0.199	0	0.583	0.218	0	0.583	0.417	0	0.199	0.801	50	
			b	0	0.220	0	0.563	0.217	0	0.563	0.437	0	0.220	0.780	41	
	mean			0	0.210	0	0.573	0.218	0	0.573	0.427	0	0.210	0.790		91
6	Barra	57	a	0	0.158	0	0.500	0.342	0	0.500	0.500	0	0.158	0.842	40	
			b	0	0.326	0	0.605	0.069	0	0.605	0.395	0	0.326	0.674	73	
	mean			0	0.242	0	0.553	0.206	0	0.553	0.448	0	0.242	0.758		113
7	Sanna	56½	a	0	0.232	0	0.367	0.400	0	0.368	0.632	0	0.232	0.768	37	37
9	Tramore	55	a	0	0.334	0	0.562	0.103	0	0.563	0.437	0	0.335	0.666	44	
			b	0	0.206	0	0.794	0	0	0.794	0.206	0	0.206	0.794	34	
	mean			0	0.270	0	0.678	0.052	0	0.678	0.322	0	0.271	0.730		78
10	Kilmichael	52½	a	0	0.240	0.118	0.314	0.327	0	0.314	0.568	0.118	0.359	0.641	102	102
12	South Angle	51½	a	0	0.104	0	0.847	0.049	0	0.847	0.153	0	0.104	0.896	68	68
13	Port Eynon	51½	a	0	0.236	0	0.763	0	0	0.763	0.237	0	0.237	0.764	241	
			b	0	0.227	0	0.758	0.015	0	0.758	0.242	0	0.227	0.773	109	
	mean			0	0.232	0	0.761	0.008	0	0.761	0.240	0	0.232	0.769		350
15	Ambleteuse	50½	a	0	0.122	0.100	0.765	0.006	0.007	0.765	0.128	0.107	0.221	0.779	95	95
17	Mawgan	50	a	0.164	0.182	0	0.514	0.022	0.116	0.680	0.204	0.116	0.346	0.654	41	
			b	0.299	0.166	0.045	0.423	0.021	0.046	0.722	0.187	0.091	0.510	0.490	69	
			c	0.203	0.191	0.080	0.460	0.065	0	0.664	0.256	0.080	0.475	0.525	145	
			d	0.244	0.222	0	0.533	0	0	0.778	0.222	0	0.466	0.534	110	
			e	0.301	0.081	0	0.567	0.034	0.017	0.868	0.115	0.017	0.382	0.618	89	
			f	0.345	0.059	0.017	0.568	0	0.011	0.912	0.059	0.028	0.420	0.580	72	
	mean			0.259	0.150	0.024	0.511	0.024	0.031	0.771	0.174	0.055	0.433	0.567		526
18	Holywell	50	a	0	0.234	0.038	0.717	0.012	0	0.717	0.245	0.038	0.271	0.729	109	
			b	0.181	0.113	0	0.661	0.001	0.043	0.843	0.115	0.043	0.295	0.705	84	
	mean			0.091	0.174	0.019	0.689	0.007	0.022	0.780	0.180	0.041	0.283	0.717		193
19	Penhale	50	a	0	0.235	0.015	0.750	0	0	0.750	0.235	0.015	0.250	0.750	34	34

Downloaded from rstb.royalsocietypublishing.org

20	Perran	50	a	0.236	0.177	0.047	0.533	0.007	0.007	0.770	0.183	0.047	0.459	0.541	87	
			b	0	0.161	0.029	0.809	0.001	0	0.809	0.162	0.029	0.190	0.810	55	
	mean			0.118	0.169	0.038	0.671	0.004	0.004	0.790	0.173	0.042	0.325	0.676		142
21	Perranporth	50	a	0.221	0.197	0.115	0.467	0.001	0	0.689	0.198	0.115	0.532	0.468	125	
			b	0.174	0.127	0.131	0.567	0.002	0	0.740	0.129	0.131	0.432	0.568	139	
			c	0.365	0.067	0.128	0.437	0	0.003	0.803	0.067	0.131	0.560	0.440	37	
			d	0.507	0.109	0.084	0.289	0.002	0.007	0.797	0.112	0.091	0.701	0.299	63	
			e	0.259	0.116	0.165	0.456	0	0.004	0.715	0.116	0.169	0.540	0.460	117	
			f	0.370	0.045	0.116	0.468	0.001	0	0.838	0.046	0.116	0.531	0.469	94	
			g	0.296	0	0.193	0.494	0.012	0.005	0.790	0.012	0.198	0.489	0.511	102	
			h	0.352	0.080	0.115	0.446	0.006	0	0.799	0.897	0.115	0.547	0.453	98	
	mean			0.318	0.093	0.131	0.453	0.003	0.002	0.771	0.096	0.133	0.542	0.459		775
22	Porth towan	50	a	0	0.151	0.078	0.709	0.002	0	0.769	0.153	0.078	0.229	0.771	104	
			b	0	0.106	0.066	0.532	0.285	0.011	0.532	0.391	0.077	0.172	0.828	95	
	mean			0	0.129	0.072	0.651	0.144	0.006	0.651	0.272	0.078	0.200	0.800		199
23	Godrevy	50	a	0.116	0.250	0.011	0.616	0.007	0	0.731	0.257	0.011	0.377	0.623	179	
			b	0.116	0.170	0.015	0.675	0.024	0	0.761	0.195	0.015	0.301	0.699	103	
			c	0.192	0.223	0.008	0.506	0.070	0	0.699	0.293	0.008	0.424	0.577	120	
			d	0	0.276	0.008	0.712	0.004	0	0.712	0.280	0.008	0.284	0.716	129	
			e	0.156	0.196	0.004	0.548	0.097	0	0.704	0.292	0.004	0.356	0.644	125	
	mean			0.116	0.223	0.009	0.611	0.040	0	0.727	0.263	0.009	0.348	0.652		656
24	Gwithian	50	a	0	0.228	0	0.768	0.004	0	0.768	0.232	0	0.228	0.772	13	
27	Fort Mahon	50	a	0.364	0.016	0	0.605	0.014	0	0.969	0.031	0	0.380	0.620	83	
			b	0.194	0.016	0	0.789	0	0	0.984	0.016	0	0.211	0.789	62	
	mean			0.279	0.016	0	0.697	0.007	0	0.977	0.024	0	0.296	0.705		145
28	Jonville	49½	a	0.437	0.074	0	0.476	0.013	0	0.913	0.087	0	0.512	0.489	84	
			b	0.244	0.081	0	0.670	0.005	0	0.914	0.086	0	0.326	0.675	55	
			c	0.280	0.083	0	0.616	0.022	0	0.896	0.014	0	0.362	0.638	91	
	mean			0.320	0.079	0	0.587	0.013	0	0.908	0.092	0	0.400	0.601		230
29	La Renaudière	49	a	0.098	0.033	0	0.838	0.031	0	0.936	0.064	0	0.131	0.869	113	113
30	Utah Beach	49	a	0.242	0.028	0.007	0.653	0.071	0	0.894	0.099	0.007	0.276	0.724	75	
			b	0.347	0.019	0.030	0.547	0.056	0	0.894	0.075	0.030	0.396	0.604	85	
			c	0.383	0.015	0	0.595	0	0.007	0.978	0.015	0.007	0.398	0.602	69	
	mean			0.324	0.021	0.012	0.598	0.042	0.002	0.922	0.063	0.015	0.357	0.643		229
31	La Barbarie	49	a	0.428	0.019	0	0.546	0.006	0	0.975	0.025	0	0.447	0.553	60	60
32	Le Conquet	48	a	0.295	0.192	0.005	0.490	0.018	0	0.785	0.211	0.005	0.492	0.508	110	
33	Pte de Trévignon	47½	a	0.181	0.100	0	0.715	0.004	0	0.896	0.104	0	0.281	0.719	36	
35	La Faute	46	a	0.403	0.175	0	0.376	0.042	0.005	0.778	0.216	0.005	0.577	0.423	99	
			b	0.448	0.151	0.016	0.326	0.058	0	0.774	0.210	0.016	0.615	0.385	95	
	mean			0.426	.163	0.008	0.351	0.050	0.003	0.776	0.213	0.011	0.596	0.404		194

Downloaded from rstb.royalsocietypublishing.org

TABLE 7 (cont.)

colony ref. no.	colony	latitude ° N	sample ref.	supergene frequency						gene frequency					size of sample	colony total
				CO 00	*CO 04*	*CO + +*	*DO 00*	*DO 04*	*DO + +*	00	04	+ +	CO	DO		
36	Le Colombier	$45\frac{1}{2}$	a	0	0	0	0.923	0.077	0	0.923	0.077	0	0	1.000	54	
			b	0.139	0.261	0.010	0.460	0.131	0	0.599	0.391	0.010	0.410	0.590	158	
	mean			0.070	0.131	0.005	0.692	0.104	0	0.761	0.234	0.005	0.205	0.795		212
37	Biarritz	$43\frac{1}{2}$	a	0.354	0.089	0	0.554	0.004	0	0.907	0.093	0	0.443	0.558	91	
			b	0.554	0.119	0	0.295	0.032	0	0.849	0.151	0	0.673	0.327	75	
	mean			0.454	0.104	0	0.430	0.018	0	0.878	0.122	0	0.558	0.443		166
38	La Barre	$43\frac{1}{2}$	a	0.439	0.071	0	0.482	0.008	0	0.922	0.078	0	0.510	0.490	73	73
39	Ilbarritt	43	a	0.315	0.011	0	0.674	0	0	0.989	0.011	0	0.326	0.674	93	
			b	0.423	0.012	0	0.561	0.004	0	0.984	0.016	0	0.435	0.565	95	
	mean			0.369	0.012	0	0.618	0.002	0	0.987	0.014	0	0.381	0.620		188
40	Bidart	43	a	0.334	0.138	0	0.455	0.074	0	0.789	0.211	0	0.471	0.529	90	90
41	Hendaye	43	a	0.420	0.257	0	0.308	0.015	0	0.728	0.272	0	0.677	0.323	98	
			b	0.324	0.259	0.032	0.384	0.001	0	0.708	0.260	0.032	0.615	0.385	97	
			c	0.384	0.250	0	0.354	0.011	0	0.739	0.261	0	0.635	0.365	84	
	mean			0.376	0.255	0.011	0.349	0.009	0	0.725	0.264	0.011	0.642	0.358		279
42	Cunndal	58	a	0	0	0	1.000	0	0	1.000	0	0	0	1.000	90	90
43	Gress	58	a	0.112	0	0	0.888	0	0	1.000	0	0	0.112	0.888	78	78
44	Coll	58	a	0	0	0	1.000	0	0	1.000	0	0	0	1.000	35	35
50	Streedagh	54	a	0.450	0	0	0.550	0	0	1.000	0	0	0.450	0.550	195	
			b	0.506	0	0	0.494	0	0	1.000	0	0	0.506	0.494	120	
	mean			0.478	0	0	0.522	0	0	1.000	0	0	0.478	0.522		315
51	Mullaghmore	54	a	0.338	0.015	0.028	0.619	0	0	0.957	0.015	0.028	0.381	0.619	37	37
55	Ferriter's Cove	52	a	0.235	0.276	0	0.487	0.003	0	0.722	0.278	0	0.510	0.490	128	128
59	Berrow	51	a	0.286	0.055	0	0.660	0	0	0.945	0.055	0	0.341	0.660	57	57
66	Deauville	49	a	0.104	0.175	0	0.702	0.016	0.003	0.805	0.191	0.003	0.279	0.721	144	144
68	Merville	49	a	0.403	0	0	0.597	0	0	1.000	0	0	0.403	0.597	80	80
70	Sables d'or	$48\frac{1}{2}$	a	0	0	0	0.980	0.020	0	0.980	0.020	0	0	1.000	102	
			b	0	0	0	1.000	0	0	1.000	0	0	0	1.000	70	
	mean			0	0	0	0.990	0.010	0	0.990	0.010	0	0	1.000		172
72	Dournenez	48	a	0.304	0.124	0	0.572	0	0	0.876	0.124	0	0.428	0.572	97	97
79	Ile D'Oléron	$45\frac{1}{2}$	a	0.141	0.274	0.094	0.437	0.053	0	0.579	0.327	0.094	0.509	0.491	119	119

Downloaded from rstb.royalsocietypublishing.org

1	Veilish	57½	a	0	0.366	0.236	0.298	0.100	0	0.298	0.466	0.236	0.601	0.399	28	
			b	0	0.387	0.150	0.400	0.063	0	0.400	0.450	0.150	0.537	0.463	45	
	mean			0	0.377	0.193	0.349	0.082	0	0.349	0.458	0.193	0.569	0.431		73
2	Nunton	57	c	0	0.370	0.120	0.509	0	0	0.509	0.371	0.120	0.491	0.509	109	
			d	0	0.348	0.092	0.559	0	0	0.560	0.348	0.092	0.440	0.560	109	
			e	0	0.391	0.127	0.453	0.029	0	0.453	0.420	0.127	0.518	0.482	45	
	mean			0	0.370	0.113	0.507	0.010	0	0.507	0.380	0.113	0.483	0.517		263
3	South Nunton	57	a	0	0.362	0.387	0.248	0.003	0	0.248	0.365	0.387	0.749	0.251	10	
			b	0	0.436	0.286	0.273	0.005	0	0.273	0.441	0.286	0.722	0.278	96	
			c	0	0.603	0.182	0.183	0.031	0	0.183	0.635	0.182	0.785	0.215	87	
			d	0	0.530	0.303	0.167	0	0	0.167	0.530	0.303	0.833	0.167	42	
			e	0	0.433	0.275	0.287	0.004	0	0.287	0.437	0.275	0.709	0.291	119	
			f	0	0.484	0.199	0.274	0.043	0	0.274	0.527	0.199	0.683	0.317	73	
			g	0	0.431	0.256	0.312	0	0	0.312	0.431	0.256	0.687	0.313	48	
			h	0	0.485	0.222	0.264	0.030	0	0.264	0.515	0.222	0.717	0.293	115	
			i	0	0.478	0.231	0.288	0.003	0	0.288	0.481	0.231	0.709	0.291	100	
	mean			0	0.471	0.249	0.255	0.013	0	0.255	0.485	0.249	0.732	0.268		690
4	Stoneybridge	57	c	0	0.538	0.172	0.285	0.005	0	0.285	0.543	0.172	0.709	0.291	116	
			d	0	0	0.091	0.643	0.266	0	0.643	0.266	0.091	0.091	0.909	11	
	mean			0	0.269	0.132	0.464	0.136	0	0.464	0.405	0.132	0.400	0.600		127
5	Kilpheder	57	c	0	0.337	0	0.535	0.128	0	0.535	0.465	0	0.337	0.663	87	
			d	0	0.363	0	0.558	0.079	0	0.558	0.442	0	0.363	0.637	89	
	mean			0	0.350	0	0.547	0.104	0	0.547	0.454	0	0.350	0.650		176
6	Barra	57	c	0	0.458	0	0.396	0.146	0	0.396	0.604	0	0.458	0.542	19	
			d	0	0.403	0	0.431	0.167	0	0.431	0.569	0	0.403	0.597	86	
			c	0	0.442	0	0.495	0.062	0	0.495	0.505	0	0.442	0.558	60	
	mean			0	0.434	0	0.441	0.125	0	0.441	0.559	0	0.434	0.566		165
8	Portstewart	55	a	0.099	0.578	0.213	0.076	0.034	0	0.175	0.612	0.213	0.890	0.111	112	112
9	Tramore	55	c	0.170	0.303	0.003	0.481	0.043	0	0.651	0.346	0.003	0.477	0.253	148	
			d	0.100	0.333	0	0.515	0.052	0	0.615	0.385	0	0.433	0.567	121	
	mean			0.135	0.318	0.002	0.498	0.048	0	0.633	0.366	0.002	0.455	0.545		269
11	Youghal	51½	a	0	0.689	0.017	0.293	0	0	0.293	0.689	0.017	0.707	0.293	29	
			b	0.137	0.647	0.002	0.176	0.038	0	0.313	0.685	0.002	0.786	0.214	231	
	mean			0.069	0.668	0.010	0.240	0.019	0	0.303	0.687	0.010	0.747	0.254		260
12	South Angle	51½	b	0	0.427	0	0.523	0.042	0.008	0.523	0.469	0.008	0.427	0.573	121	121
13	Port Eynon	51½	c	0.202	0.236	0	0.529	0.033	0	0.731	0.269	0	0.438	0.562	82	
			d	0	0.697	0	0.297	0.005	0	0.297	0.703	0	0.698	0.303	113	
			e	0	0.692	0.005	0.293	0.010	0	0.293	0.702	0.005	0.697	0.303	95	
			f	0	0.154	0	0.715	0.131	0	0.715	0.285	0	0.154	0.846	41	
	mean			0.050	0.445	0.001	0.459	0.045	0	0.509	0.490	0.001	0.497	0.504		331

Downloaded from rstb.royalsocietypublishing.org

Table 7 (*cont.*)

colony ref. no.	colony	latitude °N	sample ref.	supergene frequency						gene frequency					size of sample	colony total
				CO 00	*CO 04*	*CO* + +	*DO 00*	*DO 04*	*DO* + +	00	04	+ +	CO	DO		
14	Polzeath	50½	a	0.164	0.347	0.022	0.407	0.060	0	0.571	0.407	0.022	0.532	0.468	116	116
15	Ambleteuse	50½	b	0.266	0.203	0.057	0.447	0	0.027	0.713	0.204	0.084	0.526	0.474	106	106
16	Seaford	50½	a	0.244	0.660	0.042	0.054	0	0	0.298	0.660	0.042	0.946	0.054	49	49
17	Mawgan	50	g	0.208	0.288	0.135	0.306	0.062	0.002	0.514	0.350	0.136	0.630	0.370	75	
			h	0.241	0.316	0.020	0.356	0.005	0.063	0.596	0.321	0.083	0.577	0.423	44	
			i	0.188	0.132	0.034	0.584	0.001	0.061	0.772	0.132	0.095	0.354	0.646	88	
			j	0.322	0.153	0.032	0.473	0.003	0.016	0.795	0.156	0.049	0.507	0.493	126	
			k	0.300	0.068	0.106	0.353	0.134	0.039	0.653	0.201	0.145	0.474	0.526	89	
			l	0.276	0.185	0.072	0.350	0.013	0.104	0.626	0.198	0.176	0.533	0.467	56	
			m	0.246	0.102	0.085	0.375	0.183	0.009	0.621	0.285	0.094	0.433	0.567	101	
	mean			0.254	0.178	0.069	0.400	0.057	0.042	0.654	0.235	0.111	0.501	0.499		579
18	Holywell	50	c	0.216	0.375	0.086	0.294	0.028	0	0.510	0.404	0.087	0.678	0.322	121	
			d	0.245	0.331	0.106	0.251	0.068	0	0.495	0.399	0.106	0.681	0.319	105	
			e	0.138	0.194	0.123	0.483	0.019	0.044	0.620	0.212	0.167	0.455	0.545	62	
	mean			0.233	0.300	0.105	0.343	0.038	0.015	0.542	0.338	0.120	0.605	0.395	288	
19	Penhale	50	b	0	0.468	0.135	0.385	0.004	0.007	0.385	0.472	0.143	0.603	0.397	102	102
20	Perran	50	c	0	0.372	0.223	0.405	0	0	0.405	0.372	0.223	0.595	0.405	21	
			d	0.274	0.317	0.198	0.210	0	0	0.484	0.317	0.198	0.790	0.210	111	
	mean			0.137	0.345	0.211	0.308	0	0	0.445	0.345	0.211	0.645	0.308		132
21	Perranporth	50	i	0	0.169	0.762	0	0.056	0.012	0	0.226	0.774	0.932	0.068	38	
			j	0	0.164	0.761	0	0.034	0.041	0	0.198	0.802	0.925	0.075	76	
			k	0.418	0.112	0.270	0.200	0.002	0	0.617	0.113	0.270	0.799	0.201	116	
			l	0.305	0.121	0.195	0.351	0.028	0	0.656	0.149	0.195	0.621	0.379	111	
			m	0.311	0.117	0.183	0.389	0	0	0.700	0.117	0.183	0.611	0.389	201	
			n	0.408	0.167	0.055	0.366	0.005	0	0.773	0.171	0.055	0.630	0.370	94	
			o	0.405	0.114	0.037	0.433	0	0	0.848	0.114	0.037	0.557	0.443	109	
			p	0.297	0.153	0.088	0.452	0	0.011	0.749	0.153	0.098	0.537	0.463	91	
	mean			0.268	0.140	0.294	0.274	0.016	0.008	0.543	0.155	0.302	0.702	0.299		836
22	Porth Towan	50	c	0.080	0.353	0.143	0.293	0.120	0.012	0.373	0.473	0.154	0.575	0.425	151	151
23	Godrevy	50	f	0.234	0.543	0.042	0.178	0.002	0	0.412	0.545	0.042	0.819	0.181	121	
			g	0.229	0.507	0.083	0.181	0	0	0.410	0.507	0.083	0.819	0.181	101	
			h	0.199	0.431	0.027	0.277	0.065	0	0.477	0.496	0.027	0.658	0.342	112	
			i	0.254	0.306	0.099	0.280	0.060	0	0.534	0.366	0.099	0.659	0.341	162	
	mean			0.229	0.447	0.063	0.229	0.032	0	0.456	0.479	0.063	0.714	0.261		496

Downloaded from rstb.royalsocietypublishing.org

24	Gwithian	50	b	0.194	0.242	0.023	0.455	0.063	0.024	0.649	0.305	0.046	0.458	0.542	199	
			c	0.460	0.143	0	0.320	0.076	0	0.781	0.219	0	0.604	0.397	151	
			d	0.183	0.283	0.023	0.317	0.167	0.027	0.500	0.450	0.050	0.489	0.511	92	
			e	0.213	0.328	0.018	0.374	0.019	0.049	0.587	0.347	0.067	0.558	0.442	155	
			f	0.226	0.339	0	0.391	0.028	0.015	0.618	0.367	0.015	0.566	0.435	130	
			g	0	0.752	0	0	0.248	0	0	1.000	0	0.752	0.248	23	
	mean			0.213	0.348	0.011	0.309	0.100	0.019	0.523	0.448	0.030	0.571	0.346		750
25	Upton	50	a	0.149	0.301	0.011	0.422	0.043	0.074	0.570	0.344	0.085	0.461	0.539	98	
			b	0	0.484	0.036	0.477	0.002	0	0.477	0.486	0.036	0.520	0.480	70	
			c	0.283	0.287	0.007	0.422	0	0	0.706	0.288	0.007	0.577	0.423	74	
			d	0.572	0.199	0.025	0.160	0.034	0.010	0.731	0.234	0.035	0.796	0.204	101	
	mean			0.251	0.318	0.020	0.370	0.020	0.021	0.621	0.338	0.041	0.589	0.412		343
26	Phillack	50	a	0.095	0.336	0.036	0.401	0.132	0	0.496	0.468	0.036	0.467	0.533	113	
			b	0	0.491	0.026	0.446	0.020	0.018	0.446	0.511	0.044	0.517	0.483	117	
			c	0.233	0.393	0	0.248	0.107	0.018	0.482	0.500	0.018	0.627	0.373	56	
			d	0.249	0.300	0.019	0.364	0.068	0	0.612	0.369	0.019	0.568	0.432	133	
			e	0.283	0.333	0.062	0.206	0.094	0.022	0.490	0.427	0.083	0.678	0.322	100	
			f	0.328	0.441	0.040	0.100	0.090	0	0.428	0.531	0.040	0.810	0.190	38	
			g	0.334	0.353	0.013	0.235	0.059	0.005	0.569	0.412	0.019	0.700	0.300	108	
	mean			0.217	0.378	0.028	0.286	0.081	0.009	0.503	0.460	0.038	0.624	0.376		665
27	Fort Mahon	50	c	0.304	0.101	0	0.590	0.001	0.004	0.894	0.102	0.004	0.405	0.595	111	
			d	0	0.067	0	0.932	0	0	0.932	0.067	0	0.068	0.932	37	
			e	0.347	0.081	0.011	0.541	0.017	0.003	0.888	0.098	0.014	0.439	0.561	109	
			f	0.390	0.027	0	0.542	0.019	0.022	0.933	0.046	0.022	0.417	0.583	46	
			g	0.394	0.042	0	0.563	0	0	0.958	0.042	0	0.437	0.564	86	
	mean			0.287	0.064	0.002	0.634	0.007	0.006	0.921	0.071	0.008	0.353	0.647		389
28	Jonville	49½	d	0.286	0.122	0.005	0.573	0.014	0	0.858	0.136	0.005	0.413	0.587	92	
			e	0.375	0.053	0	0.528	0.044	0	0.904	0.096	0	0.428	0.572	71	
			f	0.385	0.107	0	0.499	0.009	0	0.884	0.116	0	0.491	0.509	165	
	mean			0.349	0.094	0.002	0.534	0.022	0	0.882	0.116	0.002	0.444	0.566		338
29	La Renaudière	49	b	0	0.173	0	0.812	0.015	0	0.812	0.188	0	0.173	0.827	100	
			c	0	0.297	0	0.702	0.001	0	0.702	0.298	0	0.297	0.703	116	
			d	0	0.324	0	0.675	0	0	0.676	0.324	0	0.324	0.676	37	
	mean			0	0.265	0	0.730	0.005	0	0.730	0.270	0	0.265	0.735		253
30	Utah Beach	49	d	0	0.143	0	0.707	0.150	0	0.707	0.293	0	0.143	0.867	96	
			e	0.097	0.159	0	0.474	0.270	0	0.571	0.429	0	0.256	0.744	92	
			f	0.272	0.049	0.084	0.554	0.041	0	0.826	0.090	0.084	0.404	0.596	90	
			g	0.305	0.103	0.062	0.514	0.016	0	0.819	0.119	0.062	0.470	0.530	94	
	mean			0.169	0.114	0.037	0.562	0.119	0	0.731	0.233	0.037	0.318	0.682		372
31	La Barbarie	49	b	0.238	0.371	0	0.349	0.041	0	0.587	0.413	0	0.610	0.391	75	
			c	0.442	0.318	0.037	0.203	0	0	0.645	0.318	0.037	0.797	0.203	42	
			d	0.186	0.313	0	0.439	0.041	0.020	0.625	0.354	0.020	0.499	0.501	99	
	mean			0.288	0.334	0.012	0.330	0.027	0.007	0.629	0.362	0.019	0.635	0.365		216

Downloaded from rstb.royalsocietypublishing.org

Table 7 (*cont.*)

colony ref. no.	colony	latitude °N	sample ref.	supergene frequency						gene frequency					size of sample	colony total
				CO 00	*CO 04*	*CO ++*	*DO 00*	*DO 04*	*DO ++*	00	04	++	CO	DO		
32	Le Conquet	48	b	0	0.197	0.148	0.489	0.089	0.077	0.489	0.286	0.225	0.345	0.655	25	
			c	0.419	0.128	0	0.408	0.036	0.008	0.827	0.165	0.009	0.547	0.453	177	
			d	0	0.185	0.123	0.538	0.132	0.022	0.538	0.317	0.145	0.308	0.692	93	
			e	0	0	0	0.690	0.261	0.049	0.690	0.261	0.049	0	1.000	21	
			f	0.117	0.098	0	0.551	0.234	0	0.668	0.332	0	0.215	0.785	65	
	mean			0.107	0.122	0.054	0.535	0.150	0.031	0.642	0.272	0.086	0.283	0.717		381
33	Pte de Trévignon	47½	b	0	0.270	0.058	0.314	0.080	0.279	0.314	0.350	0.336	0.328	0.672	118	118
34	Kerfany	47½	a	0	0.486	0.009	0.415	0.090	0	0.415	0.576	0.009	0.495	0.505	109	109
35	La Faute	46	c	0.185	0.055	0	0.526	0.234	0	0.711	0.289	0	0.240	0.760	87	
			d	0.228	0.195	0	0.464	0.109	0.004	0.692	0.304	0.004	0.423	0.577	117	
			e	0.337	0.128	0	0.378	0.146	0.011	0.715	0.273	0.011	0.465	0.535	88	
	mean			0.250	0.126	0	0.456	0.166	0.008	0.706	0.289	0.008	0.376	0.624		292
36	Le Colombier	45½	c	0.123	0.428	0.048	0.369	0.032	0	0.493	0.460	0.048	0.599	0.401	87	
			d	0.136	0.443	0.035	0.376	0.010	0	0.512	0.453	0.035	0.614	0.386	88	
	mean			0.130	0.436	0.042	0.373	0.021	0	0.503	0.457	0.042	0.607	0.394		175
37	Biarritz	43½	c	0.356	0.168	0.010	0.302	0.163	0	0.658	0.331	0.010	0.535	0.465	97	
			d	0.336	0.240	0	0.410	0.005	0.009	0.746	0.244	0.009	0.576	0.424	107	
			e	0.280	0.261	0.029	0.316	0.114	0	0.596	0.375	0.029	0.571	0.429	104	
			f	0.337	0.303	0.019	0.307	0.034	0	0.644	0.337	0.019	0.659	0.341	108	
			g	0.323	0.334	0.005	0.331	0.007	0	0.655	0.341	0.005	0.662	0.338	106	
			h	0.258	0.292	0	0.398	0.052	0	0.656	0.344	0	0.549	0.451	109	
			i	0.242	0.273	0.025	0.441	0.001	0.016	0.684	0.275	0.041	0.541	0.459	75	
	mean			0.305	0.267	0.013	0.357	0.054	0.004	0.663	0.321	0.016	0.572	0.415		706
38	La Barre	43½	b	0.300	0.210	0	0.480	0.010	0	0.780	0.220	0	0.510	0.490	72	72
39	Ilbarritt	43	c	0.257	0.171	0	0.571	0	0	0.828	0.172	0	0.428	0.572	131	
			d	0.255	0.067	0	0.582	0.095	0	0.837	0.163	0	0.322	0.678	77	
			e	0.292	0.084	0	0.549	0.074	0	0.841	0.159	0	0.376	0.624	106	
	mean			0.268	0.107	0	0.567	0.060	0	0.835	0.165	0	0.375	0.625		314
40	Bidart	43	b	0.384	0.286	0	0.307	0.023	0	0.691	0.309	0	0.670	0.330	69	
			c	0.213	0.479	0	0.307	0.001	0	0.520	0.480	0	0.692	0.308	73	
	mean			0.299	0.383	0	0.307	0.012	0	0.606	0.395	0	0.681	0.319		142
41	Hendaye	43	d	0.293	0.311	0	0.341	0.056	0	0.634	0.366	0	0.603	0.397	107	
			e	0.337	0.342	0.020	0.301	0	0	0.638	0.342	0.020	0.698	0.302	102	
	mean			0.315	0.327	0.010	0.321	0.028	0	0.636	0.354	0.010	0.654	0.350		209
49	Sheeps Haven	55	a	0	0		0.916	0.083	0	0.917	0.083	0	0	1.000	25	25

Downloaded from rstb.royalsocietypublishing.org

54	Brittas Bay	52½	a	0	0.478	0.006	0.383	0.131	0.003	0.383	0.609	0.009	0.484	0.516	183	183
58	Sangatte	51	a	0.680	0	0.092	0.227	0	0	0.908	0	0.092	0.773	0.228	98	
			b	0.504	0.010	0.111	0.375	0	0	0.879	0.010	0.111	0.625	0.375	59	
			c	0.681	0.073	0.038	0.208	0	0	0.889	0.073	0.038	0.792	0.208	68	
	mean			0.622	0.027	0.080	0.270	0	0	0.898	0.027	0.080	0.730	0.270		225
60	Richborough	51	a	0.298	0.413	0.089	0.195	0.002	0.002	0.493	0.416	0.091	0.800	0.200	104	
			b	0.319	0.345	0.044	0.288	0.004	0	0.608	0.348	0.044	0.708	0.292	47	
	mean			0.309	0.379	0.067	0.242	0.003	0.001	0.551	0.382	0.068	0.754	0.246		151
61	Fistral	50	a	0	0.458	0.088	0.451	0.002	0.001	0.451	0.460	0.089	0.546	0.454	53	53
62	Portreath	50	a	0	0.155	0	0.845	0.001	0	0.845	0.155	0	0.155	0.845	132	132
64	Whitesand Bay	50	a	0	0.159	0.109	0	0.647	0.085	0	0.806	0.194	0.268	0.732	83	
			b	0	0	0	0	0.743	0.256	0	0.744	0.256	0	1.000	47	
	mean			0	0.080	0.055	0	0.695	0.171	0	0.775	0.225	0.134	0.866		130
65	Blonville	49	a	0.585	0.141	0	0.274	0	0	0.859	0.141	0	0.726	0.274	58	
			b	0.539	0.328	0.007	0.100	0.027	0	0.639	0.355	0.007	0.874	0.127	76	
	mean			0.562	0.235	0.004	0.187	0.014	0	0.749	0.248	0.004	0.800	0.200		134
67	Villers	49	a	0.538	0.169	0	0.293	0	0	0.831	0.169	0	0.707	0.293	69	69
71	Kerhornous	48	a	0.254	0.254	0	0.221	0.271	0	0.475	0.525	0	0.508	0.492	31	31
73	Trèxen	48	a	0	0	0	0.682	0.309	0.009	0.682	0.309	0.009	0	1.000	58	58
74	Kervel	48	a	0	0.143	0	0.515	0.342	0	0.515	0.485	0	0.143	0.857	49	
			b	0	0.226	0	0.480	0.294	0	0.480	0.520	0	0.226	0.774	39	
	mean			0	0.185	0	0.498	0.318	0	0.498	0.503	0	0.185	0.816		88
76	Batz-sur-Mer	47	a	0.802	0.070	0	0.128	0	0	0.930	0.070	0	0.872	0.128	67	
			b	0.326	0.462	0	0.150	0.062	0	0.477	0.523	0	0.788	0.212	66	
	mean			0.564	0.532	0	0.139	0.031	0	0.704	0.297	0	0.830	0.170		133
77	La Parée	46½	a	0.111	0.141	0	0.644	0.104	0	0.755	0.245	0	0.252	0.748	79	79
78	Bourgenez	46	a	0	0.224	0	0.701	0.075	0	0.702	0.298	0	0.224	0.776	95	95
81	Feltrim	53½	a	0.194	0.200	0.034	0.569	0.003	0	0.763	0.203	0.034	0.428	0.572	121	121
82	Itford	50½	a	0.298	0	0	0.702	0	0	1.000	0	0	0.298	0.702	45	45
83	South Heighton	50½	a	0.390	0.268	0.033	0.309	0.001	0	0.699	0.269	0.033	0.691	0.309	78	78
84	Rousse Tower	49	a	0.496	0.088	0.059	0.345	0.012	0	0.841	0.100	0.059	0.644	0.356	96	96
85	East Rottingdean	50½	a	0.329	0.318	0.011	0.340	0	0.003	0.668	0.318	0.014	0.657	0.343	71	71
86	West Rottingdean	50½	a	0.295	0.489	0.026	0.188	0.002	0	0.483	0.491	0.026	0.810	0.190	98	
			b	0.167	0.390	0.041	0.378	0.022	0.002	0.545	0.412	0.043	0.598	0.402	83	
			c	0.237	0.364	0.054	0.343	0.003	0	0.579	0.367	0.054	0.654	0.346	77	
	mean			0.233	0.414	0.040	0.303	0.009	0.001	0.536	0.423	0.041	0.687	0.313		258

Downloaded from rstb.royalsocietypublishing.org

TABLE 7 (*cont.*)

colony ref. no.	colony	latitude ° N	sample ref.	supergene frequency						gene frequency					size of sample	colony total
				CO 00	*CO 04*	*CO + +*	*DO 00*	*DO 04*	*DO + +*	00	04	+ +	CO	DO		
							close turf									
1	Veilish	$57\frac{1}{2}$	c	0	0.458	0.218	0.272	0.053	0	0.272	0.510	0.218	0.675	0.325	95	95
2	Nunton	57	f	0	0.619	0.159	0.221	0	0	0.221	0.619	0.159	0.779	0.221	70	
			g	0	0.448	0.126	0.425	0	0	0.425	0.449	0.126	0.575	0.425	80	
			h	0	0.548	0.170	0.283	0	0	0.283	0.548	0.170	0.717	0.283	46	
	mean			0	0.538	0.152	0.310	0	0	0.310	0.538	0.152	0.690	0.310		196
3	South Nunton	57	j	0	0.794	0.051	0.137	0.012	0.006	0.137	0.806	0.057	0.845	0.155	36	
			k	0	0.523	0.322	0.123	0.032	0	0.123	0.555	0.322	0.845	0.155	124	
			l	0	0.403	0.491	0.106	0	0	0.106	0.403	0.491	0.894	0.106	66	
			m	0	0.536	0.266	0.198	0	0	0.198	0.536	0.266	0.802	0.198	106	
	mean			0	0.564	0.283	0.141	0.011	0.002	0.141	0.575	0.284	0.847	0.154		332
4	Stoneybridge	57	e	0	0.676	0.171	0.139	0.014	0	0.139	0.690	0.171	0.847	0.153	103	
			f	0	0.469	0.179	0.352	0	0	0.352	0.469	0.179	0.648	0.352	71	
	mean			0	0.573	0.175	0.246	0.007	0	0.246	0.580	0.175	0.748	0.253		174
5	Kilpheder	57	e	0	0.450	0.052	0.484	0.014	0	0.480	0.464	0.052	0.502	0.498	111	111
6	Barra	57	f	0	0.525	0	0.362	0.113	0	0.362	0.638	0	0.525	0.475	83	
			g	0	0.542	0	0.348	0.110	0	0.348	0.652	0	0.543	0.458	98	
			h	0	0.507	0	0.401	0.091	0	0.401	0.599	0	0.507	0.493	104	
			i	0	0.535	0	0.343	0.123	0	0.343	0.657	0	0.535	0.465	101	
			j	0	0.523	0	0.369	0.108	0	0.369	0.631	0	0.523	0.477	109	
			k	0	0.608	0	0.309	0.083	0	0.309	0.691	0	0.608	0.392	102	
			l	0	0.580	0.005	0.268	0.147	0	0.268	0.727	0.005	0.585	0.415	96	
	mean			0	0.546	0.001	0.343	0.111	0	0.343	0.656	0.001	0.547	0.451		693
7	Sanna	$56\frac{1}{2}$	b	0	0.834	0	0.143	0.022	0	0.143	0.857	0	0.835	0.166	37	
			c	0	0.599	0	0.399	0.002	0	0.399	0.601	0	0.599	0.401	45	
	mean			0	0.717	0	0.271	0.012	0	0.271	0.729	0	0.717	0.284		82
8	Portstewart	55	b	0	0.383	0.476	0.140	0	0	0.140	0.384	0.476	0.860	0.140	292	292
9	Tramore	55	e	0	0.835	0	0.147	0.018	0	0.147	0.853	0	0.836	0.165	34	34
10	Kilmichael	$52\frac{1}{2}$	b	0	0	0.886	0.066	0.048	0	0.066	0.048	0.886	0.886	0.114	79	
			c	0.197	0.094	0.153	0.232	0.324	0	0.429	0.418	0.153	0.444	0.556	113	
	mean			0.099	0.047	0.521	0.149	0.186	0	0.248	0.233	0.521	0.665	0.335		192
11	Youghal	$51\frac{1}{2}$	c	0	0.699	0.070	0.157	0.073	0	0.157	0.772	0.070	0.769	0.231	37	37
12	South Angle	$51\frac{1}{2}$	c	0	0.480	0	0.493	0.002	0.025	0.493	0.482	0.025	0.480	0.520	81	
			d	0	0.428	0	0.555	0.017	0	0.555	0.445	0	0.428	0.572	80	
	mean			0	0.454	0	0.524	0.010	0.013	0.524	0.464	0.013	0.454	0.546		161

Downloaded from rstb.royalsocietypublishing.org

13	Port Eynon	51½	g	0	0.488	0	0.398	0.114	0	0.398	0.602	0	0.488	0.512	25	25
14	Polzeath	50½	b	0.209	0.406	0	0.342	0.024	0.019	0.551	0.430	0.019	0.616	0.385	107	107
15	Ambleteuse	50½	c	0	0	0.970	0	0.030	0	0	0.030	0.970	0.970	0.030	50	50
16	Seaford	50½	b	0.295	0.238	0	0.390	0.078	0	0.685	0.315	0	0.533	0.467	81	81
17	Mawgan	50	n	0.427	0.178	0.040	0.267	0.009	0.078	0.694	0.188	0.119	0.645	0.355	139	
			o	0.338	0.325	0.056	0.213	0.001	0.068	0.551	0.325	0.124	0.718	0.282	142	
			p	0.465	0.167	0	0.359	0	0.010	0.824	0.167	0.010	0.631	0.369	51	
			q	0.276	0.306	0.032	0.255	0.063	0.068	0.532	0.369	0.099	0.614	0.386	53	
			r	0.332	0.407	0.039	0.129	0	0.092	0.461	0.408	0.132	0.779	0.221	118	
			s	0.291	0.326	0.059	0.240	0.007	0.076	0.531	0.333	0.136	0.677	0.323	91	
			t	0.366	0.186	0.042	0.274	0.052	0.080	0.640	0.238	0.122	0.594	0.406	105	
	mean			0.356	0.271	0.038	0.248	0.019	0.067	0.605	0.290	0.106	0.665	0.335		699
18	Holywell	50	f	0.090	0.554	0.178	0.075	0.092	0.011	0.165	0.646	0.189	0.822	0.178	111	
			g	0.238	0.336	0.109	0.284	0.033	0	0.522	0.369	0.109	0.683	0.317	84	
			h	0.129	0.190	0.218	0.280	0.184	0	0.409	0.373	0.218	0.536	0.464	69	
			i	0	0.301	0.161	0.376	0.099	0.063	0.376	0.400	0.224	0.462	0.538	98	
			j	0	0.317	0.287	0.234	0.123	0.038	0.235	0.440	0.325	0.605	0.395	90	
			k	0.096	0.594	0.172	0.048	0.087	0.003	0.144	0.681	0.175	0.862	0.138	97	
	mean			0.092	0.382	0.188	0.216	0.103	0.019	0.309	0.485	0.207	0.662	0.338		549
19	Penhale	50	c	0.103	0.481	0.292	0.049	0.073	0.002	0.152	0.554	0.293	0.876	0.124	86	86
20	Perran	50	e	0	0.243	0.278	0.400	0.072	0.008	0.400	0.315	0.286	0.521	0.479	97	
			f	0.081	0.198	0.237	0.334	0.149	0.001	0.415	0.347	0.238	0.516	0.484	151	
			g	0.090	0.250	0.326	0.257	0.057	0.021	0.347	0.306	0.347	0.665	0.335	124	
			h	0.127	0.301	0.269	0.296	0.007	0	0.424	0.308	0.269	0.697	0.303	116	
			i	0.154	0.090	0.388	0.279	0.048	0.040	0.433	0.138	0.428	0.633	0.367	122	
			j	0.222	0.164	0.254	0.177	0.183	0	0.399	0.347	0.254	0.641	0.359	56	
	mean			0.112	0.208	0.292	0.291	0.086	0.012	0.403	0.294	0.304	0.612	0.388		666
21	Perranporth	50	q	0.337	0.295	0.180	0.156	0.001	0.031	0.493	0.297	0.210	0.812	0.188	77	
			r	0.144	0.164	0.634	0.045	0.007	0.007	0.188	0.171	0.641	0.941	0.059	193	
			s	0.211	0.104	0.464	0.173	0.027	0.022	0.384	0.130	0.486	0.778	0.222	94	
			t	0.195	0	0.680	0.112	0.013	0	0.307	0.013	0.680	0.875	0.125	72	
			u	0.206	0.184	0.348	0.261	0.001	0	0.467	0.185	0.348	0.738	0.262	41	
			v	0.198	0.157	0.348	0.269	0.005	0.022	0.467	0.162	0.371	0.704	0.296	126	
			w	0.177	0.209	0.476	0.165	0.003	0.030	0.282	0.211	0.507	0.802	0.198	119	
			x	0.356	0.124	0.257	0.232	0.031	0	0.589	0.154	0.257	0.737	0.263	108	
			y	0.288	0.147	0.386	0.178	0	0	0.467	0.147	0.386	0.821	0.179	73	
			z	0.349	0.222	0.274	0.154	0	0	0.503	0.222	0.274	0.846	0.154	66	
			aa	0.374	0.220	0.189	0.189	0.028	0	0.563	0.248	0.189	0.783	0.217	112	
	mean			0.252	0.166	0.385	0.170	0.011	0.010	0.428	0.176	0.395	0.803	0.197		1081
22	Porth towan	50	d	0	0.378	0.164	0.408	0.038	0.011	0.409	0.416	0.176	0.542	0.458	150	150

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Table 7 (*cont.*)

colony ref. no	colony	latitude ° N	sample ref.	supergene frequency						gene frequency					size of sample	colony total
				CO 00	*CO 04*	*CO* + +	*DO 00*	*DO 04*	*DO* + +	00	04	+ +	CO	DO		
23	Godrevy	50	j	0.098	0.773	0.058	0.053	0.010	0.008	0.150	0.783	0.066	0.929	0.071	124	
			k	0.182	0.641	0.038	0.071	0.056	0.011	0.253	0.697	0.050	0.861	0.139	62	
			l	0.124	0.398	0.059	0.334	0.084	0	0.458	0.483	0.059	0.581	0.419	70	
			m	0	0.862	0.021	0.098	0.007	0.012	0.098	0.869	0.033	0.883	0.117	109	
			n	0	0.520	0.118	0.319	0.042	0	0.319	0.562	0.118	0.639	0.361	78	
			o	0	0.505	0.119	0.377	0	0	0.377	0.505	0.119	0.623	0.377	69	
			p	0	0.895	0.038	0.066	0.001	0	0.066	0.896	0.038	0.933	0.067	67	
			q	0	0.885	0.048	0.065	0.002	0	0.065	0.887	0.048	0.933	0.067	75	
			r	0.087	0.846	0.032	0	0.036	0	0.087	0.881	0.032	0.964	0.036	128	
			s	0.180	0.530	0.018	0.262	0.010	0	0.442	0.540	0.018	0.728	0.272	114	
			t	0	0.900	0.065	0.034	0	0	0.035	0.900	0.065	0.966	0.035	87	
			u	0	0.854	0.069	0.055	0.003	0.020	0.055	0.856	0.089	0.923	0.077	106	
			v	0.140	0.745	0.039	0.060	0	0.016	0.200	0.745	0.055	0.924	0.076	84	
			w	0	0.863	0.041	0.089	0.007	0	0.089	0.870	0.041	0.904	0.096	63	
			x	0.152	0.759	0.057	0.022	0.001	0.009	0.174	0.760	0.066	0.967	0.033	94	
			y	0.090	0.757	0.100	0	0.049	0.004	0.090	0.806	0.104	0.947	0.053	117	
			z	0.109	0.681	0.132	0.061	0.017	0	0.170	0.698	0.132	0.922	0.078	94	
			aa	0.123	0.588	0.247	0.035	0.002	0.004	0.158	0.591	0.252	0.959	0.041	75	
			ab	0.177	0.724	0.038	0.043	0.005	0.013	0.220	0.729	0.051	0.939	0.061	101	
			ac	0	0.891	0.048	0	0.048	0.012	0	0.939	0.061	0.939	0.061	68	
			ad	0.152	0.762	0.032	0.041	0	0.014	0.193	0.762	0.045	0.946	0.054	135	
			ae	0.098	0.752	0.083	0.036	0.017	0.014	0.134	0.768	0.097	0.933	0.067	108	
			af	0.120	0.696	0.115	0.063	0.006	0	0.183	0.702	0.115	0.931	0.069	83	
			ag	0.104	0.785	0.055	0.035	0.009	0.013	0.138	0.794	0.067	0.943	0.057	100	
			ah	0.157	0.523	0.037	0.276	0.007	0	0.433	0.530	0.037	0.717	0.283	124	
	mean			0.084	0.725	0.068	0.100	0.017	0.006	0.183	0.743	0.074	0.877	0.123		2535
24	Gwithian	50	h	0.177	0.424	0	0.391	0.008	0	0.568	0.432	0	0.601	0.399	130	
			i	0.174	0.496	0.005	0.290	0.015	0.021	0.464	0.511	0.026	0.674	0.326	159	
			j	0	0.631	0.009	0.351	0.005	0.005	0.351	0.635	0.014	0.639	0.361	182	
			k	0	0.632	0.125	0.139	0.239	0.003	0	0.871	0.129	0.758	0.242	108	
	mean			0.088	0.546	0.035	0.258	0.067	0.007	0.346	0.612	0.042	0.668	0.332		579
25	Upton	50	e	0.370	0.331	0.041	0.228	0.018	0.012	0.598	0.349	0.054	0.743	0.257	134	
			f	0.410	0.438	0	0.142	0.002	0	0.560	0.440	0	0.856	0.145	120	
			g	0.396	0.463	0	0.111	0	0.030	0.507	0.463	0.030	0.859	0.141	51	
	mean			0.392	0.411	0.014	0.160	0.007	0.014	0.555	0.417	0.028	0.819	0.181		305
26	Phillack	50	h	0.354	0.369	0.060	0.157	0.055	0.004	0.511	0.424	0.065	0.783	0.217	88	
			i	0.249	0.338	0.009	0.332	0.073	0	0.581	0.411	0.009	0.595	0.405	118	
			j	0.252	0.398	0.011	0.328	0.001	0.011	0.580	0.399	0.021	0.661	0.339	71	
	mean			0.285	0.368	0.027	0.272	0.043	0.005	0.557	0.411	0.032	0.680	0.320		277
27	Fort Mahon	50	h	0.409	0.123	0.010	0.441	0.018	0	0.850	0.141	0.010	0.541	0.459	105	105

Downloaded from rstb.royalsocietypublishing.org

29	La Renaudière	49	e	0.137	0.400	0	0.440	0.023	0	0.577	0.423	0	0.538	0.463	68	68
31	La Barbarie	49	e	0.327	0.383	0.007	0.246	0.032	0.005	0.573	0.415	0.012	0.717	0.283	210	210
34	Kerfany	47½	b	0	0.693	0.009	0.298	0	0	0.298	0.693	0.009	0.702	0.298	57	57
35	La Faute	46	f	0.424	0.283	0	0.186	0.081	0.026	0.610	0.364	0.026	0.707	0.293	78	78
36	Le Colombier	45½	e	0.273	0.578	0.030	0.114	0.002	0.003	0.387	0.580	0.033	0.881	0.119	77	
			f	0.206	0.424	0.031	0.192	0.148	0	0.398	0.572	0.031	0.660	0.340	50	
	mean			0.240	0.501	0.031	0.153	0.075	0.002	0.393	0.576	0.032	0.771	0.230		127
37	Biarritz	43½	j	0.459	0.372	0.005	0.150	0.013	0	0.610	0.386	0.005	0.836	0.164	110	
			k	0.583	0.311	0	0.102	0.004	0	0.685	0.315	0	0.894	0.106	130	
			l	0.529	0.320	0	0.130	0.021	0	0.659	0.341	0	0.849	0.151	168	
	mean			0.524	0.334	0.002	0.127	0.013	0	0.651	0.347	0.002	0.826	0.140		408
39	Ilbarritt	43	f	0.441	0.042	0	0.270	0.246	0	0.712	0.288	0	0.484	0.517	77	77
40	Bidart	43	d	0.343	0.255	0	0.373	0.029	0	0.716	0.284	0	0.599	0.402	78	
			e	0.430	0.282	0	0.249	0.038	0	0.679	0.321	0	0.713	0.288	65	
	mean			0.387	0.269	0	0.311	0.034	0	0.697	0.303	0	0.656	0.345		143
45	Valtos	58	a	0	0.266	0.406	0.267	0.060	0	0.267	0.327	0.406	0.672	0.328	51	51
46	Starasta	57½	a	0	0	0.687	0.276	0.037	0	0.276	0.037	0.687	0.688	0.312	64	
			b	0	0.303	0.254	0.443	0	0	0.443	0.303	0.254	0.557	0.443	79	
	mean			0	0.152	0.471	0.360	0.019	0	0.360	0.170	0.471	0.623	0.378		143
47	Pollachar	57	a	0	0.546	0.162	0.292	0	0	0.292	0.546	0.162	0.708	0.292	101	101
48	Scarinish	56	a	0	0.595	0.209	0	0.177	0.019	0	0.772	0.228	0.804	0.196	99	99
52	Corballis	53	a	0.077	0.792	0.070	0.050	0.010	0	0.128	0.802	0.070	0.939	0.061	222	222
53	Dog's Bay	53	a	0.431	0.284	0	0.097	0.070	0.117	0.528	0.354	0.117	0.715	0.285	86	86
56	Ventry	52	a	0.243	0.543	0.089	0.116	0.009	0	0.359	0.552	0.089	0.875	0.125	95	95
57	Marloes	51½	a	0	0.899	0	0.099	0.001	0	0.100	0.900	0	0.899	0.101	194	194
63	Porth Farm	50	a	0.463	0.262	0	0.275	0	0	0.738	0.262	0	0.725	0.275	106	106
69	St Pabu	48½	a	0.281	0.532	0	0.162	0.001	0.024	0.443	0.533	0.024	0.813	0.187	63	
			b	0	0.623	0.004	0.337	0.003	0.034	0.337	0.626	0.037	0.627	0.373	204	
	mean			0.141	0.578	0.002	0.250	0.002	0.029	0.390	0.580	0.030	0.720	0.280		267
75	Le Poldu	47½	a	0.391	0.521	0.009	0.067	0.008	0.004	0.458	0.529	0.013	0.921	0.079	119	
			b	0.515	0.370	0.014	0.086	0.011	0.005	0.601	0.381	0.018	0.898	0.102	83	
			c	0.339	0.552	0.006	0.047	0.056	0	0.387	0.608	0.006	0.897	0.103	87	
	mean			0.415	0.481	0.010	0.067	0.025	0.003	0.482	0.506	0.012	0.906	0.095		289
80	Pte Espagnole	45½	a	0.318	0.256	0.074	0.290	0.061	0	0.608	0.318	0.074	0.648	0.352	79	79

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The regression coefficients of the frequencies of the supergene *CO 00* on latitude, in both these contrasting habitats, show quite significant departures from zero and they are not significantly different from each other (figure 12). The frequency of the supergene *CO 00* is thus shown to be independent of the habitat in which it occurs. It is evidently determined by some selective factor related to latitude. In the extreme north of the range where the frequency of *CO 00* approaches very closely to zero, the frequencies of both the component genes CO and 00, in both types of habitat, are significantly greater than zero. In other words, the component genes are present in the populations but there is gametic disequilibrium brought about by a deficiency of the supergene *CO 00*. Selection appears to be operating not against either of the constituent genes CO and 00 but against the supergene that includes them both and the extent of this selection decreases progressively southwards.

TABLE 8. REGRESSION PARAMETERS: SUPERGENE AND GENE FREQUENCIES ON LATITUDE

regression ref. number	gene or supergene	habitat	mean latitude	mean frequency	regression constant 95 % confidence limits			standard errors from zero	regression coefficient
1	CO 00	s.	50.4	0.169	0.281	0.347	0.413	−5.3	−0.024 ± 0.0046
2	CO 00	t.	51.3	0.159	0.331	0.404	0.477	−6.6	−0.029 ± 0.0045
3	CO 04	s.	50.4	0.133	0.072	0.120	0.169	+0.5	+0.002 ± 0.0034
4	CO 04	t.	51.3	0.424	0.178	0.297	0.415	+2.1	+0.015 ± 0.0072
5	DO 00	s.	50.4	0.631	0.425	0.507	0.590	+2.9	+0.017 ± 0.0057
6	DO 00	t.	51.3	0.239	0.151	0.226	0.301	+0.4	+0.002 ± 0.0046
7	DO 04	s.	50.4	0.047	−0.038	+0.006	+0.051	+1.8	+0.006 ± 0.0031
8	DO 04	t.	51.3	0.045	0.032	0.064	0.095	−1.2	−0.002 ± 0.0019
9	CO	s.	50.4	0.320	0.419	0.485	0.551	−4.9	−0.022 ± 0.0046
10	CO	t.	51.3	0.707	0.624	0.702	0.780	+0.1	+0.001 ± 0.0048
11	00	s.	50.4	0.800	0.770	0.854	0.938	−1.3	−0.007 ± 0.0058
12	00	t.	51.3	0.398	0.527	0.630	0.734	−4.4	−0.028 ± 0.0063
13	DO	s.	50.4	0.680	0.449	0.515	0.581	+4.9	+0.022 ± 0.0046
14	DO	t.	51.3	0.293	0.222	0.300	0.378	−0.2	−0.001 ± 0.0048
15	04	s.	50.4	0.180	0.049	0.126	0.203	+1.4	+0.007 ± 0.0053
16	04	t.	51.3	0.469	0.247	0.360	0.474	+1.9	+0.013 ± 0.0069
17	CO 00	m.v.	50.1	0.175	0.229	0.307	0.386	−3.3	−0.019 ± 0.0056
18	CO 04	m.v.	50.1	0.292	0.130	0.208	0.287	+2.1	+0.012 ± 0.0056
19	DO 00	m.v.	50.1	0.408	0.323	0.414	0.504	−0.1	−0.001 ± 0.0065
20	DO 04	m.v.	50.1	0.069	0.024	0.078	0.132	−0.3	−0.001 ± 0.0039
21	CO	m.v.	50.1	0.512	0.387	0.489	0.592	+0.4	+0.003 ± 0.0074
22	00	m.v.	50.1	0.584	0.624	0.717	0.810	−2.8	−0.019 ± 0.0067
23	DO	m.v.	50.1	0.486	0.404	0.508	0.611	−0.4	−0.003 ± 0.0074
24	04	m.v.	50.1	0.356	0.194	0.274	0.354	+2.0	+0.012 ± 0.0058
25	CO ++	s.	50.4	0.018	0	0.018	0.036	0	0 ± 0.0012
26	CO ++	m.v.	50.1	0.045	−0.043	−0.012	+0.018	+3.7	+0.008 ± 0.0022
27	CO ++	t.	51.3	0.125	−0.110	−0.001	+0.109	+2.3	+0.015 ± 0.0067
28	DO ++	s.	50.4	0.002	−0.001	+0.002	+0.005	−0.2	−0.0001 ± 0.0002
29	DO ++	m.v.	50.1	0.012	−0.001	+0.020	+0.041	−0.8	−0.001 ± 0.0015
30	DO ++	t.	51.3	0.008	−0.002	+0.010	+0.022	−0.3	−0.0002 ± 0.0007
31	++	s.	50.4	0.020	+0.001	+0.020	+0.039	0	0 ± 0.0013
32	++	m.v.	50.1	0.058	−0.029	+0.010	+0.049	+2.5	+0.007 ± 0.0028
33	++	t.	51.3	0.133	−0.099	+0.010	+0.118	+2.2	+0.015 ± 0.0067

The regression coefficients of the frequencies of the supergene *DO 04* on latitude similarly are not significantly different from each other in the two contrasting habitats but, unlike those of the supergene *CO 00*, they do not show any significant departure from zero. The values are:

in (s.) +0.006 ± 0.003 and in (t.) +0.002 ± 0.002

Downloaded from rstb.royalsocietypublishing.org

and in neither habitat does the frequency exceed a value of 0.1 throughout the latitude range covered by the survey. Thus, it is evident that the frequency of that supergene, namely *DO 04*, is not only independent of the habitat in which it occurs but is also independent of latitude. Throughout the range, it maintains a consistently low value (figure 12).

The frequencies of the other two supergenes *CO 04* and *DO 00* are, however, significantly different in the two habitats but these and the frequencies of their constituent genes are most conveniently discussed taking each habitat separately.

In sandy habitats (s.), the frequency of the gene 00 is high and, throughout the range 43° N to 58° N, remains so independently of latitude; the regression coefficient minus 0.007 ± 0.006 showing no significant departure from zero. That of the supergene *DO 00*, however, has a

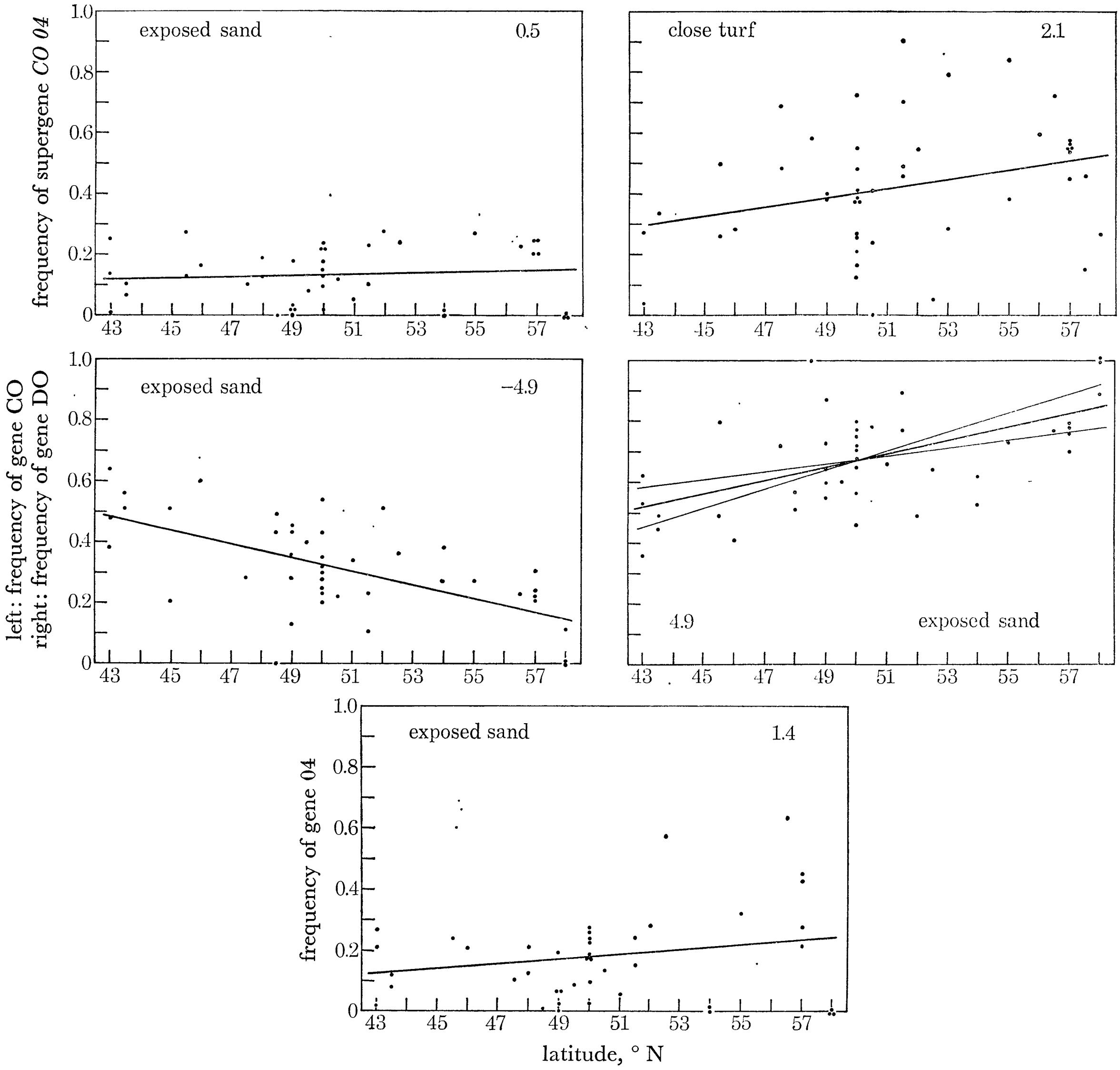


FIGURE 13. Relationships between colonial supergene and gene frequencies and latitude. In each diagram the type of habitat is shown and also a figure giving the number of times the standard error by which the regression coefficient departs from zero, a value of ± 1.96 being significant at the 5 % level. The 5 % confidence limits are drawn on either side of the fitted line of linear regression in the gene DO/exposed sand diagram; in the others the regression line alone is shown.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

value of $+0.017 \pm 0.006$, a value which is significantly different from zero (figure 12). The gene 00 is evidently favoured in sandy habitats and this is probably the result of visual selection (see § 3 (*a*) (ii)). In the northern part of the range, this gene occurs almost entirely as a component of the supergene *DO 00* but progressively southwards, as selection against the supergene *CO 00* becomes diminished, an increasing proportion occurs in coupling with the gene CO. At a latitude of 43° N, the southern limit of the present survey, the frequency of the supergene *CO 00* just exceeds 0.3 in both habitats and it may be inferred that further south still, even higher frequencies of it will be found.

Although the frequency of the supergene *CO 04* in sandy habitats remains at a low value which is independent of latitude, this is not the case for both its component genes. One of these, 04 (the gene determining 00040) does remain at a low frequency independently of latitude in sandy habitats but the other does not (figure 13). The frequency of the gene 04 is

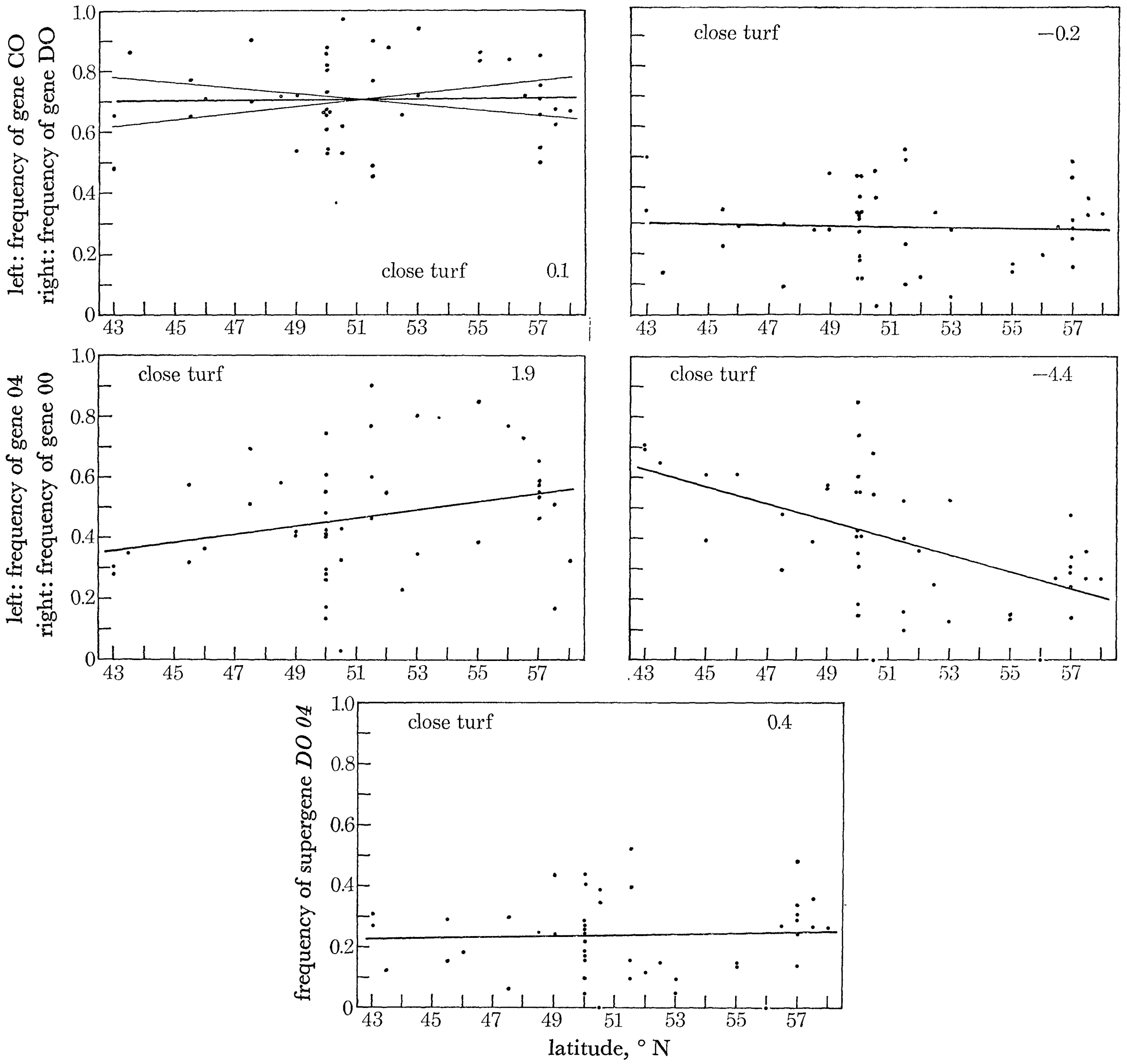


Figure 14. Regression diagrams similar to figures 12 and 13 showing relationships between supergene and gene frequencies and latitude.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

the sum of the frequencies of the two supergenes, *DO 04* and *CO 04*, which in sandy habitats both remain at constant frequency throughout the latitude range. Selection against these two particular supergenes themselves or against either of their component genes could determine this. The supergene *DO 04* is at a low frequency, less than 0.1, in both types of habitat and it is thus unlikely that its low frequency will be determined by factors directly related to a sandy one. The frequency of *CO 04* in turfy habitats (figure 13) varies with latitude and, if this were a response due to the supergene *CO 04* itself, some similar variation would be expected to be evident in the other habitat but it is not. *CO 04* in sandy habitats remains at low frequency independently of the latitude. The frequencies of the three component genes of these two supergenes *CO 04* and *DO 04* do differ from each other, however, in sandy habitats. That of DO is significantly higher than that of 04 and so is that of CO except in the extreme north of the latitude range. It is only 04 that remains consistently low (figure 13). In sandy habitats therefore selection does not appear to act against the features determined by the genes DO and CO but against banding. Visual selection acting upon banding characteristics of the shell and favouring the absence of bands against a sandy substrate thus seems to provide the most likely explanation. Selection against the presence of band 4 keeps the frequency of the gene 04 at a low value and in consequence that of the supergene *CO 04* also. This conclusion is just the same as that reached by an independent consideration, discussed above, of the frequency in sandy habitats of the gene 00 and those of the supergenes *DO 00* and *CO 00*.

In turfy habitats the frequency of the gene CO is high and quite significantly above that of its allele DO (figure 14). Throughout the latitude range 43° N to 58° N their regression coefficients, namely, for the gene CO, $+0.0006 \pm 0.0048$ and, for DO, -0.0008 ± 0.0048, remain very close to zero. The constancy of this difference in frequency over such a considerable range of latitude is clearly an indication that the difference is due, in some way, to habitat. The frequency of the supergene *CO 04* however decreases southwards, the regression coefficient on latitude having a value of $+0.0152 \pm 0.0072$, a significant departure from zero of 2.1 times the standard error. In the extreme south of the range, the gene CO occurs in both the supergenes *CO 00* and *CO 04*, occurring at a slightly higher frequency as a component of *CO 00* than of *CO 04*. Proceeding northwards, as selection against *CO 00* progressively increases, the proportion in repulsion with the gene 04 steadily increases until, at the most northerly end, only a very small proportion is found in linkage with the gene 00, the frequency of *CO 04* having dwindled to a value closely approaching zero and the frequency of *CO 00* having reached a maximum value.

The supergenes *DO 00* in turfy habitats (figure 14) responds in a manner resembling that of *CO 04* in sandy habitats. Similarly, although its frequency throughout the range 43° N to 58° N is maintained independently of the latitude, the same is true for one only of its constituent genes, that determining the discontinuity of shell opacity. The frequency of a supergene such as *DO 00* is determined by selection acting upon one or other of its constituent genes, upon the supergene itself or, to some extent, on both. In this instance, while the frequency of the component gene DO remains constant that of 00 shows a significant rise southwards. Thus it seems most unlikely that it can be selection influencing the genes at the banding locus that limits the frequency of *DO 00* but rather that it is selection acting either upon the gene DO or upon the supergene itself that does so. Throughout the whole of the latitude range the frequencies of both of these, in sandy habitats, are significantly higher than the corresponding frequencies in turfy habitats. For turfy habitats, comparisons, on the one hand, of the frequencies of *DO 00* with those of the other supergenes and, on the other, of those of the gene DO with those of its

Downloaded from rstb.royalsocietypublishing.org

allele CO show that there is a consistent frequency difference associated with the gene DO but no consistent frequency difference associated with the supergene *DO 00*. The frequency of the gene DO is rather more than half the value of that of the gene CO throughout the whole range, a clear indication that selection is acting either to augment the gene CO or to restrict DO. Whichever is the case, it appears to be a consequence of this selection that keeps the frequency of *DO 00* low in turfy habitats.

The results of this analysis are summarized in table 9.

TABLE 9

ref. no.	supergene or gene	differences related to habitat	differences related to latitude		conclusions
			exposed sand	close turf	
1 2	*CO 00*	no	yes: significant increase southwards	yes: significant increase southwards	frequency determined by some factor directly related to latitude
3 4	*CO 04*	yes: frequency higher in t.: difference diminishes southwards	no: low value constant throughout latitude range	yes: decline in frequency southwards – just significant	the two preferred supergenes; differential selection in the two habitats varies with latitude, greatest in north of range
5 6	*DO 00*	yes: frequency higher in s.: difference diminishes southwards and would disappear below 43° N	yes: significant decline southwards	no	
7 8	*DO 04*	no: frequency low and independent of habitat	no: frequency low and independent of latitude	no: frequency low and independent of latitude	selection favours other supergenes at all latitudes and in both habitats
9 10	CO	yes: frequency higher in t. but difference decreases southwards	yes: significant increase southwards	no: high frequency independent of latitude	selection probably favouring CO in (t.)
11 12	DO	yes: higher in s. throughout latitude range	yes: significant decrease southwards	no	
13 14	00	yes: higher in s. but difference decreases southwards	no	yes: significant increase southwards	selection probably favouring 00 in (s.)
15 16	04	yes: higher in t. throughout but difference decreases southwards	no: low value independent of latitude	yes: decline southwards just significant	

B. *Linear regressions of frequency on latitude, nos.* 17–24. These involve the alleles C.O., D.O., unbanded (00) and one-banded (04) in mixed vegetation type habitats. The regression diagrams are shown together in figure 15 and a summary of the results of analysing them comparatively is given in table 10.

C. *Linear regressions of frequency in latitude, nos.* 25–33. The regression diagrams are shown together in figure 16 and a summary of their more important characteristics is given in table 11.

D. *Comparative analysis of regressions.* A comparison of the results summarized in tables 9 and 10 leads to the general and important conclusion that the properties of the populations which occur in the habitats which I have termed mixed vegetation type resemble very much more closely those of the 'turfy' populations than they do those of the 'sandy' ones. Of the three habitat types two, namely exposed sand and close turf are quite distinct and, respectively,

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

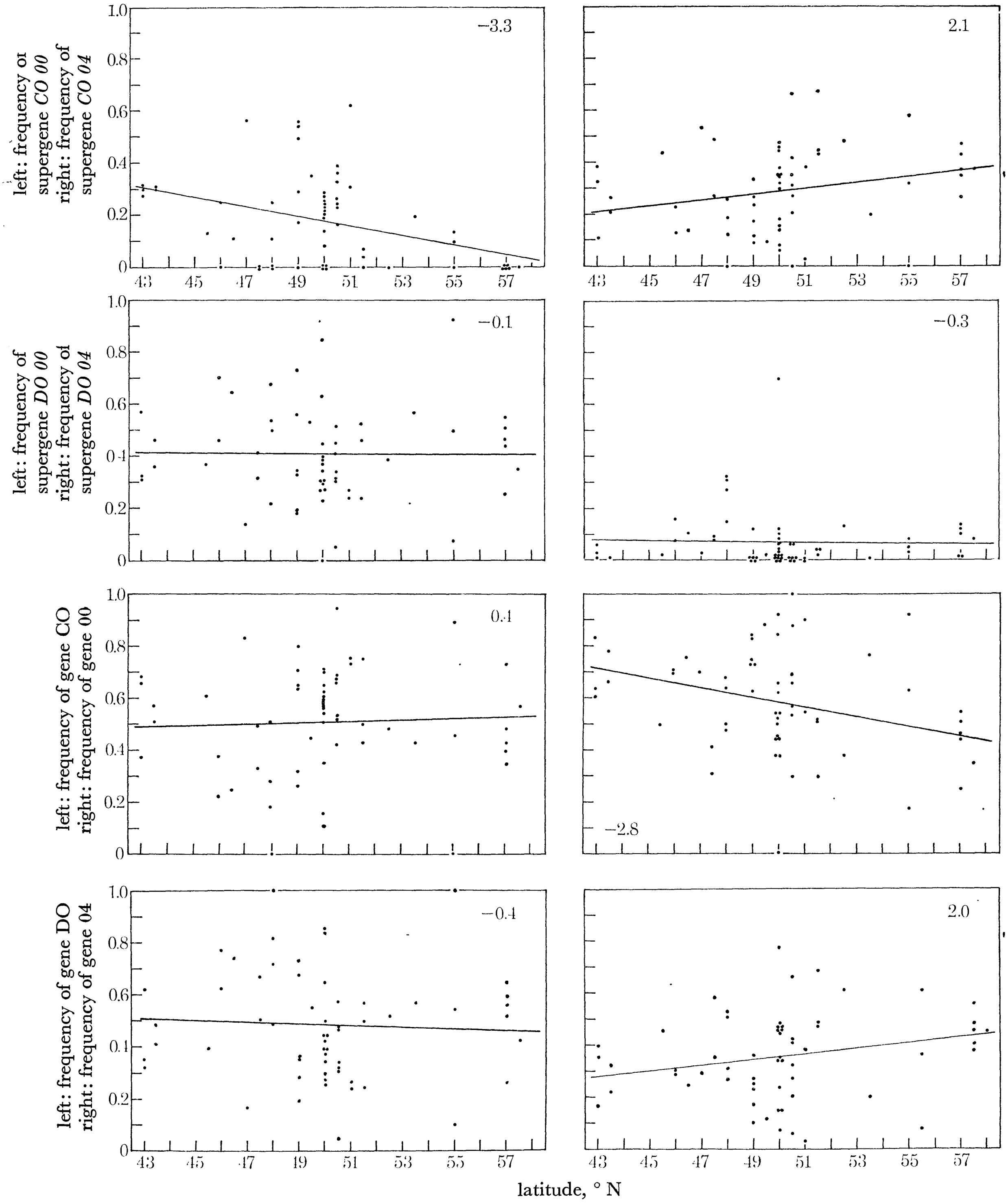


FIGURE 15. Relationships between colonial supergene and gene frequencies and latitude for mixed vegetation type habitats. Fitted regression lines are drawn and, in each diagram, a figure is included which indicates the significance of the departure from zero of the slope of that line; a value of ±1.96 is significant at the 5% level.

Downloaded from rstb.royalsocietypublishing.org

uniform in character, but in contrast mixed vegetation, which includes all the habitats not assigned to either of the other two, is much less uniform in character. However, most of the habitats referred to that type do have a coverage of vegetation. For that reason, in general their *appearance* is nearer to that of close turf than to that of exposed sand. Since the genetic properties of the mixed vegetation populations are similarly so inclined, there is a clear indication that the significant difference between habitats, which influences the compositions of the inhabiting population of *Cochlicella acuta*, neglecting for the present the actual colour of the sand, is whether or not the sand is exposed, that is to say, whether or not the snails have a background of green vegetation or one almost entirely composed of the sandy substrate itself.

Table 10

ref. no.	gene or supergene	differences related to latitude	habitat type showing similar relationship	conclusion
17	*CO 00*	frequency increases significantly southwards	both s and t	provides confirmation that frequency independent of habitat type
18	*CO 04*	frequency decreases significantly southwards	t	—
19	*DO 00*	none	t, but frequency significantly lower	—
20	*DO 04*	none: frequency remains at low value	both s and t	provides confirmation that frequency is independent of both habitat and latitude
21	CO	none: not significantly different from that of DO	t	—
22	DO	none	t, but frequency significantly lower	habitat types designated close turf and mixed vegetation probably not significantly different
23	00	frequency increases significantly southwards	t	
24	04	frequency decreases significantly southwards	t	

Table 11

A, frequency change in relation to latitude; B, supergene or gene showing similar relationship.

supergene or gene	exposed sand		mixed vegetation		close turf	
	A	B	A	B	A	B
CO ++	none	*CO 04* in s	decrease southwards significantly below *CO 04* frequency	*CO 04*	decrease southwards: above m.v. but below *CO 04* frequency	*CO 04*
DO ++	none: exceedingly low at all latitudes	*DO 04*	none	*DO 04*	none	*DO 04*
++	none	04	significant decrease southwards	04	significant decrease southwards	04

The results summarized in table 10 confirm those in table 9; they show the latitude dependence of the frequency of the supergene *CO 00* and the independence of both latitude and habitat type of that of *DO 04*.

Comparisons between table 11 and tables 9 and 10 show that there is a general similarity between the relationships involving the genes determining the one-banded morph 00040 and

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

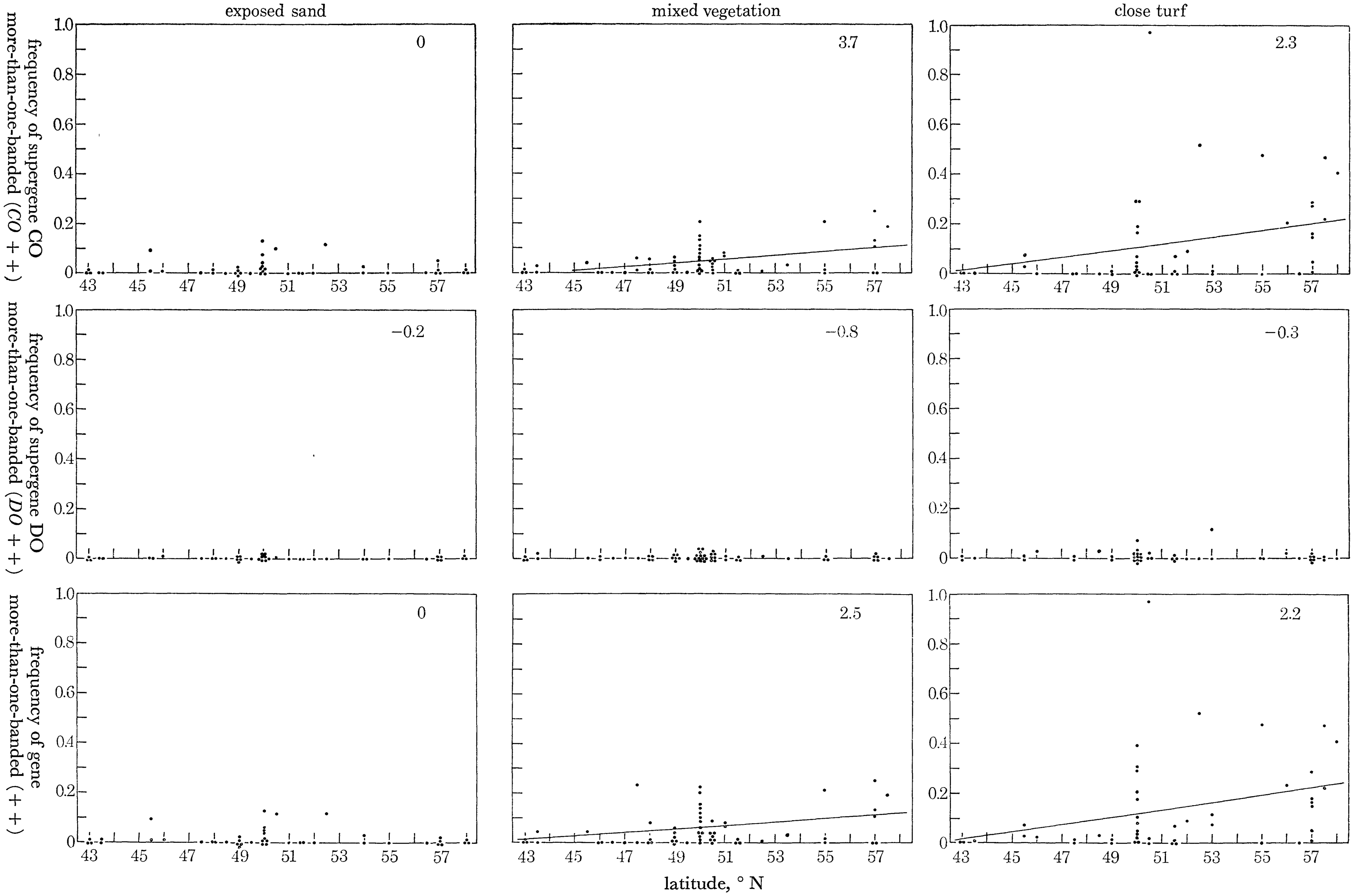


FIGURE 16. Relationships between latitude and colonial supergene and gene frequencies involving the gene more-than-one-banded, depicted by the symbol + +, for the habitat types exposed sand, mixed vegetation and close turf. Only those fitted regression lines with a slope which departs significantly from zero have been drawn.

Downloaded from rstb.royalsocietypublishing.org

those (here treated collectively) producing more-than-one-bandeds. For example, in sandy habitats, the frequency of the supergene *CO* + + is low and remains so independently of latitude. So does that of *CO 04*. In the other two types of habitat, close turf and mixed vegetation, there is a gradual increase northwards in the frequency of banded forms, irrespective of the number of bands but, since this does not occur similarly in sandy habitats, it must be concluded that at least two different kinds of selection are involved, the one being related to habitat, the other to latitude. In the non-sandy habitats, the frequencies of the genes determining one-bandeds 00040 and more-than-one-bandeds are not equally frequent, however. At all latitudes, the frequency of the supergene *CO 04* and that of the gene determining 00040 are quite significantly higher than are those of the supergene CO + + and the gene + +, respectively.

5. Discussion and conclusion

The broad conclusions that may be drawn from all these studies are that the frequencies of certain supergenes and genes, which are components of the supergene system by which the shell polymorphism in *Cochlicella acuta* is mainly controlled, change in relation to habitat type, others alter in relation to latitude while those of a third category appear to be independent of both latitude and habitat type. Such variations may reasonably be considered to be the results of selection which must include at least three different kinds, respectively identified by being related directly to habitat type, to latitude and thirdly, to neither.

The cryptic appearance of heavily-banded morphs against dark backgrounds, of DO unbandeds on sandy substrates and the existence of at least one visual predator, namely the rook, *Corvus frugilegus*, together provide good reasons for concluding that visual selection is one of the kinds probably the major kind related to habitat. Selection of that kind, that is selection related to the appearance of the background of a particular habitat and brought about by avian visual predation is known to occur in other species. It has been convincingly demonstrated for *Cepaea*, by Sheppard (1951), Cain & Sheppard (1954) and Currey, Arnold & Carter (1964) and for the moth *Biston betularia* by Kettlewell (1955, 1956). It seems unlikely that rooks will be the only visual predators of *C. acuta* but since their range (Peterson, Mountford & Hollom 1954) extends beyond that over which the habitat/morph frequency relationship has been demonstrated it is possible that rooks alone could be responsible for the visual predation. If their predation is selective and it seems unnecessary to concede that it could be otherwise, rooks seem likely to be the principal agents involved in the habitat-related selection.

Such avian visual selection cannot be the only habitat-related selection that is acting. This is well illustrated by the frequencies of the supergenes *CO 04* and *CO* + +. In sandy habitats irrespective of latitude the frequencies of both remain low (see figures 13 and 16); in other words, both are selected against in favour of unbandeds. Yet, in non-sandy habitats, their frequencies differ markedly. That of *CO 04* predominates and that frequency difference is maintained in non-sandy habitats, as the frequencies of both progressively increase in a northerly direction. That is to say, in sandy habitats, selection does not favour either of those two supergenes but in non-sandy ones it does. Since the morphs that these supergenes determine, namely CO one-banded (CO 00040) and CO more-than-one-banded, are different in appearance and, as neither is very cryptic in most of the situations in which they are found, it seems that visual selection can be playing only a minor part in determining their relative frequencies. Some non-visual habitat-related selection, which seems likely to be microclimatic in nature, must be

Downloaded from rstb.royalsocietypublishing.org

involved. It is evident that within and between habitats of similar appearance, there will be differences of a microclimatic nature. As an example, the close turf on a cliff top within a few yards of the sea itself must provide a very different microclimate from that afforded by habitats of similar appearance situated a mile inland near the limit of the dune slacks. Between habitats of different type, the microclimates must vary to an even greater extent. The effects of microclimatic factors, if they do have selective influences, may be considerable for, as Lamotte (1959) has pointed out, the diversity of microclimates to which colonies are exposed may be considerable, much greater than meteorological averages show.

Differences in morph frequencies brought about by selection that is related to habitat variation, whether visual or non-visual, will tend to persist and be more pronounced in a species such as *Cochlicella acuta*, the populations of which are very nearly always localized and discontinuous, since such differences will not be smoothed out by gene flow to the extent they would be if the populations were more continuous.

In the analyses reported in this paper, the latitude-related variations that have been demonstrated depend largely upon variations in the frequency of the supergene *CO 00*. This is primarily determined by selection acting against the phenotype CO unbanded, which is the universal recessive (Lewis 1975). This selection acts most strongly in northern colonies where the morphs CO 00040 and DO 00000 are the most commonly occurring ones. If heterozygote advantage is the mechanism by which this part of the polymorphism is maintained, the situation is of particular significance since for both the morphs CO 00040 and DO 00000 the only known heterozygote genotypes that could exist include the supergene *CO 00*. These genotypes are $\frac{CO\ 04}{CO\ 00}$ and $\frac{DO\ 00}{CO\ 00}$. In the northern colonies, the rate of loss of homozygous CO unbandeds must therefore be considerable both in sandy habitats, in which DO unbandeds are the most frequently occurring morphs, and in non-sandy ones, in which CO one-bandeds are. High rates of homozygous mortality have been reported in other species, for example in *Drosophila tropicalis* (Dobzhansky & Pavlovsky 1955). Moreover, in that particular instance, in a different locality the high mortality of the homozygote concerned was much diminished. This also occurs in the case of *C. acuta* in which the CO unbanded homozygotes increase progressively in frequency southwards.

The nature of the latitude-related selection which could influence the frequency of the supergene *CO 00* is not evident. Since in neither sandy nor non-sandy (close turf and mixed vegetation together) habitats does the CO unbanded morph seem to be at a disadvantage visually, the factor or factors responsible are very probably non-visual. Mayr (1963) asserts that 'the strong geographic variation of most cases of polymorphism, often closely parallelling climate gradients, is evidence of correlated physiological effects of polymorphic genes'. In *C. acuta*, the distribution of the latitude-related variation strongly suggests that climate is involved, but at present direct evidence of climatic selection or what aspects of climate may have a selective influence is lacking. In *Cepaea*, however, the influence of climatic factors has been demonstrated. Lamotte (1959) has reported differential survival between different phenotypes when they have been subjected to different conditions of temperature and humidity, and Wolda (1963, 1965) has shown that temperature influences the reproductive capacities of morphs differentially. Lamotte used adult snails in his investigations and based his conclusions on these studies alone. Cain & Sheppard (1961) have drawn attention, however, to the importance of selection acting upon juveniles. In *C. acuta*, evidence derived from sub-fossil

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

material taken in Cornwall from a site far from the fringes of the range of the species (unpublished data) shows that mortality of juveniles is very considerable and it also indicates that this mortality occurs during the winter period, which suggests strongly that climatic factors are involved. For a review of climatic selection in snail populations see Jones (1973). A relationship between climate and gene frequencies has also been demonstrated for some plant species. Harland (1947) found that climatic factors determined the frequency ratio of two allelic forms of the Castor oil plant, *Ricinus communis* at Lima in Peru. Daday (1954*a*, *b*) has shown a close correlation between a cline (Huxley 1938, 1974) extending southwest to northeast across Europe in the frequency of the gene responsible for the presence of cyanogenic glucosides, which is the dominant condition (Atwood & Sullivan 1943), in *Trifolium repens* and January mean temperatures and, in addition, between the frequency of cyanogenic plants of the same species and altitude in the Alps. Warm winter temperatures favour high frequencies, a relationship shown to exist for populations of *T. repens* in Euro-Asia, North America and Japan (Daday 1958), also.

The nature of the selection, which keeps the frequency of the supergene *DO 04* at a consistently low value must be of a different kind again, since it is apparently neither habitat-related nor latitude-related. It is suggested that interaction of some kind between the component genes producing some physiological disadvantage may be responsible.

These three kinds of selection act together upon the same gene system. They act in different directions and, in different places and at different times, to varying and differing degrees. They are unlikely to be the only kinds of selection influencing the shell variation but they are probably the principal elements of a dynamic equilibrium of selective forces that determine, in any population of *C. acuta*, the distribution of the genes responsible for the shell polymorphism.

I am most grateful to Professor A. J. Cain and I thank him for his generous help and encouragement while the work was being done and, also, for his invaluable advice during the course of the preparation of this paper. I wish to thank Professor P. M. Sheppard, F.R.S., Professor E. B. Ford, F.R.S., and B. C. Clarke, also, for guidance and advice, Professor J. W. S. Pringle, F.R.S., for the facilities that he provided in the Department of Zoology, Oxford and Professor A. C. Thomas for permitting me to work on his land at Gwithian. To the Leverhulme Trust, I express my very grateful thanks for financial assistance.

REFERENCES

Arnold, R. W. 1968 Climatic selection in *Cepaea nemoralis* (L.) in the Pyrenees. *Phil. Trans. R. Soc. Lond.* B **253**, 549–593.

Atwood, S. S. & Sullivan, J. T. 1943 Inheritance of a cyanogenic glucoside and its hydrolysing enzyme in *Trifolium repens*. *J. Hered.* **34**, 311–320.

Bailey, N. T. J. 1959 *Statistical methods in biology*. Cambridge University Press.

Boyd, W. C. 1954*a* Maximum likelihood method for estimation of gene frequencies from MNS data. *Am. J. hum. Genet.* **6**, 1–10.

Boyd, W. C. 1954*b* Shortened maximum likelihood estimation of Rh gene frequencies. *Am. J. hum. Genet.* **6**, 303–318.

Boyd, W. C. 1955 Simple maximum likelihood methods for calculating Rh gene frequencies in Pacific populations. *Am. J. Phys. Anthrop.* **13**, 447–453.

Clarke, B. 1960 Divergent effects of Natural Selection in two closely-related polymorphic snails. *Heredity* **14**, 423–443.

Clarke, B. 1975 The causes of biological diversity. *Scient. Am.* **233** (2), 50–60.

Clarke, B. & Murray, J. 1969 Ecological genetics and speciation in land snails of the genus *Partula*. *Biol. J. Linn. Soc.* **1**, 31–42.

Downloaded from rstb.royalsocietypublishing.org

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

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. 1961 Visual and physiological selection in *Cepaea*. *Am. Nat.* **95**, 61–64.

Carter, M. A. 1968 Thrush predation of an experimental population of the snail, *Cepaea nemoralis* (L.). *Proc. Linn. Soc. Lond.* **179**, 241–249.

Crampton, H. E. 1916 Studies on the variation, distribution and evolution of the genus *Partula*, the species inhabiting Tahiti. *Publ. Carneg. Instn* **228**, 1–311.

Crampton, H. E. 1932 Studies on the variation, distribution and evolution of the genus *Partula*, the species inhabiting Moorea. *Publ. Carneg. Instn* **410**, 1–335.

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.

Daday, H. 1954*a* Gene frequencies in wild populations of *Trifolium repens*. 1. Distribution by latitude. *Heredity* **8**, 61–78.

Daday, H. 1954*b* Gene frequency in wild populations of *Trifolium repens*. 2. Distribution by altitude. *Heredity* **8**, 377–384.

Daday, H. 1958 Gene frequencies in wild populations of *Trifolium repens* L. 3. World distribution. *Heredity* **12**, 169–184.

Dobzhansky, Th. & Pavlovsky, O. 1955 An extreme case of heterosis. *Proc. Natn. Acad. Sci. U.S.A.* **41**, 289–295.

Ellis, A. E. 1926 *British snails*. Oxford: Clarendon Press.

Fisher, R. A. 1946 The fitting of gene frequencies to data on rhesus reactions. *Ann. Eugen. Lond.* **13**, 150–155.

Fisher, R. A. 1947 Note on the calculations of the frequencies of rhesus allelomorphs. *Ann. Eugen. Lond.* **13**, 223–224.

Ford, E. B. 1940 Polymorphism and taxonomy. In *The new systematics* (ed. J. S. Huxley), pp. 493–519. Oxford: Clarendon Press.

Ford, E. B. 1971 *Ecological genetics*, 3rd ed. London: Methuen.

Germain, L. 1930 Mollusques terrestres et fluviatiles Faune de France, XXI, 477.

Harland, S. C. 1947 An alteration in gene frequency in *Ricinus communis* L. due to climatic conditions. *Heredity* **1**, 121–125.

Huxley, J. S. 1938 Clines: an auxiliary principle. *Nature, Lond.* **142**, 219–220.

Huxley, J. S. 1974 *Evolution: the modern synthesis*, 3rd ed. London: Allen and Unwin.

Jones, J. S. 1973 Ecological genetics and natural selection in molluscs. *Science, N.Y.* **182**, 546–552.

Jones, J. S. 1974 Environmental selection in the snail *Cepaea vindobonensis* in the Lika area of Yugoslavia. *Heredity* **32** (2), 165–170.

Jones, J. S., Briscoe, D. A. & Clarke, B. 1974 Natural selection in the polymorphic snail *Hygromia striolata*. *Heredity* **33** (1), 102–106.

Kettlewell, H. B. D. 1955 Selection experiments on industrial melanism in the Lepidoptera. *Heredity* **9**, 323–342.

Kettlewell, H. B. D. 1956 Further selection experiments on industrial melanism in the Lepidoptera. *Heredity* **10**, 287–301.

Lamotte, M. 1951 Recherches sur la structure génétique des populations naturelles de *Cepaea nemoralis* L. *Bull. Biol. France Suppt* **35**, 1–239.

Lamotte, M. 1959 Polymorphism of natural populations of *Cepaea nemoralis*. *Cold. Spr. Harb. Symp. quant. Biol.* **24**, 65–86.

Lewis, G. 1975 Shell polymorphism in the snail *Cochlicella acuta* (Müller) and some data on its genetics. *Biol. J. Linn. Soc.* **7**, 147–160.

Lewontin, R. C. 1974 *The genetics basis of evolutionary change*. New York: Columbia University Press.

Mayr, E. 1963 *Animal species and evolution*. Harvard University Press.

Peterson, R., Mountford, G. & Hollom, P. A. D. 1954 *A field guide to the birds of Britain and Europe*. London: Collins.

Porpora, L. & Sacchi, C. F. 1958 Ricerche su *Euparypha arietina* (Rossmaessler). II. *Ann. Istit. Mus. Zool. Univ. Napoli* **9** (7), 1–43.

Sacchi, C. F. 1956 Relazioni tra colori ed ambienti in popolazioni naturali spagnuole di *Pseudotachea* (*Stylommatophora*, Helicidae). B *Zool.* **23**, (2), 461–502.

Sacchi, C. F. 1965 Ecological and historical bases for a study of Iberian terrestrial Mollusca. *Proc. 1st Europ. Malac. Congr.* (1962), 243–257.

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

Wolda, H. 1963 Natural populations of the polymorphic land snail *Cepaea nemoralis* (L.). *Arch. Néerl. Zool.* **15** (4), 381–471.

Wolda, H. 1965 The effects of drought on egg production in *Cepaea nemoralis* (L.). *Arch. Néerl. Zool.* **16** (3), 387–399.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

FIGURE 7. An aerial photograph of the site at Godrevy showing the principal features of the area. The line drawn on the photograph represents the transect (see figure 9).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES