VARIATION IN SHELL COLOUR AND PATTERN CORRELATED WITH MICROCLIMATE IN THE STRIPED SNAIL *CERNUELLA VIRGATA* (DA COSTA, 1778) (GASTROPODA, PULMONATA, HYGROMIIDAE)

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Abstract *Polymorphisms for shell colour and pattern in* Cernuella virgata *are illustrated. Populations of* C. virgata *in north-east England are described in which white shells are predominant in an open habitat exposed to the sun, and brown shells occur more commonly in shaded sites. This could well be a result of climatic selection. Other populations of* C. virgata *in north-east England and on the east coast of Scotland do not show any correlation with microclimate, and it is suggested that other factors such as founder effects and evolutionary bottlenecks might be responsible for the present day incidence of different shell pattern morphs.*

Key words Cernuella virgata*, polymorphism, climatic selection, founder effect, evolutionary bottleneck*

Introduction

Many species of snail belonging to the superfamily Helicoidea show more or less striking patterns of polymorphism of shell colour and banding. Among these species, *Cepaea nemoralis* has been studied in considerable detail. Although earlier workers suggested that the shell patterns were random, and not subject to selection, it now appears that various selective forces act to produce these polymorphisms (e.g. Cain, 1977; Jones *et al*., 1977; Silvertown *et al.,* 2011). *Cepaea nemoralis* is subject to predation by birds, especially the Song Thrush *Turdus philomelos,* which select those snails that stand out most clearly against the background (Cain & Sheppard, 1954). A correlation with climate has also been established, such that pale-shelled individuals tend to be commoner in warmer habitats, and dark-shelled individuals (including heavily banded ones) tend to be commoner in cooler habitats (Jones, 1973). Richardson (1974) showed that this difference could well be a result of a selective process. Polymorphisms have been studied in a number of other species of helicid snails, including *Arianta arbustorum* (Burla & Stahel, 1983), *Cepaea hortensis* (Cameron, 2013), *Cepaea vindobonensis* (Jones, 1973), *Cochlicella acuta* (Lewis, 1977), *Xerolenta obvia* (Lazaridou & Chatziionnaou, 2005), and *Theba pisana* (Baker & Vogelzang, 1988; Johnson, 2011). Many, but not all, of these studies showed a correlation between degree of exposure and shell colour, but Lewis (1977) also found that darker forms of *Cochlicella acuta* were more commonly found on dark substrates, and suggested that this might be a result of visual selection by Rooks (*Corvus frugilegus*), although there was no direct evidence for this.

Shell colour polymorphisms have also been studied in the Striped Snail *Cernuella virgata* (Da Costa, 1778) (also known as the Vineyard or White Snail) (Lewis 1977; Baker 1988a, 2012). No clear evidence emerged from these studies to correlate polymorphisms with microclimate, although Lewis (1977) found that darker specimens of *Cernuella virgata* were commoner on dark substrates, like *Cochlicella acuta*, and suggested that this was a result of selective predation.

In 2014 two adjacent populations of *Cernuella virgata* were discovered that showed striking differences in shell colours and pattern. This study was carried out to see if these differences could be correlated with the local habitat or climate. These findings were compared with observations from several other populations on the east coast of the northern part of Great Britain to see if any such correlations might be of general occurrence.

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Material and Methods

Sampling methods

Cernuella virgata appears to live in discrete colonies, separated from each other by areas

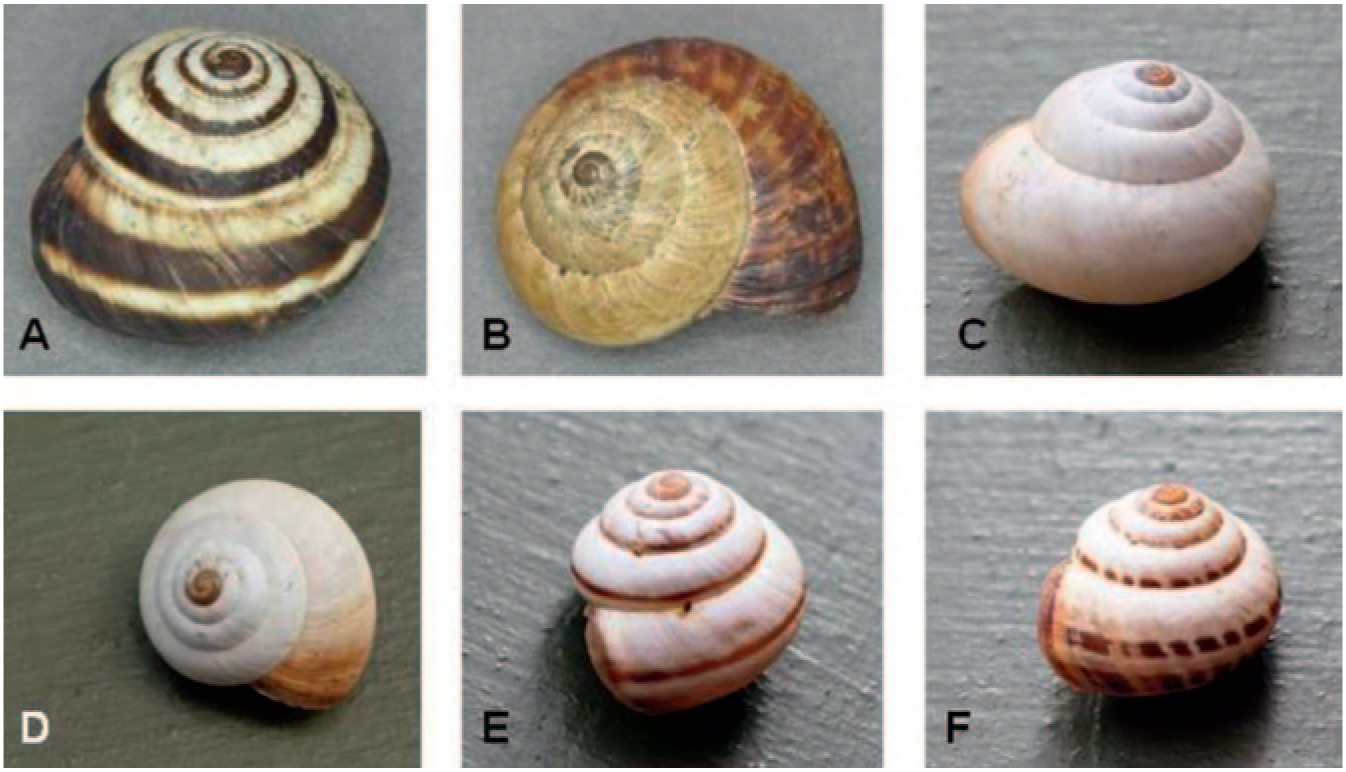

Figure 1 A "typical" form of *Cernuella virgata* – banded; B brown form; C white form; D white shell showing dark purplish-red colour behind lip of shell; E single-banded shell. F shell with broken bands.

containing no, or very few, specimens of this species (see Results). As far as possible the polymorphisms of all the live adult snails in a colony were recorded. Three main classes were predominant: white, banded, and brown (Fig. 1). These are described in more detail in the Results. The British National Grid References of each site were determined with a Garmin Etrex GPS.

Temperature measurements

Surface temperatures were measured with an Infrared Non-contact Thermometer (model TN1, Electronic Temperature Instruments Ltd., Worthing, West Sussex BN14 8HQ, United Kingdom) set for an emissivity of 95% as recommended by the manufacturer. Air temperatures were measured at heights of approximately 5cm and 125cm above the surface of the ground using a Vertical Barrel Digital Test Thermometer (Brannan Thermometers, Cleator Moor, Cumbria CA25 5QE, United Kingdom).

Results

Polymorphisms

All authors agree that *Cernuella virgata* is a very variable species; many varieties have been described (Taylor, 1921; Ellis, 1969), and a limited number of these have been illustrated (e.g. Kerney & Cameron, 1979; Pfleger & Chatfield, 1988; Fechter & Falkner, 1990). Although it is possible to recognise a number of distinct types, it must be realised that there is considerable gradation between the different morphs. The following account refers only to specimens found during the present study, and is necessarily an over-simplification.

The "typical" form (Fig. 1A) has a white background, a broad dark band near the periphery of the shell, visible from above, and a number of finer bands on the underside of the shell; according to Ellis (1969) there are seven, but the number is in fact variable. This form has a very black and white appearance, particularly in live animals, but the bands are in fact dark brown. In addition, the background colour of the shell is often not pure white, but may be very pale brown.

The brown form (Fig. 1B) has a medium brown colour, usually shading to a paler colour on the upper side of the shell. Although at first sight the coloration seems to be uniform, faint bands can often be discerned on close examination. A common variant has a pale peripheral band;

this seems to correspond with the variety *leucozona* (Taylor, 1921; Ellis 1969). Most of the brown shells found in this study belong to this variety.

White shells (Fig. 1C) are pure white all over, except for a region of deep purplish red just behind the lip. The extent of this pigment is very variable and was quite small in most of the snails found in this study, although it can extend further back in a few individuals (Fig. 1D). This corresponds to the variety *albicans* (Taylor, 1921; Ellis 1969). Some brown shells are very pale, and may approximate to the class of white shells rather than that of brown shells.

Single-banded shells (Fig. 1E) form only a small proportion of the shells, but are widespread. In their simplest form they appear to have only a single band at the periphery of the shell. This band is usually rather narrow, and gives the shell a distinct appearance even when the underside of the shell is not visible. In many cases, however, faint bands are visible on the underside of the shell. In fact, these shells appear to be a poorly pigmented version of the "typical" banded shell. These are not equivalent to "mid-banded" shells in *Cepaea*, which result from the absence of bands above and below the central one.

Shells from one site show what I have called broken bands (Fig. 1F). The pattern on the shell is basically that of the typical banded shell, except that the bands are interrupted at fairly regular intervals.

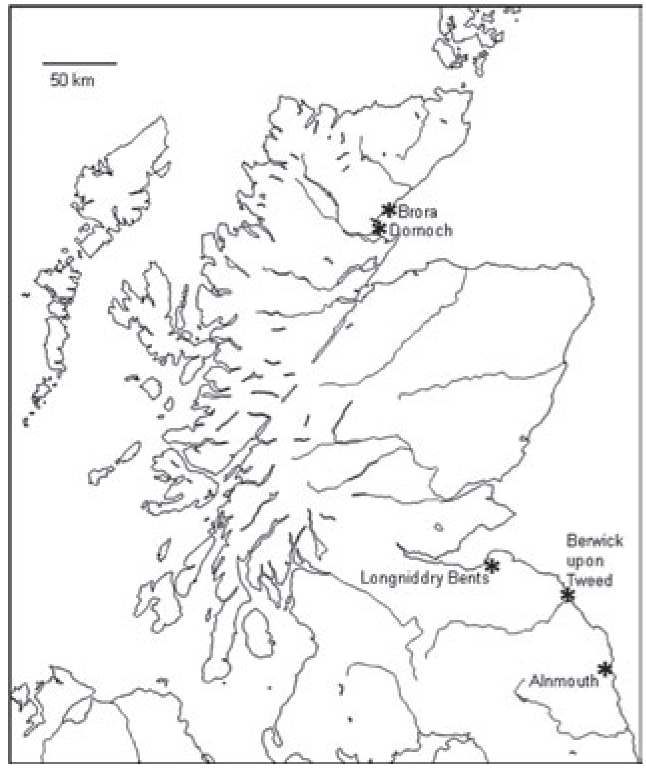

Figure 2 Map of the northern part of Great Britain, showing the location of the sites studied.

Sites sampled — The locations of the sites studied are shown in Fig. 2.

Berwick-upon-Tweed (55° 46′ N) The site at Berwick-upon-Tweed, Northumberland, England, where the populations were found that prompted this study, is an area of flat ground north of the breakwater at the mouth of the Tweed estuary, bounded to the west by higher ground, and to the east by the beach and the North Sea. The breakwater at this point runs very roughly from north-north-west to south-south-east; in fact, it faces 62° east of north. As a result, the landward side of it only receives sunshine during the morning, and by 12 noon BST (~10.52 a.m. local time, Berwick-upon-Tweed being at longitude 2° 00′ west) the sun is aligned along the direction of the breakwater, which is thus in shade for the greater part of the day. The breakwater is built of masonry, with a narrow strip of bare ground at its base. At the head of the breakwater, and in line with it, is a house (Fig. 3A). A short distance from the breakwater is mown grass, and nearer the beach a variety of coastal vegetation, mainly grasses. Further up the coast the typical coastal vegetation has been invaded by ivy, *Hedera helix* (Fig. 3B), although there were still large areas of open grassland. This site is more open, and would receive sunshine for much of the day.

The site at Berwick-upon-Tweed was visited three times, once in 2014, and twice in 2016. The snails were found over a distance of approximately 30 m along the breakwater, and extending out into the adjacent grassland for about 50 m, at which distance they were very sparse. Whereas snails were abundant on the breakwater and adjacent ground in 2014, they were much scarcer there in 2016. Nevertheless, the results were essentially similar at all visits. At the breakwater, shells are predominantly banded, but with a good proportion of brown shells also (Fig. 4 and Table 1). White and single-banded shells are rare here. The area of coastal vegetation nearest to the breakwater shows a similar pattern, although the snails are relatively uncommon in this area. However, on the coastal vegetation further up

Figure 3 The different habitats at Berwick-upon-Tweed. A the shady side of the breakwater, including the house at the landward end; B open coastal vegetation further up the coast, where white shells predominate.

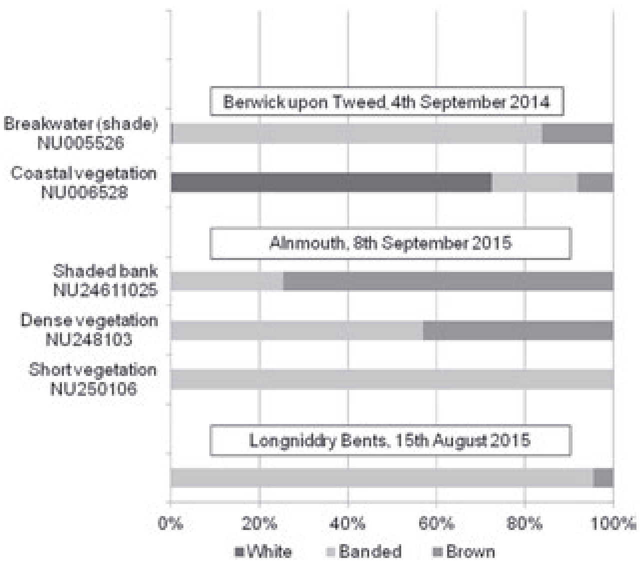

Figure 4 Bar chart showing examples of the proportions of different morphs of shell colour and banding at Berwick upon Tweed, Alnmouth, and Longniddry Bents. Except for the breakwater at Berwick-upon-Tweed (NU005526) and the shaded bank at Alnmouth (NU24611025), all the sites are open and would be in the sun for most of the day.

the coast, the great majority of shells are white, with only small numbers of the other morphs. In 2014, 72.6% of shells were white at this site, while on the two visits in 2016 the proportion of white shells was over 90%. This last area extends for a distance of 20–30 m, and is separated from the previous one by a distance of the order of 150 m in which there were no specimens of *C. virgata*, or at most very few.

A series of temperature measurements were taken on 16th August 2016, a warm summer day. Air temperatures, both near the breakwater and over the area of coastal vegetation, were very similar, in the range 19.4–20.9ºC. Measurements of the surface temperature of the breakwater gave an interesting set of values (Table 2). In the late morning, shortly before the sun went off the north-easterly side of the breakwater, temperature readings adjacent to individual snails averaged 21.7ºC, and on the side of the house, which was painted a pale colour (Fig. 3A), 19.5ºC. In the afternoon, when this side of the breakwater and house had been in shade for some 2.5 h, the corresponding temperatures were 19.7ºC and 16.8ºC, so that the temperature here was falling at a time when temperatures generally would still be rising. However, the surface temperature of the top of the breakwater, measured adjacent to the few snails that were there, averaged 29.5ºC in the afternoon, with a highest reading of 32.6ºC.

Alnmouth (55º 23′ N) Alnmouth is about 50 km south of Berwick-upon-Tweed on the coast of Northumberland and has a good population of *C. virgata* along its coasts. Three areas are of particular interest. The first is a site overlooking the mouth of the River Aln, where a bank slopes down steeply to the beach and is overshadowed by a small tree (Fig. 5A). When studied in 2015, this small area, only 3–4 m across, which faces due south, had three times as many brown shells as banded ones (Fig. 4 & Table 3). A nearby area of well-vegetated dunes, open to the sun (Fig. 5B), had a majority of banded snails, but also a substantial number of brown snails. The difference is highly significant (χ^2=17.67 with 1 degree of freedom, $p < 0.001$). It was not clear whether

Table 1 Counts of the various polymorphic forms of *C. virgata* at Berwick-upon-Tweed

Date	Habitat	Grid refs.	White	Single-banded	Banded	Brown
4th September 2014	Breakwater (shaded)	NU005526 NU005527	1	0	426	82
	Coastal vegetation	NU005526 NU006527	8	3	90	28
	Coastal vegetation	NU006528	82	11	11	9
16th August 2016	Breakwater (shaded)	NU005527	0	0	21	11
	Coastal vegetation	NU006527	0	0	5	0
	Coastal vegetation	NU005529 NU006528 NU006529	208	9	4	8
17th October 2016	Breakwater (shaded)	NU005527	0	0	36	10
	Coastal vegetation	NU006527 NU005526 NU006527	0	1	12	16
	Coastal Vegetation	NU005529 NU006528 NU006529	121	0	1	7

Table 2 Temperature measurements at Berwick-upon-Tweed on 16th August 2016. Measurements were made of the surface of the breakwater in the morning (11.26–11.47 BST) when the stonework had been irradiated by the sun for several hours, and in the afternoon (14.10–14.17 BST) after the stonework had been in shade for more than 2h. The sunny side of the breakwater had been exposed to the sun for approximately 2.5 h. All measurements were taken in the area of grid reference NU005527.

Time	Substrate	Mean temperature±s.d.	N
11.26–11.47	Wall of breakwater	21.7±1.44°C	18
	Wall of house	19.5±0.42°C	2
14.10–14.17	Wall of breakwater	19.7±0.91°C	9
	Wall of house	16.8±0.61°C	4
14.25–14.30	Sunny side of breakwater	29.5±1.61°C	12

there was an area between these sites from which *Cernuella virgata* was absent. On two visits in 2016, the number of snails in the shady area under the tree was very small, but still the great majority were brown.

Further round towards the sea there was a long narrow strip of very short vegetation, about 170 m long, between a region of dunes and a car park (Fig. 5C). This coast faces about 30° south of east, and with flat ground inland of the site must be exposed to the sun all day. This area contained predominantly banded snails, but with a significant proportion of brown shells; these were, however, a paler brown than those recorded at the previous site, or by the breakwater at Berwick-upon-Tweed. It was noticeable that the snails were concentrated in discrete colonies, with only a few sparsely distributed snails in between. Moreover, the pale brown snails were commoner at each end of this strip of very short vegetation, and absent in the middle, where only banded snails were present. Because of the great density of vegetation between this site and the previous one, it was not possible to determine if they were separated by an area from which *Cernuella virgata* was absent.

Figure 5 The habitats at Alnmouth, Northumberland. A a steep bank above the beach, which is overshadowed by a small tree (grid ref. NU2461 1025). B the well vegetated dunes near the site shown in A. C the strip of very short vegetation between the sand dunes and a car park (grid refs NU249105 to NU250107).

Table 3 Counts of the various polymorphic forms of *C. virgata* at Alnmouth, Northumberland

Date	Habitat	Grid refs.	Single-Banded	Banded	Brown
8th September 2015	Shaded bank above beach	NU2461 1025	0	15	44
	Dunes with dense vegetation	NU248103	0	139	105
	Short coastal vegetation	NU250106	0	87	0
26th August 2016	Shaded bank above beach	NU2461 1025	0	1	8
	Short coastal vegetation	NU249105 NU250106 NU250107	3	344	92
12th October 2016	Shaded bank above beach	NU2461 1025	1	2	9
	Dunes with dense vegetation	NU248103 NU248104	1	42	30
	Short coastal vegetation	NU249105 to NU250107	0	1530	181

Longniddry Bents, East Lothian (55° 58′ N) Longniddry Bents is a coastal area of flat ground, both sandy and stony, approximately 400 m long, facing north over the Firth of Forth, which would be exposed to the sun for most of the day. The snails here are predominantly banded. On 15th August 2016, 213 banded snails were found, and only 10 brown snails (Fig. 4). On previous occasions, only banded snails, or banded snails with only one or two specimens of other morphs, were present.

Embo (57° 54′ N) to Dornoch (57° 52′ N), Sutherland Populations of *C. virgata* between Embo and Dornoch, on the east coast of Sutherland, were sampled on 20th September 2016. There were several discrete populations, each only a few metres across, with few or no specimens of *C. virgata* in between. The Dornoch Beach site faced roughly south, whereas the rest faced roughly east. All were on fairly flat ground, and would therefore be exposed to the sun for most of the day. Each of the populations sampled appeared to have different proportions of the different morphs (Table 4; Fig. 6). The two populations at Embo, which were about 200 m apart, occupy different habitats, and they differ significantly in their ratios of banded to brown shells (χ^2=13.35 with 1 degree of freedom, probability, $p < 0.001$). Similarly, the two populations on coastal grassland north of Dornoch, which were about 2 km apart, differ significantly (χ^2=8.35 with 1 degree of freedom, $p < 0.01$). For this calculation, single-banded snails are included with banded snails, as the numbers of the former are small. The more

Table 4 Counts of the various polymorphic forms in east Sutherland

Date and site	Habitat	Grid refs.	Single-banded	Banded	Brown
20th September 2016					
Embo Pier	Sand dunes	NH819921 NH819922 NH820921	0	5	23
Embo caravan site	Grassland	NH817921	0	19	8
North of Dornoch	Coastal grassland	NH812916	5	34	56
North of Dornoch	Coastal grassland	NH807896	15	23	19
Dornoch Beach	Sand dunes	NH805894	16	83	5
22nd September 2016					
Brora	River bank	NH909038	2	51	30
Brora	Coastal grassland	NH910039	9	34	31
Brora	Coastal grassland	NH911040	4	79	26

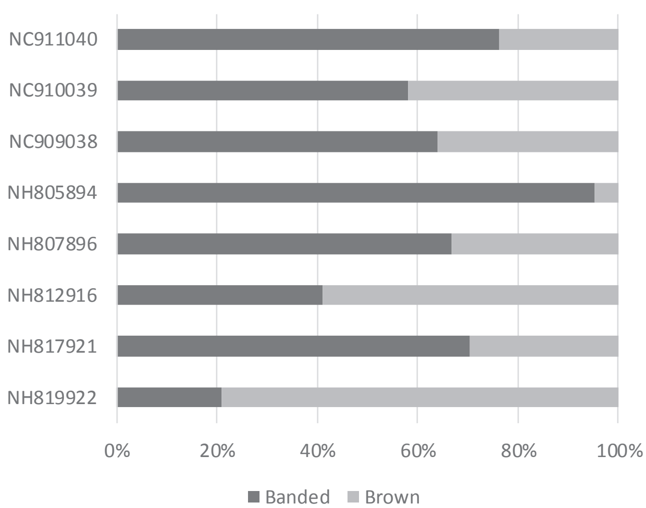

Figure 6 Bar chart showing the proportions of the different morphs of *C. virgata* at Dornoch and Brora. Black indicates banded shells (including a small number of single-banded shells), and grey indicates brown shells. Note the great variation in the proportions of different morphs. Grid references NH817921 and NH819922 are at Embo; NH807896 and NH812916 are north of Dornoch; NH805899 is at Dornoch beach; and NC909038, NC910039 and NC911040 are at Brora.

northerly of these two populations (NH812916) was about 700 m from the nearest population at Embo, and was unique among those sampled in having a significant proportion of shells with broken bands (Fig. 1F). The population on the sand dunes at Dornoch Beach (NH805894), which is about 280 m from the next one, is also clearly different, with a much higher proportion of banded shells than at the other sites. No pure white snails were found at any of these sites.

Brora, Sutherland (58° 0′ N) At Brora, snails were sampled on 22nd September 2016 (Table 4). All three populations, which covered only a few metres across, were on banks above the beaches; the bank at NH909038 faced approximately due south (Fig. 7), and the others roughly eastwards, and would receive the sun for most of the day. Adjacent populations were about 100 m from each other. As at Dornoch and Embo, the sites would be exposed to the sun for much of the day. The first two (NH909038 and NH910039) were not significantly different in the proportions of the different morphs, but the third one (NH911040) differed from the first two (χ^2=6.23 with 1 degree of freedom, $0.05 > p > 0.01$) (Fig. 6). Again, no pure white snails were found.

DISCUSSION

In this paper I report on populations of the Striped Snail *Cernuella virgata* at Berwick-upon-Tweed, Northumberland, England, that differ in their proportions of shell polymorphisms according to habitat and microclimate. Snails living on or adjacent to the breakwater, where they were in the shade for a significant part of the day and would therefore be less subject to the heat of the sun, nearly all have banded or brown shells, whereas the predominant morph in a population

Figure 7 One of the sites where *C. virgata* was found at Brora (grid reference NC909038) on a bank above the River Brora.

living on open coastal vegetation is pure white, with only a small proportion of other morphs. This observation is consistent with many reports in a variety of species of polymorphic snails that paler snails with less banding tend to occur in more open habitats, and that darker and more heavily banded snails tend to occur more often in shady habitats. This has been found in, for example, *Cepaea nemoralis* (Jones, 1973; Richardson, 1974; Cameron *et al.*, 2011; Ożgo, 2012); *Cepaea vindobonensis* (Jones, 1973), and *Theba pisana* (Johnson, 2011). In *Cochlicella acuta* and *Cernuella virgata*, Lewis (1977) found that darker and more heavily banded snails tended to occur more commonly on dark substrates. In some cases it seems that this distinction is most probably the result of climatic selection (Bantock, 1974; Jones *et al.*, 1977; Richardson, 1974; Johnson, 2011). Cain (1977) pointed out that snails that live predominantly in shaded areas, or are mainly nocturnal, tend to be fairly dark coloured, while at the other extreme, snails living in hot dry areas are normally white; snails living in intermediate habitats tend to be polymorphic. It therefore seems reasonable to suppose that the difference in the proportions of the different morphs in the populations at Berwick-upon-Tweed could be the result of climatic selection. Snails that live out in the open would be subject to the heating effect of the sun for longer, and would therefore tend to become hotter; possession of a white shell would reduce the heating effect.

As well as the population at Berwick-upon-Tweed, there is another population with a high proportion of brown shells, in the shade of a tree at Alnmouth. A correlation between darker shells and shady or cooler habitats has been noted in other species (Jones, 1973; Richardson, 1974; Cameron *et al.*, 2011; Johnson, 2011), but not in *C. virgata* in Australia (Baker, 1988a, 2012), where only banded and white shells have been reported. Bantock (1974) found that brown-shelled *Cepaea nemoralis* survived better than other morphs in cold valley bottoms. Jones (1973) showed that darker-shelled specimens of *C. vindobonensis* warm up more quickly, and become active sooner, than pale-shelled ones. Experiments have shown that snails with dark shells reach higher temperatures than those with pale shells when exposed to the sun (Heath, 1975; Tilling, 1983). On the other hand, Lewis (1977) found that in both *Cochlicella acuta* and *C. virgata,* darker snails were found on darker substrates, which he attributed to selective predation by birds. Both factors could be operating at Berwick-upon-Tweed and at Alnmouth: the sites with higher proportions of brown shells are both shady, and at Berwick-upon-Tweed, at least, the brown shells appear less conspicuous than the banded ones, both on the masonry of the breakwater, and on the bare ground at the foot of the breakwater. However, no evidence of selective predation was observed.

There are various objections to explaining the proportions of the different morphs at Berwick-upon-Tweed by climatic selection. Firstly, it might be wondered whether temperatures on the north-east coast of England are high enough to be lethal. Average maximum temperature for Berwick-upon-Tweed over the years 1981–2010 is 17.9ºC (Meteorological Office 2016), although individual days would be hotter. Moreover, it is not air temperature that is important, but the temperature of the snail, and a dark snail will heat up more in the sun than a pale one (Jones *et al*. 1977; Heath 1975; Tilling 1983). Pomeroy (1968) showed that the temperature of a snail exposed to the sun could rise to up to 10ºC more than the ambient temperature. Lethal temperatures for various snails have been reported as being in the region of 40ºC (Cowie 1985; Riddle 1990). It was not possible in this study to measure the actual temperature of the snails, but it seems unlikely that they would reach such temperatures in northern Britain. However, temperature can affect different morphs in different ways without necessarily being lethal. In *Arianta arbustorum*, pale morphs can remain active in sunlight for longer, while darker morphs seek shelter (Burla & Gosteli 1993). Similarly, Staikou (1999) found greater activity among paler morphs of *Cepaea vindobonensis* in sunny conditions. Burla & Stahel (1983) have suggested that shell colour might help to regulate the amount of heat that each population is adapted to. These behavioural differences appear to be related to physiological differences between morphs (Kavaliers 1992). Thus paler shells could have an advantage in areas more exposed to the sun, without temperatures being lethal.

Secondly, none of the other populations investigated – those at Alnmouth, south of Berwick-upon-Tweed, and those much further north on the east coast of Sutherland – has a significant proportion of white shells. Alnmouth is sufficiently close to Berwick-upon-Tweed for their climates to be similar, yet pure white snails are absent. There is, however, plenty of evidence that several different selective forces, besides selective predation and climatic selection, can act on different populations in different sites, (Jones *et al.,* 1977). In any case, selection can only act on the available variation in the population, and if the appropriate genotype is not present a particular phenotype (for example, a white shell) could not be produced.

Another factor that should be considered is that *Cernuella virgata* lives in a number of relatively small populations that may have only limited interaction with each other, and which in some circumstances may be reduced to quite small numbers. As a result, the proportions of the different morphs could be affected by chance. Among the populations studied here, there are at least two where this might happen. At Berwick-upon-Tweed, the population in the shade of the breakwater consisted of many hundreds of snails in 2014, while in 2016 it was reduced to much smaller numbers, and in fact snails were quite difficult to find. However, there was no evidence of a significant change in the proportion of the different morphs (Table 1). Again, on a visit to Embo Pier in June 2009, before the start of this study, there were so many snails that they were making the grasses up which they had climbed bend over with their weight; in 2016 there were so few snails that they had become difficult to find. Evidence of a different sort comes from the population at grid reference NH812916, north of Dornoch. This was the only population where snails with broken bands were found (Fig. 1F). If broken bands are under genetic control, this suggests that there may be little interchange between populations. It is generally believed that snails do not move far by themselves (Goodhart, 1962; Johnson, 1981; Cowie, 1984; Baker, 1988b; Aubry *et al.,* 2006), in which case little mixing of individuals from adjacent populations would be expected, and each might evolve in its own way. The distances between the populations studied here are generally greater, sometimes very much greater, than the dispersal distances described in the papers just cited.

In addition, many Scottish populations are isolated, and may be chance introductions. Thus only certain morphs might have been present in the original populations. At Brora, Baillie (1884, 1889) introduced *C. virgata* to areas where he had already established that this species was absent, and the present populations could well be descended from his introduction. In South Australia, where only white and banded morphs have been reported (Baker 2012), this could also be because the original introduced population lacked brown-shelled specimens, although these could well have been selected against in the hotter Australian climate.

In conclusion, in some of the populations of *Cernuella virgata* studied, the frequency of the different polymorphic forms seems most likely to be the result of adaptation to environments with different temperature regimes, with white-shelled snails predominating in an open habitat, and with a high proportion of brown shells in shady habitats. Other populations in exposed sites do not show this differentiation, and indeed most populations are different from each other. This could perhaps be due to founder effects or evolutionary bottlenecks, as populations are sometimes reduced to small numbers, and are to some extent isolated from each other. Selective predation does not seem a likely explanation of the results, however.

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