Systematic effects on morph frequency in the polymorphic mangrove snail *Littoraria pallescens*

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General observations of the polymorphic mangrove snail *L. pallescens* suggest that frequencies of the dark morph are lower in places where it shares its leaf habitat with a congeneric species than where it is present alone. The other species involved resemble the dark morph. This possibility was tested by comparing the composition of samples from two genera of mangrove trees which differ in their likelihood of having the alternative species on the leaves. The results showed the same pattern. This is a systematic effect on morph frequency, possibly selective predation, because the colonies on the different species of trees are drawn from the same larval population.

INTRODUCTION

The factors which maintain visible polymorphisms in a wide range of animal species are imperfectly understood. In molluscs, about 30 per cent of species are polymorphic in some groups, and there is an association of background homogeneity with monomorphism, and heterogeneity with polymorphism (Clarke *et al.*, 1978; Cain, 1977, 1988). An effect of visual predators is implied, and the polymorphism may develop because the background favours an appropriate type of behaviour either on the part of the predators or of the prey (Cook, 1986a). The majority of the work to investigate these factors has probably been carried out on the helicid snail *Cepaea nemoralis*. The results have only been partially successful (*e.g.*, Clarke *et al.*, 1978; Jones *et al.*, 1977), and it is still possible to argue that much of the variation in morph frequency is due to random factors (Selander and Ochman, 1983).

A very promising alternative system is presented by the prosobranch genus *Littoraria*, in which species restricted to uniform root and bark substrates are monomorphic while those restricted to leaves are polymorphic (Reid, 1986). *L. pallescens* is a polymorphic species which invites comparison with *C. nemoralis*. Both have distinct dark brownish, yellow and reddish morphs. *C. nemoralis* is widespread in Europe and lives in a wide variety of habitats. It is always polymorphic, but variable

in phenotype frequency from one place to another. *L. pallescens* occurs from east Africa to the western Pacific, but in a rather constant habitat consisting of mangrove trees. It is always polymorphic, but with relatively invariant frequencies, darks being the commonest morph, yellows comprising one quarter to one third of the population and orange about five per cent. *Cepaea nemoralis* is terrestrial, with low mobility and has a small effective population size (Greenwood, 1975). *L. pallescens* is effectively terrestrial when it has settled, but has a planktonic larval stage and a high effective population size. In each case, the scale of variation in morph frequencies may be interpreted as a consequence either of effective population size or selection resulting in background matching. In each case there is evidence for selection, but it cannot be said conclusively that it generates the patterns observed.

C. nemoralis has a very similar congener, *C. hortensis*, which is also polymorphic. They are often sympatric, and there is evidence that morph frequencies are more divergent between the two when they are sympatric than when they are allopatric (Clarke, 1962). This may be interpreted as evidence of selective predation, although other selective explanations are possible (Carter, 1967; Clarke, 1969; Clarke *et al.*, 1978).

There are several other *Littoraria* species which occur sympatrically with *L. pallescens*. In most cases they exhibit sharp habitat separation, living

almost exclusively on bark on mangrove trees. Bark-living species are monomorphic dark brown, resembling most closely the dark morph of *L. pallescens*. Sometimes, bark-living species extend onto leaves, and occasionally *L. pallescens* is found on bark, although there is strong substrate specificity. The investigation presented here was designed to investigate whether any inter-species effects on morph frequency occur.

The question of inter-species interaction arose from a comparison of morph frequencies in *L. pallescens* from Papua New Guinea and from Kenya. A survey in Papua New Guinea (Cook, 1986b) showed that samples taken over some 100 km of coast had a rather constant frequency of dark individuals, with a mean of 66·2 per cent (68 samples; the mean and standard error for arcsin transformed frequencies are 56·4±0·76). They were collected in an area where *L. pallescens* is present alone on leaves. In Kenya there is a second sympatric species, *L. subvittata*, which is monomorphic with diagonal dark stripes (Reid, 1986). It most resembles the dark form of *L. pallescens* and occurs both on bark and on leaves. In January 1988, eight samples were collected over 150 km of coast, in which the *L. pallescens* frequencies were homogeneous with 56·3 per cent dark. The transformed frequency is 48·4±3·08. In these samples the frequency of *L. subvittata* as a fraction of all snails on leaves was 50·8 per cent. Thus, in a region where leaves are also occupied by a second species resembling the dark morph, the frequency of darks in *L. pallescens* is lower than in an area where it occurs alone. This agrees with an earlier observation by Dr M. A. Beaumont (personal communication), who found even lower frequencies of darks. There are many other reasons why the frequencies should differ between the two regions, but the result suggested that a further test of the hypothesis of interaction should be carried out under better controlled conditions.

MATERIALS AND METHODS

The survey was carried out on the island of Phuket, in southern Thailand. Mangroves are established in many of the bays on the east and south of the island, with a few small outliers to the west. On the seaward side, the dominant trees are usually *Rhizophora apiculata* and *R. mucronata* or *Avicennia alba* and *A. marina*, interspersed with *Sonneratia alba*. A number of other species are to be found to landward. Reid (1985) and Frith *et al.* (1976) describe the vegetation at Ao Nam Bor,

where the mangrove is very extensive, and the small mangrove at Ao Yon is described by Hylleberg (1987). *Littoraria pallescens* is abundant, as is *L. intermedia*, a species which is monomorphic and typically lives on the roots and trunks. It is sometimes to be found on leaves, however, where it closely resembles the dark form of *L. pallescens*.

The survey took place in October and November 1988 in bays around the coast of Phuket Island (Cook and Garbett, 1990). A total of 50 samples was examined, in which morph frequencies were scored. Samples observed on *Rhizophora* were distinguished from those on *Avicennia* and scored for morph frequency in *L. pallescens* and ratio of *L. pallescens* to *L. intermedia* in order to test for associations with type of tree. At each site the dominant tree species were either *Avicennia* or *Rhizophora*, and in all cases the sample was taken exclusively from leaves of trees of one or other genus.

RESULTS

The composition of the collections is given in table 1. This shows the number of individuals in each morph category in *L. pallescens* and the number of *L. intermedia*. The frequency of dark in *L. pallescens*, and *L. intermedia* as a fraction of all snails on leaves, are listed. The last column indicates whether the sample was taken from *Avicennia* or *Rhizophora*. The sites are listed geographically from northeast of the island (Site 1) to the middle of the west coast (Site 14). Using Kendall's coefficient the correlation of frequency of dark in *pallescens* with Site numbers is not significant (Tau = −0·17, $t = 1·74$), so that there is no evidence that morph frequency varies geographically. Using the Mann-Whitney test, the frequency of *L. intermedia* is found to be significantly higher in samples from *Avicennia* than in those from *Rhizophora* ($z = 3·47$, $P < 0·001$). This is probably because foliage descends lower on *Avicennia* than on *Rhizophora*, and *L. intermedia* is therefore more likely to be forced onto leaves at high tide.

In *L. pallescens* the frequency of the dark morph is significantly lower in samples from *Avicennia* than in those from *Rhizophora* ($z = 3·77$, $P < 0·001$). The result is that *intermedia* frequency and dark frequency in *pallescens* are negatively correlated (Kendall's Tau = −0·21, $t = 2·18$, $P < 0·05$). The relation is shown in fig. 1. It can be seen that samples from *Avicennia* and *Rhizophora* are widely distributed among each other, and not

Table 1 Individuals of two species of *Littoraria* from sites on Phuket Island, Thailand. Numbers of three morphs of *L. pallescens* are shown, followed by numbers of *L. intermedia*. The next two columns show frequency of dark in *L. pallescens*, and *L. intermedia* as a fraction of total sample. Last column indicates whether sample was from *Rhizophora* or *Avicennia*. Sites are, 1: Ban Rak Mai, 2: Phara, 3: Bang Rong, 4: Ban Pa Klok, 5: Ban Sapam, 6 Ao Nam Bor, north, 7: Ao Nam Bor, 8: Laem Phan Wa, 9: Ao Yon, 10: Ao Chalong, east, 11: Ao Chalong, north, 12: Ao Chalong, west, 13: Kata, 14: Ban Layan

Sample	Site	L. pallescens			L. intermedia	% dark	% intermedia	Mangrove
		Orange	Yellow	Dark				
1	1	2	10	52	8	81	11	RH
2	1	0	2	11	17	84	56	AV
3	1	0	2	46	11	95	18	RH
4	1	0	3	12	13	80	46	AV
5	2	1	4	23	10	82	26	RH
6	2	2	2	26	26	86	46	RH
7	3	0	3	3	54	50	90	RH
8	3	0	3	18	42	85	66	RH
9	3	0	1	9	85	90	89	RH
10	4	1	9	23	44	69	57	AV
11	·4	0	6	18	28	75	53	AV
12	5	1	6	13	64	65	76	AV
13	6	1	5	33	13	84	25	RH
14	6	0	2	21	14	91	37	RH
15	7	0	2	29	17	93	35	RH
16	7	1	17	68	8	79	8	RH
17	7	1	10	64	1	85	1	RH
18	7	1	12	94	8	87	6	RH
19	7	2	36	207	63	84	20	RH
20	7	0	8	62	22	88	23	RH
21	8	5	63	132	44	66	18	AV
22	8	1	51	123	47	70	21	AV
23	9	0	8	92	5	92	4	RH
24	9	1	1	38	12	95	23	AV
25	9	2	2	35	5	89	11	RH
26	9	0	3	72	1	96	1	RH
27	9	0	6	38	11	86	20	RH
28	9	1	8	56	5	86	7	RH
29	9	4	7	73	2	86	2	RH
30	10	2	13	64	0	81	0	RH
31	10	1	7	33	2	80	4	AV
32	10	0	6	37	9	86	17	AV
33	10	0	21	55	0	72	0	RH
34	10	4	28	74	2	69	1	RH
35	11	4	19	78	0	77	0	RH
36	11	1	8	87	0	90	0	RH
37	11	1	16	90	4	84	3	RH
38	11	1	16	66	33	79	28	AV
39	11	2	12	59	4	80	5	RH
40	11	0	10	74	4	88	4	RH
41	12	2	11	47	24	78	28	AV
42	12	0	10	45	44	81	44	AV
43	12	0	27	13	23	32	36	AV
44	12	0	14	14	33	50	54	AV
45	12	0	11	22	54	66	62	AV
46	12	4	25	44	46	60	38	AV
47	12	0	7	14	56	66	72	AV
48	13	3	9	42	11	77	16	RH
49	13	0	8	70	5	89	6	RH
50	14	1	13	56	14	80	16	AV

clumped into particular parts of the distribution. A negative correlation would be expected if, for example, predators selected for a modal frequency determined by frequency of background elements,

and did not distinguish between the two species. If that were so, the frequency of dark in the two species taken together should be more uniform than in *L. pallescens* alone. Using arcsin
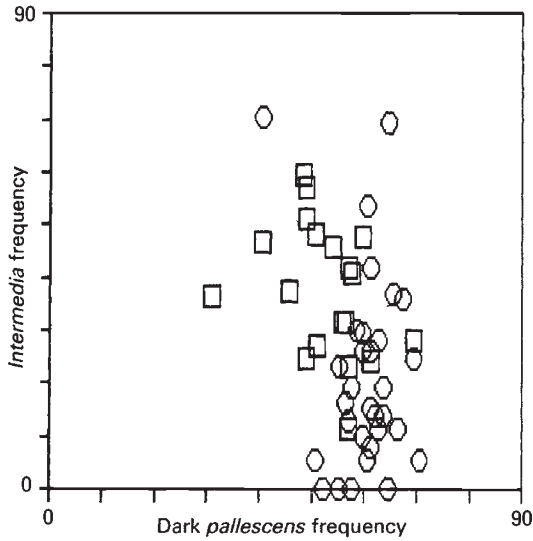
Figure 1 Relation of fraction of *L. intermedia* in sample to fraction of dark in *L. pallescens* (arcsin transformed frequencies). Rectangles: samples from *Avicennia*, circles: samples from *Rhizophora*.

transformed data this is found to be the case ($F = 1\cdot73$, $P < 0\cdot05$).

DISCUSSION

The general correlation of polymorphic species with foliage-living and of monomorphic species with bark-living in the genus *Littoraria* (Reid, 1986) appears to favour selection as an explanation for polymorphism, but it could be suggested that the foliage habitat removes the animals from predation pressure, so that variant mutant forms are not eliminated (Rosewater, 1970). The only practical way of countering this possibility is to show that systematic forces are at work. Seasonal changes in morph frequency have been demonstrated by Hughes and Mather (1986), Reid (1987) and Cook (1986*b*). There are differences in heating properties and shell strength between the morphs (Reid, 1987; Cook and Freeman, 1986; Cook *et al.*, 1985; Cook, 1990). Evidence for apostatic selection has been obtained in the similar polymorphic species *L. filosa* (Reid, 1987), although predators have not been caught in the act of selection.

Associations of morph frequency with local features are also good evidence for systematic effects. Reid (1987) demonstrated that dark *L. filosa* has a higher frequency on bare *Avicennia* trees and yellows on leafy trees, which suggests visual selection for crypsis. The positive result

reported here is that morph frequency in *L. pallescens* appears to compensate for the presence of another species, *L. intermedia*, which looks like one of the morphs. This supports the prediction from the earlier comparison between frequencies in two regions. It could be an effect of predators selecting for a modal morph frequency. Alternatively, the conditions which lead more *L. intermedia* to utilize the leaves of *Avicennia* than of *Rhizophora* could also favour the non-dark morphs of *L. pallescens*. Since the individuals on *Avicennia* and *Rhizophora* are recruited from the same larval population and are replenished by annual spawning, a systematic effect of some kind must be involved.

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