NOTES AND COMMENTS

FURTHER ASSOCIATIONS BETWEEN MORPH-FREQUENCY AND COEXISTENCE IN *CEPAEA*

WALLACE ARTHUR

Department of Biology, Sunderland Polytechnic, Sunderland SR1 3SD

Received 10.xii.79

ATTEMPTS to demonstrate evolutionary change resulting from interspecific competition have until recently been based on continuously variable characters whose heritability is at best poorly understood. Because of the difficulty in interpreting variation in such characters, it is of interest to examine polymorphic variation, whose genetic basis is known, in relation to the relative distributions of a pair of closely related species. In an earlier paper (Arthur, 1978), I described the variation in the frequency of unbanded shells in populations of *Cepaea nemoralis* in relation to the distribution of its congener, *Cepaea hortensis*, as well as the variation in unbanded *C. hortensis* in relation to the distribution of *C. nemoralis*. This was a preliminary study in that only three areas were surveyed. Since then, analyses of several other authors' data have been performed, and the results suggest that selection resulting from interspecific competition is a fairly widespread phenomenon in *Cepaea*, though it certainly does not characterise all mixed-species populations.

Data from the following papers have been analysed: Schilder and Schilder (1953), Clarke (1960), Clarke (1962), Cain and Currey (1963), Arnold (1969), Parkin (1972), Greenwood (1974) and Arthur (1978). The analysis took the form of comparing, with respect to the frequency of banded/unbanded, the mixed and single-species groups of samples within each survey. In some cases only one or other species could be compared between allopatry and sympatry, while in other cases such a comparison was possible for both species. In one instance (Parkin, 1972), the related species *Arianta arbustorum* was compared—between allopatric areas and areas of coexistence with *Cepaea*. In all, 16 allopatric/sympatric comparisons were possible, from a wide geographical area including populations from a number of localities in Britain as well as German and Spanish populations. The results are shown in table 1.

It can be seen that in seven cases the degree of "bandedness" increased significantly in sympatry, and in one case there was an almost-significant increase ($P \approx 0.08$). In contrast, there were no significant (or even nearly-significant) declines in the frequency of bandeds in sympatry. The probability of these eight cases all showing trends in the same direction by chance is $\frac{1}{2^8} = 0.008$. However, since the surveys by Schilder and Schilder (1953) and Parkin (1972) used different variables to the others, they should perhaps be excluded from the overall analysis. Even when this is done, the trend for bandeds to increase in sympatry is still significant ($P = \frac{1}{2^5} =$

TABLE 1

Summary of allopatric/sympatric comparisons of morph-frequency

Species	Area	Survey conducted by	Statistical test used	P	Direction of change in the frequency of bandeds on entering sympatry (see note (i))
<i>C. nemoralis</i>	Pyrenees	Arnold (1969)	U	< 0.005	↑
	Montrose	Arthur (unpub.)	U	n.s.	—
	Derbyshire	Arthur (1978)	t	< 0.05	↑
	Northumberland	Arthur (1978)	U	< 10 ⁻⁴	↑
	Salisbury Plain	Cain & Currey (1963)	U	n.s.	—
	Worcestershire	Greenwood (1974)	U	n.s.	—
	Hiddensee	Schilder & Schilder (1953)	χ^2	n.s.	—
	Hiddensee*	Schilder & Schilder (1953)	χ^2	n.s.	—
<i>C. hortensis</i>	Northumberland	Arthur (1978)	r	< 0.005	↑
	Somerset	Arthur (1978)	χ^2	< 0.001	↑
	Anglesey	Arthur (unpub.)	U	n.s.	—
	Salisbury Plain	Cain & Currey (1963)	U	≈ 0.08	↑
	Oxfordshire	Clarke (1960, 1962)	U	n.s.	—
	Hiddensee	Schilder & Schilder (1953)	χ^2	n.s.	—
	Hiddensee*	Schilder & Schilder (1953)	χ^2	< 10 ⁻⁵	↑
<i>A. arbustorum</i>	Derbyshire	Parkin (1972)	Sign test	< 0.001	↑

Notes:

- (i) Directions of change are only given where there is some indication that a change in morph-frequency has occurred ($P < 0.1$). Where sympatric and allopatric samples were very similar in morph-frequency, it is impossible to give a clear statement of the direction of change since different measures of morph-frequency in the two groups of samples (mean, median, sum of ranks, etc.) may give different "directions".
- (ii) All P-values given are two-tailed.
- (iii) Where parametric tests were used, frequencies were arcsin-transformed.
- (iv) Samples with $N < 10$ (of the appropriate species) were omitted from the analyses.
- (v) Sympatry, for either *Cepaea* species refers to areas of coexistence with the congener; for *Arianta* it means areas of coexistence with either or both species of *Cepaea*.

* Variable examined in these cases is index of band-fusions (see text).

0.031). This group of significant changes in morph-frequency between allopatry and sympatry is most easily explained in terms of competitive selection—*i.e.*, unbanded snails being weaker interspecific competitors than bandeds. The reasons why this explanation is preferable to explanations involving other forms of selection will be discussed shortly, but first it is necessary to give some details of those individual analyses (other than the ones already dealt with in Arthur (1978)) which departed from the basic

t- or U-test, or which dealt with a different measure of "bandedness" than the simple frequency of banded/unbanded in the sample.

In Parkin's (1972) study, the variable examined was the frequency of yellow unbanded. Due to strong linkage disequilibrium between colour and banding loci, there were very few yellow banded or brown unbanded. In each of 22 localities, Parkin correlated the frequency of yellow unbanded *A. arbustorum* with the proportion of *Cepaea* shells in the sample. This latter proportion should be an estimator of the degree of interspecific competition, from *Arianta*'s point of view, though species-proportions are known to be somewhat error-prone. (This problem has been discussed by Clarke (1962) and Arthur (1978).) Since the number of samples in each locality was small, Parkin used a sign test on the distribution of the signs of the correlation coefficients, rather than looking for a significant relationship within any one area. It is the result of this test that is given in table 1.

In the Hiddensee population (Schilder and Schilder, 1953), the frequency of banded in either species showed no significant association with areas of coexistence. However, another measure of shell darkness did exhibit such an association. This measure, an index of band fusion, was the proportion of 5-banded shells exhibiting fusions, weighted for the number of fusions per shell. An increase in the darkness of the shell due to increased fusion is phenotypically equivalent—at least in terms of radiant heat uptake—to an increase in darkness through the addition of bands. The test carried out on the data of Schilder and Schilder was a $2 \times N \chi^2$ (mixed, single $\times N$ categories representing different proportions of fused-banded shells in the sample). The P-value given in the table is for the trend component of the overall χ^2 , and indicates that there has been a general shift towards darker shells in sympatry. (The "departure from trend" component was not significant.)

Returning to the question of which selective agent is responsible for the widespread increase in bandedness in sympatry, it is clear that competitive selection with darker shells conferring an (interspecific) competitive advantage, could give rise to all the changes in morph-frequency observed (though the reason for this difference between morphs in competitive ability remains obscure—see Arthur (1978)). Note that phenotypic darkness is achieved in most sympatric populations by an increase in the frequency of bandeds, but by an increase in the frequency of fused-bandeds in Schilder and Schilder's (1953) study, and an increase in the frequency of brown bandeds in the *A. arbustorum* populations surveyed by Parkin (1972). The occurrence of some areas of sympatry without any apparent effect is hardly surprising, on this hypothesis, since mixed populations occur in a variety of habitats and need not necessarily entail interspecific competition in all of them.

A number of other selective agents have been observed, or suspected of, acting on the colour and banding loci in *Cepaea*. Consequently it will strengthen the case put forward here to show not only that competitive selection could cause all the changes in morph-frequency observed, but also that none of the other selective agents, acting alone, could do so. The forms of selection which will be discussed are—climatic selection, apostatic selection and visual selection for crypsis. The possibility of interspecific hybridisation will also be considered.

(i) *Climatic selection.* It is likely from geographical (Taylor, 1914)

physiological (Cameron, 1970a, b) and ecological evidence (Cameron, 1970c) that the various types of colony fall into the following microclimatic series from warmer and drier areas to colder and damper ones: *C. nemoralis*→*C. nemoralis*+*C. hortensis*→*C. hortensis*→*C. hortensis*+*A. arbustorum*→*A. arbustorum*. (The position of *C. nemoralis*+*A. arbustorum*, and of three-species colonies, is not clear). If such a series does exist in general, then a move from allopatry to sympatry should produce an opposite evolutionary response, considering any pair of the three species, if climatic selection is operating (*i.e.*, if the frequency of bandeds increases in one species, it should decrease in the other). As has been seen, this does not happen: all the changes in morph-frequency in the three species are in parallel.

(ii) *Apostatic selection*. It has been suggested (Clarke, 1962) that apostatic selection would produce an inverse relationship between the frequency of a particular morph in *C. nemoralis*, and its frequency in *C. hortensis*, on considering a number of mixed-species samples. It would also be expected, on similar reasoning, that apostatic selection would result in divergence of the frequency of banded *C. hortensis* (say) away from the frequency of bandeds in *C. nemoralis*, on entering a mixed colony with *C. nemoralis*. However, the results observed constitute a mixture of convergences and divergences within individual areas (see Arthur (1978) for further details).

(iii) *Visual selection for crypsis*. The parallel changes in morph-frequency in areas characterised by widely differing habitats do not suggest any simple pattern of selection for crypsis, unless the habitats of sympatric populations are consistently darker than those of allopatric populations, which is most unlikely and certainly not true of the habitats which I have personally observed.

(iv) *Interspecific hybridisation*. This process, if it occurred (and the evidence suggests it usually does not—see Jones *et al.* (1977)), would lead to convergence in sympatry, and as already mentioned, consistent convergence in sympatry is not found.

It is clear, then, that none of the above four processes, acting alone, would produce all the significant allopatric/sympatric shifts in morph-frequency that have been observed here. However, acting in combination they might do so and this possibility cannot of course be ruled out, though it is a less parsimonious hypothesis.

One further point deserves mention. The most striking increase in the frequency of banded shells in sympatry occurs at Seaton Sluice, Northumberland. Here, the selection in sympatry against unbanded *C. nemoralis* is so great that the banding polymorphism effectively disappears in the area of coexistence with *C. hortensis*. (One sympatric sample of *C. nemoralis* contained one unbanded shell, the other nine contained none.) This area is ecologically unique in that it appears to be the only English dune population of *Cepaea* where both species coexist right up to the marine border of the marram, where there is little or no other vegetation. The lack of mixed colonies in such habitats elsewhere has been attributed to strong interspecific competition leading to the competitive exclusion of *C. hortensis* (Oldham, 1928). If this interpretation is correct, then the colony at Seaton Sluice is likely to be undergoing severe competition. (A further intensive survey of this population is now being planned.)

Finally (and on a more general level) regardless of the identity of the selective agent, parallel genic variation in closely-related (but non-hybridis-

ing) species constitutes one of the strongest lines of evidence for the action of selection in natural populations. There has already been a number of reports of such variation in various species (see, for examples, Clarke (1975) and Harrison (1977)). Further studies of this kind, including those concerned with enzyme loci, may help to assess the importance of selective influence on gene-frequencies in nature.

Acknowledgments.—I would like to thank Professor A. J. Cain, Professor B. Clarke and Dr D. T. Parkin for their helpful comments.

REFERENCES

- ARNOLD, R. W. 1969. The effects of selection by climate on the land-snail *Cepaea nemoralis* (L.). *Evolution*, 23, 370-378.
- ARTHUR, W. 1978. Morph-frequency and coexistence in *Cepaea*. *Heredity*, 41, 335-346.
- CAIN, A. J., AND CURREY, J. D. 1963. Area effects in *Cepaea* on the Larkhill Artillery Ranges, Salisbury Plain. *J. Linn. Soc. (Zool.)*, 45, 1-15.
- CAMERON, R. A. D. 1970a. The survival, weight-loss and behaviour of three species of land-snail in conditions of low humidity. *J. Zool. Lond.*, 160, 143-157.
- CAMERON, R. A. D. 1970b. The effect of temperature on the activity of three species of helioid snail (Mollusca: Gastropoda). *J. Zool. Lond.*, 162, 303-315.
- CAMERON, R. A. D. 1970c. Differences in the distributions of three species of helioid snail in the limestone district of Derbyshire. *Proc. Roy. Soc. Lond., B*, 176, 131-159.
- CLARKE, B. 1960. Divergent effects of natural selection on two closely-related polymorphic snails. *Heredity*, 14, 423-443.
- CLARKE, B. 1962. Natural selection in mixed populations of two polymorphic snails. *Heredity*, 17, 319-345.
- CLARKE, B. 1975. The contribution of ecological genetics to evolutionary theory: detecting the direct effects of natural selection on particular polymorphic loci. *Genetics*, 79, 101-113.
- GREENWOOD, J. J. D. 1974. Visual and other selection in *Cepaea*: a further example. *Heredity*, 33, 17-31.
- HARRISON, R. G. 1977. Parallel variation at an enzyme locus in sibling species of field crickets. *Nature*, 266, 168-170.
- JONES, J. S., LEITH, B. H., AND RAWLINGS, P. 1977. Polymorphism in *Cepaea*: A problem with too many solutions? *Ann. Rev. Ecol. Syst.*, 8, 109-143.
- OLDHAM, C. 1928. *Cepaea hortensis* (Muller) and *Arianta arbustorum* (L.) on blown sand. *Proc. Malac. Soc. London*, 18, 144-146.
- PARKIN, D. T. 1972. Climatic selection in the land snail *Arianta arbustorum* in Derbyshire, England. *Heredity*, 28, 49-56.
- SCHILDER, F. A., AND SCHILDER, M. 1953. *Die Bänderschnecken. Eine Studie zur Evolution der Tiere*. Fischer Verlag, Jena.
- TAYLOR, J. W. 1914. *Monograph of the Land and Freshwater Mollusca of the British Isles*. Vol. 3. Taylor Brothers, Leeds.