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CURRENT PROBLEMS IN THE RESEARCH OF *CEPAEA* POLYMORPHISM

MAŁGORZATA OŻGO

Institute of Biology, Pomeranian University, Arciszewskiego 22B, 76-200 Słupsk, Poland
(e-mail: mozgo.biol@interia.pl)

ABSTRACT: Shell polymorphism in the land snails of the genus *Cepaea* has been studied for more than a century. Although these studies have taught us much about the ways in which evolutionary forces work at the population level, many problems are still unresolved. Studies of shell polymorphism, especially in populations living at the edges of the species' geographical distribution, long-term surveys of morph frequencies in selected populations, studies of the dispersal abilities of *Cepaea* snails and of differences in physiology and behaviour among morphs will help to answer outstanding questions, which have direct relevance to our understanding of microevolutionary processes generally.

KEY WORDS: ecogenetics, edge of the range, evolution, land snails, *Cepaea*, natural selection, population genetics, snail mobility, species distribution

The polymorphic land snails of the genus *Cepaea* are perhaps the most striking species in the European land snail fauna. They are also among the best studied animals, their variation having attracted the attention of biologists for more than a century (CAMERON 1997). Although these studies have taught us much about the ways in which evolutionary forces work at the population level, many problems are still unresolved. Interest in these problems has grown in recent years, and there is scope for much further work. The aim of this paper is to give a short review of the current state of the research of *Cepaea* shell polymorphism, and to draw attention to some of the questions that remain unanswered.

There are four species of *Cepaea* inhabiting Europe: *Cepaea nemoralis* (Linnaeus), *C. hortensis* (O. F. Müller), *C. vindobonensis* (Férussac), and *C. silvatica* (Draparnaud). *C. nemoralis* and *C. hortensis* are western European species. Their ranges largely overlap, but *C. hortensis* reaches further to the north, and possibly to the east. *C. vindobonensis* ranges from the northern Caucasus to eastern Austria, the Czech Republic and south-eastern Poland. The range of *C. silvatica* is limited to the western Alps (KERNEY et. al. 1983, RIEDEL 1988). Among those species, *C. nemoralis* and *C. hortensis* are the most polymorphic – their shells are yellow, pink or brown with a variety of shades, and bear up to five bands which can fuse together giving the shell an overall dark appearance. This variation of colour and banding is genetically controlled. Brown shells are dominant to pink, pink are recessive to brown and dominant to yellow, and yellow are recessive to both. The unbanded condition is dominant to banded and there are several interactions among genes for banding; five-banded is recessive to all other forms of banding (JONES et al. 1977). Polymorphism of *C. vindobonensis* and *C. silvatica* is much simpler. The ground colour of their shells is always yellowish to white and the usual number of bands is five. In *C. vindobonensis* two major forms occur: dark-banded, with dark-brown bands, and faint-banded, with straw-colored bands. In *C. sylvatica* bands can be reduced to a series of flecks. No information on the formal genetics of these two species is available.

Cepaea have become model species in the study of ecogenetics, i.e. the effects of environment on the genetic structure of populations. Initially, the variation of shell colour and banding was regarded as non-adaptive and resulting solely from chance events

(CAMERON 1997). Today we know that although chance events can play an important role, shell features are adaptive and natural selection does affect their frequencies in populations. Of the selective forces shown to operate, two are most importatnt: visual selection for crypsis and climatic selection. Among snail predators hunting by sight the song thrush (*Turdus philomelos)* is probably most efficient; it also has a very convenient way of breaking open snail shells on stones and other hard objects such as pieces of brick or railways, and leaving empty shells behind. This allowed the comparison of morph frequencies among the snails predated by birds with those of snails living nearby. In a series of careful observations and experiments involving marking and recapture of the marked snails it was shown that predators predominantly chose those snails whose shells stood out most against the background. The conclusion was that the colour of the shell and the pattern of banding can protect the snails from the attack of a predator (CAIN & SHEPPARD 1950, 1954, SHEPPARD 1951).

Another major influence is climate. ARNOLD (1968) demonstrated this in altitudinal clines, and a first synthesis was given by JONES (1973a) and JONES et al. (1977) who correlated the frequencies of yellow shells of *Cepaea nemoralis* with mean July temperature in Europe. A clear north-south cline of increasing frequency of yellow shells was found, giving a climatic explanation to the large-scale geographic pattern. A similar effect was expected to result from climatic selection operating on the scale of habitats (CLARKE et al. 1978). This however was more difficult to establish, as microclimatic selection can give very similar results to selection exerted by birds. Populations of *Cepaea nemoralis* living in south-eastern Poland, at the eastern edge of the species' distribution, provided a convenient opportunity to study those problems (OŻGO 2005). No visual predation was observed there, whereas the sub-continental climate, rather harsh for a western European species, is probably one of the important factors limiting its further eastern expansion. Correlation of the frequencies of dark shells (pink and heavily banded) with shaded habitats and of light shells (yellow and relatively unbanded) with open habitats was very strong there. Such relationships occur in other regions, too. The large scale cline of increasing frequency of yellow shells from the north to the south of Europe is observed in both open and in shaded habitats, but in most regions there are significant differences between those habitat types. As a rule, the frequency of yellow shells is higher in open habitats than in shaded ones.

However, many studies fail to find environmental correlations with morph frequencies (CAIN & CURREY 1963, 1964), and it is clear that many populations are influenced by past bottlenecks (founder effect) and by genetic drift. The enigmatic geographical patterns, known as "area effects", seem to be best explained by previous bottlenecks and colonisation from small relics with founder effects (CAMERON et al. 1980, CAMERON & DILLON 1984, CAMERON & PANNETT 1985, DAVISON & CLARKE 2000). Thus, the genetic structure of populations very often results not only from the effect of some, not always recognised, selective forces, but also from random processes. There may also be a time lag in the response of a population, either to a newly colonised habitat, or to changes in one already occupied. In effect morph frequencies may reflect only dimly the environmental conditions present at the place and time they are examined (COOK 1998). In some circumstances however the evolutionary response can be very rapid. In south-eastern Poland, in three replicate situations of habitat subdivision accompanied by the possibility of population growth, morph frequencies were observed to differentiate in a way consistent with the expectations of climatic selection within only 18 to 30 years (OŻGO & KINNISON 2008). Such rapidity of response may be characteristic of geographically marginal populations: at the edges of species distribution the extremes of climate are likely to have a very strong selective effect.

Visible variation in snails of the genus *Cepaea* is in some ways an ideal tool in the study of ecogenetics. The advantage lies in a clear polymorphism with a known genetic basis, in wide ecological tolerance resulting in a broad geographical range and a variety of habitats inhabited by those snails, in their general low mobility, and in the fact that they often live in distinct colonies. Additionally, the snails are common in many areas of their distribution and thus it is possible to make numerous large samples at a low cost. The cost in time and money of identifying molecular variation in several thousand specimens would be far greater. Because of those clear advantages the *Cepaea* snails are often regarded as very easy to study. However, the difficulty comes with interpretation. Doubtlessly the snails do respond to selection, but most often they do so very slowly, and by the time any effect might be seen, the direction of selection has already changed (COOK 1998); needless to say, a particular character may be subject to several different selection pressures at once. Apart from this, the precise mechanisms by which selective forces affect populations are not fully recognised. It can be simple mechanistic links such as between thermal properties of the shells and the climate or microclimate, but differences among morphs may go deeper and involve differences in physiology or behaviour (STEIGEN 1979, JONES 1982, TILLING 1983, CHANG 1991, OŻGO & KUBEA 2005). There is also the problem of genetic environment, i.e. the way in which various genes interact.

In this respect very puzzling are the differences in morph composition between *C. nemoralis* and *C. hortensis.* No matter if the major selective factor is predation or climate (or both) one would expect a positive correlation between morph frequencies when those species live in the same regions or habitat types, and especially in places where they occur together. This is not the case: agreement between morph frequencies is observed very rarely. Most often the correlation is very weak or even negative (LAMOTTE 1959, CLARKE 1962). It has been argued that even though the genes controlling shell polymorphism are homologous in both species, the genetic environment differs. *C. hortensis* is usually less polymorphic than *C. nemoralis*, and thus its reactions to selective pressures are different. For example, in woods where pink unbanded *C. nemoralis* predominate, the most common form of *C. hortensis* is yellow five-banded with the bands fused together. Both forms give a generally dark appearance, not very conspicuous on a dark background of a beech forest (CLARKE 1962). This explanation notwithstanding, the problem remains largely unresolved (CAIN 1983).

Similarly unresolved remains the problem of coexistence of *C. nemoralis* and *C. hortensis.* Although it does not relate directly to polymorphism, it often becomes apparent during morph survey studies. *C. hortensis* is more northerly and prefers cooler and damper climates than *C. nemoralis,* but their geographical ranges largely overlap, and so do their ecological preferences. Yet in the regions where both species occur, only 20% of the colonies contain both of them (JONES et al. 1977). There is a well known but not at all understood phenomenon of "*nemoralis* countries" and "*hortensis* countries" – areas occupied exclusively by, or with a very strong predominance of one of the species (CAIN 1983). As the occurrence of very subtle climatic differences between such areas is not a very likely explanation, those distributional patterns suggest some kind of competition. Competition is also suggested by the results of experimental studies (TILLING 1985a, b). There is however no clue as to the nature or mechanism of this competition (CAIN 1983, ARTHUR et al. 1993). What limits our understanding of this problem is mainly the lack of sufficient field and experimental data. We do not even know the extent to which the current geographic ranges of those species overlap, and there are some more questions. In the areas where the ranges do overlap, do the species inhabit the same kinds of habitats? If yes, do they occur together at the same sites? What are the proportions of those species and do they change with time? And finally, what are morph frequencies in sympatry and in allopatry? Answers to those questions that are presently available are at most fragmentary.

No large-scale pattern in the distribution of morph frequencies has been found in *C. hortensis.* Even though the species is less polymorphic than *C. nemoralis*, a general decrease in the frequencies of darker shells from the north to the south of its range, and from open to shaded habitats might be expected. This is not the case. If anything, the yellow morph seems to increase in frequency towards the north, with the majority of the northernmost populations being 100% yellow (ROST 1952, OWEN & BENGTSON 1972, HÄKKINEN & KOPONEN 1982). Similarly, eastern populations seem to contain only yellow-shelled individuals (SVERLOVA 2001, 2002). However, the major problem with establishing any patterns in this species is a general lack of data from large parts of its distribution.

Even less is known about the other two species of *Cepaea*, i.e. *C. vindobonensis* and *C. silvatica,* and they are no less interesting. Their simpler polymorphism possibly provides a more suitable system for the study of the complicated interactions of genetics, ecology and evolution. The frequencies of shell variants of *C. vindobonensis* show clear associations with topography (JONES 1974), large-scale climatic variables (HONĚK 2003), and habitat (ROTARIDES 1926, OŻGO & KOMOROWSKA 2008), all of them indicating the effect of climatic selection. Those studies were however carried out in marginal western and southern populations of the species. Populations inhabiting more central parts of the range show higher polymorphism (KRAMARENKO et al. 2007, SVERLOVA & KIRPAN 2004), but nearly nothing is known about morph frequencies and factors affecting them in the vast areas of the central and eastern parts of the distribution range of this species. The least is known about *C. silvatica;* polymorphism in this species has not been studied at all.

From the viewpoint of the study of polymorphism, the question of morph frequencies in natural populations remains the most important. No general conclusions can be drawn without careful mapping of gene frequencies in various regions of species distribution; in many cases it is the lack of field data that limits our understanding of evolutionary processes operating in the wild. Yet, even in *C. nemoralis,* the best studied of all *Cepaea* species, large parts of the range have never been surveyed. This concerns geographically central populations as well as populations at the margins of the species distribution. These latter ones are possibly most interesting, as in marginal populations living in the face of environmental stress that prevents the species from further extending its range, the effects of natural selection can be expected to be most pronounced (JONES 1973b).

In some areas, very detailed studies of morph frequencies were carried out already a few decades ago. This provides an excellent opportunity to study changes in the genetic composition of populations over time. Some such studies were already performed, giving valuable insights into the ways in which selective forces operate in the wild (e.g. CAMERON 1992, 2001, ARTHUR et al. 1993, COWIE & JONES 1998, COOK et al. 1999). There is however a problem of interpretation in studies in which long time intervals passed between sampling occasions. If differences in morph frequencies are found this can mean that either the environment is gradually changing or that it is constant but the fluctuations are large enough to produce the differences found every once in a while. If no significant changes are found this can mean that either morph frequencies are indeed stable, or that the various phases of positive and negative selection have by chance more or less cancelled each other (Wolda 1969, Cameron 1992). There are only few long term studies monitoring morph frequencies in selected populations (Wolda 1969, Cain et al. 1990); such studies are very much needed to establish the range of yearly fluctuations. Also, they might allow to "catch evolution in action", i.e. to record changes in gene frequencies brought about by short periods of intense directional selection. Most promising in this respect are newly established or newly subdivided populations, as those are the conditions that promote rapid evolution (Rheznic & Ghalambor 2001).

In the research of polymorphism there are two major question groups: one relating to the factors that affect morph frequencies and the other to the mechanisms that maintain polymorphism. Directional selection, such as visual or climatic selection, tends to unify morph frequencies. How is it possible than that the great majority of *Cepaea* populations are highly polymorphic? In the current view, selection of changing direction combined with migration should be sufficient to maintain polymorphism (Cook 1998). But what are the migratory abilities of *Cepaea*? Surprisingly little is known about that. Snails are slow movers with extremely high cost of locomotion (Denny 1980), and it is generally assumed that they have a very strong tendency to stay put (Cook 1998). The most often cited studies estimate the yearly movement of *C. nemoralis* to be no more than 5–10 m (Lamotte 1951, Goodhart 1962). A limited active dispersal ability is also suggested by a deme-like structure of genetic patterns determined within a continuous *C. nemoralis* population in the absence of barriers (Schweiger et al. 2004). There are however observations of a much higher mobility. In *C. hortensis* an extensive wandering was recorded, with several marked individuals covering an average distance of about 85 m in a year (Day & Dowdeswell 1968). In a different study, a distance of 23 m was covered in just 6 days by one of the marked *C. hortensis* individuals (Bengtson et al. 1976). In *Cepaea nemoralis* a dispersal of 25 m in a week was observed (Merritt G. Gillilland III, Michigan State University, personal communication 2006). It can be hypothesised that the snails are stationary when undisturbed, but become quite mobile after displacement, most probably due to their homing behaviour. The spatial genetic structure of *C. nemoralis* populations indicates a marked philopatry (Schweiger et al. 2004), but otherwise it has not been studied. Clearly, a more precise estimation of the mobility of those snails is needed.

A different kind of observations might also be very informative. Changes in the distribution of *C. hortensis*, and especially *C. nemoralis* indicate that they are currently in an easterly expansion in Europe (Honěk 1995, Ożgo 2005). *C. nemoralis* also expands its range in North America, where it was introduced at the end of the 19th century. Monitoring the changes in the distribution of those snails should give information on their effective migratory abilities, including passive dispersal, and help verify the current theory on the mechanisms maintaining polymorphism. The problem of range expansion is very interesting in itself. It is doubtlessly facilitated by increased human mobility but possibly relates also to global climatic changes, which makes it all the more worth studying.

Finally, very intriguing are differences in physiology and behaviour among various morphs. To date, only few studies were carried out on that (e.g. Steigen 1979, Wolda 1967, Jones 1982, Tilling 1983, Chang 1991, Staikou 1999, Ożgo & Kubea 2005). Better knowledge of the biology of *Cepaea* species, with special regard to the differences among morphs might give the clue to their extraordinary variation.

After intensive study for more than a century the phenotypic variety of *Cepaea* snails is still not understood. As has been stressed by Cook et al. (1999) the challenge should not be abandoned because the problem is difficult to unravel. The study of *Cepaea* polymorphism helps to explain the way in which various selective forces affect genetic composition of natural populations but it can also shed light on the origins and maintenance of biodiversity at large.

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