

Contingency and determinism during convergent contemporary evolution in the polymorphic land snail, *Cepaea nemoralis*

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ABSTRACT

Questions: How replicable is short-term evolution? Do populations recently exposed to analogous habitat gradients show analogous adaptations? Conversely, how important are chance historic events and genetic constraints in shaping the unique aspects of contemporary evolution?

Organisms: Three *Cepaea nemoralis* population pairs, each pair inhabiting adjacent open and shaded habitats in sub-optimal climatic conditions of south-eastern Poland. Population pairs likely arose through separate, single introductions and were isolated from other populations.

Methods: We compared the frequencies of genetically determined shell variants 18–28 years after the establishment of the populations.

Conclusions: The manner by which adaptive divergence proceeded varied by geographic location, but the effect in terms of darkness of the shells was convergent, resulting in higher frequencies of dark-shelled snails in shaded habitats and light-shelled snails in open habitats. Estimated selection coefficients were large (0.236, 0.370, and 0.420) with respect to other studies for this species. The relatively simple inheritance system of shell colour in this species ensures that observed differences are heritable and allows insights into the likely historical roles of genetic architecture and restricted genetic variation in driving shared and unique elements of adaptive divergence.

Keywords: climatic selection, genetic architecture, introduced species, microclimate, natural selection, parallel evolution.

INTRODUCTION

Evolution in contemporary time has been observed under a broad range of ecological and evolutionary conditions involving many taxa and many kinds of traits. Such changes are currently regarded as part of the normal processes of evolution rather than exceptional phenomena (Thompson, 1998; Hendry and Kinnison, 1999; Kinnison and Hendry, 2001; Hairston *et al.*, 2005). These

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studies have been particularly important in demonstrating the role of natural selection as a deterministic process leading to predictable trait evolution (Grant and Grant, 1995; but see Grant and Grant, 2002). However, theory and laboratory studies suggest that a full appreciation of the nature of adaptations must also recognize the role of history and constraints ['contingency' (Gould, 1990; Travisano *et al.*, 1995)]. Unfortunately, most cases of contemporary evolution in the wild are not replicated, limiting our ability to infer the importance of history and chance. One way to discern the relative effects of adaptive determinism and contingency in the wild is to study cases of parallel or convergent contemporary evolution.

Convergent or parallel evolution arises when independent lineages evolve functionally similar adaptations in response to similar selective environments. Parallel evolution is commonly associated with closely related taxa and striking homoplasy, which is thought to arise through similar modifications of the same developmental pathways (Futuyma, 1998). In contrast, convergent evolution is usually identified with characters that are functionally analogous, but less strictly identical, owing to origins from non-homologous antecedents or different developmental pathways (Futuyma, 1998). Hence, convergent evolution is most often seen in comparisons of distantly related taxa. The unique aspects of adaptations witnessed in cases of parallel or convergent evolution are generally considered to reflect the role of contingency in shaping the nature of adaptations (Gould, 1990). Although greater evolutionary divergence between taxa may increase the opportunity for contingent outcomes, there is no reason to believe contingency cannot contribute to the evolution of unique aspects of adaptations in very closely related lineages (e.g. Huey *et al.*, 2000; Collyer *et al.*, 2005). In contrast, genetic constraints associated with historical founding processes might be expected to substantially influence the nature of adaptive evolution in new populations, at least until genetic variation arises that might permit populations to adopt more similar adaptive trajectories.

The polymorphic land snail *Cepaea nemoralis* is a model organism in the study of ecology, genetics, and evolution. Shells of this species can be yellow, pink or brown, each of these categories being divisible into several shades, with shells bearing up to five usually dark bands. This variation is genetically determined by an allelic series (for reviews, see Jones *et al.*, 1977; Cook, 1998), darker colours dominating paler ones, and unbanded dominating banded ones. Genes controlling shell colour and the presence or absence of bands are closely linked and segregate together [recombination rate of just 0.2% (Cook, 2005)]. Other unlinked loci modify the number of bands on a banded shell.

Shell colour varies geographically. The frequencies of yellow shells show a significant association with mean July temperatures, and there is a clear cline of increasing frequency of yellow shells with increasing temperature from the north to the south of western Europe (Jones, 1973; Jones *et al.*, 1977). Within this trend there are significant differences between open and shaded habitats; in most regions, the frequencies of yellow shells are higher in open than in shaded sites (Ozgo, 2005). These geographic patterns suggest that variation in shell colour is associated with shell thermal properties and this hypothesis is supported by prior work. Yellow shells and unbanded shells have greater reflectance in the visible and infrared spectra than pink and banded shells (Chang, 1991), and the internal temperatures of pink or banded snails are significantly higher for a given level of solar radiation [0.32–0.46°C difference (Heath, 1975)]. Although higher internal temperatures may be metabolically beneficial to snails at higher latitudes or in shaded habitats (i.e. increased activity, growth, and fecundity), darker snails lose more weight through dehydration when exposed to sunlight and suffer higher differential mortality under heat load (Richardson, 1974; Chang, 1991). Selection on colour

due to thermal performance of these snails may thus be very strong, as has been shown in other invertebrates (e.g. Kingsolver, 1996). Detection by predators has also been suggested to contribute to this pattern of colour divergence in some parts of the species range (for a review, see Jones *et al.*, 1977). However, striking colour and banding variation often exists among populations inhabiting similar habitats. Indeed, such variation may be expected on the grounds of contingency, as hypothesized as early as 1956 by Goodhart: 'There is furthermore the possibility that in a species showing balanced polymorphism for a considerable number of genes, as is probably the case in *C. nemoralis*, several different combinations may be capable of establishing a satisfactory equilibrium in similar environments so that even where selection is of paramount importance the particular combination selected may owe much to the chance constitution of the original population upon which selection has been acting'.

Here we consider contemporary colour and banding adaptations in *Cepaea nemoralis* populations that invaded sites in south-eastern Poland, 600 km outside the natural range of the species (Kerney *et al.*, 1983; Riedel, 1988). The study system consists of three population pairs inhabiting adjacent open and shaded habitats. Each population pair likely arose through a single introduction (accidental or purposeful) of a small number of individuals, independent of the other two introductions, and was isolated from other such populations. This isolation was maintained by the very restricted dispersal ability of these animals [just 5–10 m per year (Lamotte, 1951; Goodhart, 1962)], which confined populations to local urban environments, while many similarly suitable sites remained unoccupied. These three population pairs thus represent independent natural experiments that can be used to assess the general issue of the extent to which adaptive evolution in contemporary time is replicable or unique as a result of contingency and constraint. More specifically, we investigated the following questions in our study system:

1. Did *Cepaea nemoralis* populations in adjoining open and shaded habitats diverge in their shell characteristics in contemporary time?
2. Are patterns of shell divergence consistent with expectations for this environmental gradient?
3. Did the population pairs accomplish analogous adaptations through similar or unique aspects of shell colour and banding variation?

MATERIAL AND METHODS

Study area and sample collection

All samples were collected in 1998 from recently established populations inhabiting adjacent open and shaded habitats. The populations were found in three towns in south-eastern Poland: Jarosław (22°39'10"E; 50°01'11"N), Rzeszów (22°01'56"E; 50°01'57"N), and Tarnów (20°58'17"E; 50°01'06"N). The climate of this area is characterized by relatively hot, dry summers (average July temperature is 17.7°C) and cold winters (average January temperature is -3.3°C), with yearly temperature amplitudes reaching 70°C. Such climatic conditions may well be one of the limiting factors for a species whose geographical range centre is closer to the middle of western Europe.

The populations in Jarosław (see Fig. 1) inhabited an old orchard (J02) and part of a cemetery grown only with short grass (J01) [*note*: population numbers are consistent with



Fig. 1. Adjoining open and shaded habitats at Jarosław, and *Cepaea nemoralis* shells illustrating banding polymorphism. The three-banded shell is rotated slightly to better show additional bands that distinguish it from the mid-banded phenotype.

Ożgo (2005)]. The trees in the orchard were approximately 80 years old, and it can be assumed that the snail population was of at least the same age. The adjoining cemetery was built in 1980 by cutting down part of the orchard and piling there a layer of earth 2.5 m high. A concrete wall was built between the orchard and the cemetery. Searching the whole cemetery did not reveal a single *Cepaea nemoralis* anywhere but in the closest vicinity of the orchard. It is therefore likely that the cemetery was colonized by the snails originating in the orchard. This is supported by the fact that pink snails in both habitats at Jarosław were extremely faint, similar in appearance to yellow individuals.

The populations in Rzeszów inhabited a dense walnut orchard (R16) separated from the road by a south-facing roadside covered with herbaceous vegetation (R15). The road, together with several other roads in Rzeszów, was built in about 1980. The populations analysed were likely founded during road construction, as were other more distant populations along those roads. At Rzeszów, the species was abundant in the populations in the direct vicinity of the road, but became scarce and disappeared approximately 300 m further away from it.

The populations in Tarnów inhabited a willow stand (T04) north of a 2.5 m high garage, and an open area (T08) with grass and some herbs. The two sites were connected by a 20 m long footpath with some grasses and herbs growing on both sides. Until 1970, this area was an arable field, a habitat type that is not inhabited by *Cepaea nemoralis*. Afterwards the area was included in the township and garages with small gardens were built; this is the earliest time at which the species could have been introduced. Shared ancestry of the open and shaded populations is supported by the general resemblance of banding morphs, particularly the resemblance of banding morphs in yellow shells ($\chi^2 = 2.054$, $P > 0.05$). By 2007, only the Tarnów open site remained unaltered; for this reason no follow-up study was possible.

Visual selection was unlikely to have played an important role in this system. The song thrush *Turdus philomelos* does not occur in urban environments in Poland (Tomiałojć and

Stawarczyk, 2003), and the blackbird *Turdus merula* is rare in the study areas (personal observation). Indeed, we observed no signs of predation by birds at the study sites. In contrast, the microclimates (temperature and moisture) of open and shaded habitats are clearly different and this difference may be particularly important given that these populations are probably near the climatic limits of the species (Ozgo, 2005).

We collected live snails in areas of less than 400 m², covered with relatively uniform vegetation; the boundary (approximately 10 m wide) between adjacent open and shaded habitats was omitted. Only mature individuals were included. Shells were scored according to a standard system (Cain and Sheppard, 1950). In this system, the bands are numbered from 1 to 5, with the uppermost being 1. Thus a five-banded shell is represented by 12345, a shell with the middle band only as 00300, and one with no bands as 00000. There were no brown shells in the samples, only pink, yellow, and banding variations of those colours. Using chi-square tests, we compared and tested the frequencies of the major morphs occurring in the studied populations: yellow vs. pink, unbanded vs. banded, and mid-banded vs. five-banded among banded forms.

Selection coefficients

Selection coefficients can be calculated using integration, morph ratios or iteration (Clarke and Murray, 1962b; Cook *et al.*, 1999). As all give rather similar figures (Cameron, 2001), we calculated integration estimates, according to the formulas:

$$s = \frac{\ln[q_n(1 - q_0)/q_0(1 - q_n)] - 1/q_n + 1/q_0}{n + \ln(q_n/q_0) - 1/q_n + 1/q_0}$$

where s refers to the dominant morph, and

$$s = \frac{\ln[q_0(1 - q_n)/q_n(1 - q_0)] + 1/q_n - 1/q_0}{n + \ln(1 - q_n/1 - q_0)}$$

where s refers to the recessive morph; q_0 and q_n are the initial and final gene-frequencies and n is the number of generations (Clarke and Murray, 1962b).

For simplicity, we assumed divergence to represent primarily evolution of one of the populations, and hence we used the time since populations split from a common ancestor as the estimate of time interval (Kinnison and Hendry, 2001). The generation time in *Cepaea nemoralis* is generally assumed to be 3–5 years (Clarke and Murray, 1962b; Cain and Currey, 1968; Wall *et al.*, 1980; Cowie and Jones, 1998; Cook *et al.*, 1999). In eastern parts of the species distribution, where snail activity usually lasts only about 4 months a year and is often interspaced with prolonged periods of inactivity, the snails do not mature before their third year and generation time is closer to 5 years. We calculated selection coefficients using both of these generation lengths.

RESULTS

The composition of the samples is shown in Fig. 2 and differences in the frequencies of colour and banding morphs are given in Table 1. In Tarnów, the main difference between the studied populations was the frequency of colour morphs. In the open habitat, the frequency of yellow shells was 96.3%, while in the shaded habitat it was only 44.6%. The difference in the frequency of unbanded shells reflected much of the divergence in

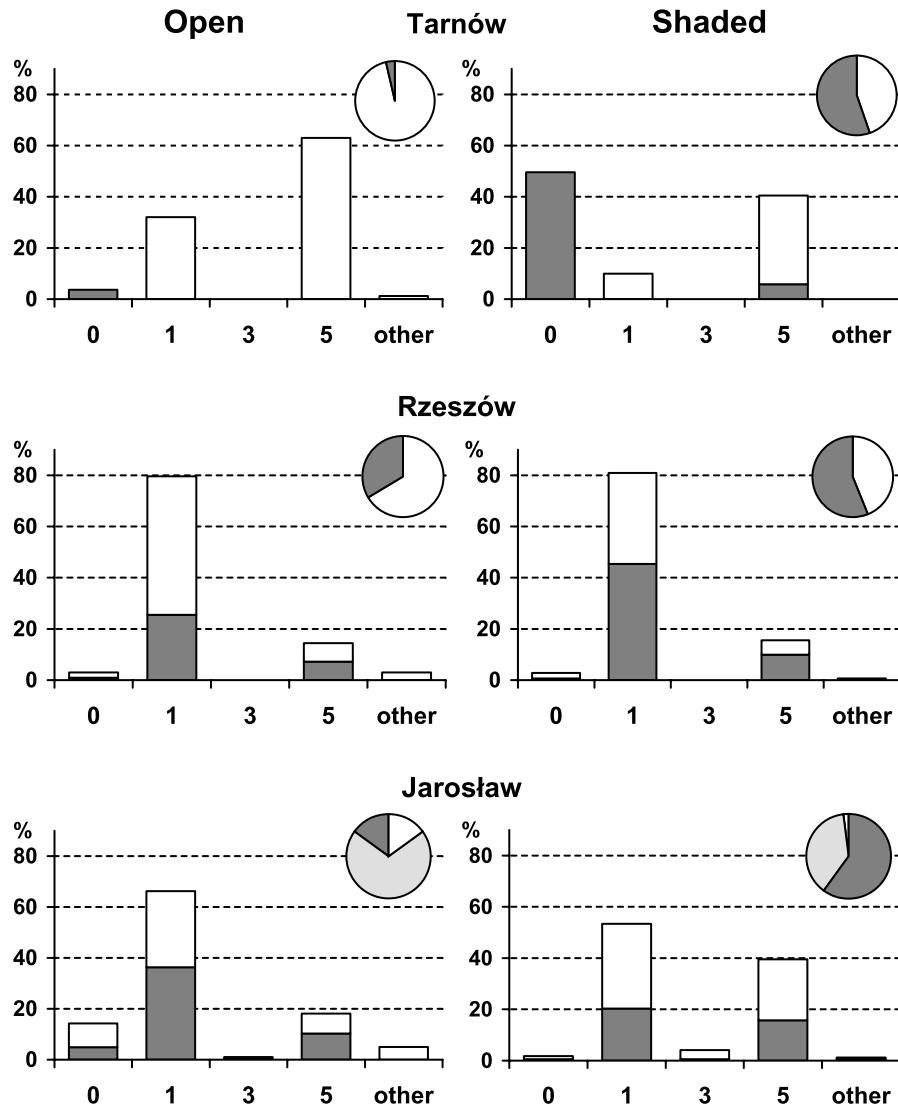


Fig. 2. Frequencies of *Cepaea nemoralis* banding and colour morphs in habitat pairs. Histograms: grey sectors, pink shells; white sectors, yellow shells. 0 = unbanded; 1 = mid-banded; 3 = three-banded; 5 = five-banded; other = other banding morphs. Tarnów and Rzeszów pie charts: grey sectors, pink shells; white sectors, yellow shells. Jarosław pie charts: white sectors, unbanded shells; dark grey sectors, banded shells; light grey sectors, five-banded shells.

background colour, as all unbanded shells were pink. In the case of Tarnów populations, it was not clear which was the original site of introduction. If it was the open habitat, then selection operated against the recessive (yellow) when snails entered the shaded site and the selection coefficients are 0.420, variance 0.0049 (assuming 6 generations, 4.7 year generation time) and 0.314, variance 0.0027 (assuming 9 generations, 3.1 year generation time). If the shaded population was established first, then divergent selection operated most strongly

Table 1. Differences in the frequencies of colour and banding morphs

Site	Habitat	Yellow	Unbanded	Mid-banded	Five-banded	Sample size
Tarnów	open	96.3%	3.7%	33.3%	65.4%	81
	shaded	44.6%	49.6%	19.7%	80.3%	121
	χ^2	57.200 ***	47.596 ***		3.388 [#]	—
Rzeszów	open	66.4%	3.0	82.0	14.9	235
	shaded	44.0%	2.8	83.2	16.1	141
	χ^2	18.168 ***	0.006 [#]		0.040 [#]	—
Jarosław	open	48.0	14.2	77.1	21.1	204
	shaded	62.2	1.7	54.4	40.2	172
	χ^2	7.557 **	18.641 ***		16.886 ***	—

Note: Frequencies of mid-banded and five-banded calculated as proportions of all banded morphs; significance of differences in the chi-square test. [#]Not significant.

against the dominant (pink) in the open habitat, and the selection coefficients are 0.542, variance 0.0082 (assuming 6 generations, 4.7 year generation time) and 0.378, variance 0.0040 (assuming 9 generations, 3.1 year generation time).

In Rzeszów, the frequency of yellow shells was 66.4% in the open habitat and 44.0% in the shaded habitat. Here, the main difference between populations was the frequencies of yellow and pink, while the frequency of all banding phenotypes remained stable across habitats. Colonization proceeded most probably from the open to the shaded habitat. We inferred this from the observation that the snails were abundant in the open habitat, but their number decreased further away from it; only the part of the shaded habitat neighbouring the open one was inhabited even though the whole site appeared similar and suitable for the species. For selection against yellow shells in the shaded site, the selection coefficients are 0.236, variance 0.0027 (assuming 4 generations, 4.5 year generation time) and 0.165, variance 0.0013 (assuming 6 generations, 3 year generation time).

Divergent selection at Jarosław mostly affected the banding pattern of the shells. The frequency of banded shells was 98.3% in the shaded habitat and 85.8% in the open one. Selection coefficients against banded snails are 0.370, variance 0.0101 (assuming 4 generations, 4.5 year generation time) and 0.279, variance 0.0058 (assuming 6 generations, 3 year generation time). It is noteworthy that the overall decrease in banded shells when moving from the shaded to open habitat was paralleled by a decrease in five-banded individuals (the darkest morph) among the banded forms from 40.2% to 21.1%, while the frequency of mid-banded (less dark) among banded forms increased from 54.4% to 77.1%. Selection coefficients for five-banded are 0.298, variance 0.0045 (assuming 4 generations, 4.5 year generation time) and 0.205, variance 0.0021 (assuming 6 generations, 3 year generation time). Selection coefficients for the mid-banded are 0.319, variance 0.0040 (assuming 4 generations, 4.5 year generation time) and 0.221, variance 0.0019 (assuming 6 generations, 3 year generation time).

DISCUSSION

In this study, we observed sharp differences in snail morph frequencies between directly adjoining open and shaded habitats. The study area lies outside of the natural range of *Cepaea nemoralis* and these populations all originated from recent introductions. The populations described here can thus be regarded as a natural experiment in contemporary evolution with three replicates, in which colonization of adjoining open and shaded habitats imposed similar patterns of divergent selection for shell darkness or lightness. However, the specific nature of contemporary adaptations in the different sites contained a substantial element of contingency, reflected in the fact that the different population pairs diverged along different heritable components of shell coloration. At Jarosław, divergence took the form of shell banding patterns, irrespective of background colour. In Rzeszów and Tarnów, differences between open and shaded habitats largely concerned the background colour of the shells, but with different implications for associated banding. This latter result conforms to the general pattern observed in south-eastern Poland in which adaptation to shaded habitats proceeds in two major ways: one towards the predominance of pink unbanded shells (e.g. Tarnów) and one towards the predominance of pink banded shells (e.g. Rzeszów) (Ożgo, 2005). Although we studied only a single species, the patterns of divergence at the different sites involved substantially different aspects of shell colour, and thus different developmental pathways. Hence, we refer to this as convergent contemporary evolution.

Although several studies have shown evidence of parallel (or convergent) evolution in a wide range of taxa (e.g. Jones *et al.*, 1992; Reznick *et al.*, 1997; Losos *et al.*, 1998; Blackledge and Gillespie, 2004; Langerhans and DeWitt, 2004), little research has examined the role of contingency or constraint in contemporary time. Huey and colleagues (Huey *et al.*, 2000; Gilchrist *et al.*, 2001) provided evidence for parallel clines of wing size evolution in introduced populations of *Drosophila subobscura*, but also showed that the wing proportions contributing to these clines differed among continents. Similarly, Collyer *et al.* (2005) showed that pupfish (*Cyprinodon tularosa*) translocated from a saline river to a saline spring developed deeper bodies as expected based on a wild population in a similar habitat. However, the translocated population did so in a morphologically different fashion. The strength of the current study, relative to such previous investigations, is that the simple genetic system of inheritance for shell colour in *Cepaea* not only assures us that the differences we have detected are genetically based, but also provides some insights into the role of particular genetic factors as underlying mechanisms of contingency. In other words, this genetic system allows us to interpret unique aspects of population divergence within the framework of Goodhart's (1956) hypothesis (see quote in Introduction).

One obvious form of constraint that contributes to contingency involves the limited genetic variation of small founding groups. Some evidence of this is probably seen at the broadest geographic scale in our study. The number of bands possessed by banded individuals is controlled by two loci that segregate independently of loci influencing colour and the presence or absence of banding. One of these loci has the potential to suppress just two bands, creating the three-banded phenotype. Given the paucity of three-banded forms in all of our populations, it is likely that little variation remains at this locus in south-eastern Poland. In contrast, the other locus suppresses four of the bands, creating the distinction between mid-banded and five-banded phenotypes. Most banded forms in our populations conform to variation at this locus.

Another mechanism by which founding processes can constrain adaptation involves the role of genetic architecture, such as linkage among loci and associated patterns of linkage disequilibria inherited from founding sources. Although such disequilibria usually decline with time, in a population originated from a small number of individuals and with a recombination rate of less than 1%, even a few hundred years could pass before the proportions were close to equilibrium (Cook, 2005). At Tarnów, the dramatic increase in pink shells in shaded habitats was accompanied by a correlated decrease in the presence of banding, even though banding also makes shells darker. This decrease in the frequency of banded individuals likely arose due to direct linkage between the colour locus and the banded/unbanded locus and an associated strong disequilibrium in which alleles for pink are almost entirely associated with an absence of banding in this population pair. Again, this result conforms to the general pattern observed in south-eastern Poland (Ożgo, 2005). Interestingly, there is some sign that this disequilibrium may be eroding at Tarnów, since there was also evidence of the emergence of pink five-banded shells in the shaded site (Fig. 2). Given time, selection on such variation could allow deterministic processes to override linkage-derived contingency.

Reduced genetic diversity and genetic architecture do not necessarily function in isolation. Unbanded phenotypes were very rare at both sites at Rzeszów, suggesting that the successful founders may have been largely fixed at the banded locus. At the same time, and in contrast to Tarnów, linkage disequilibrium was limited, with no excess of unbanded in either colour. In combination, the rarity of unbanded individuals and greater variation in colours linked to banding may have allowed colour evolution at this site to occur without divergence in the proportion of unbanded and banded individuals. In fact, colour evolution at this site apparently occurred irrespective of banding, with the frequencies of mid-banded and five-banded remaining unchanged.

Finally, a phenotypic anomaly at the Jarosław site provides an especially compelling example of the importance of genetic variation and architecture in shaping adaptations. Although less fully assorted than at Tarnów, divergence in the frequency of unbanded shells tended to be associated with a shift in the frequency of pink snails, consistent with linkage of these loci. However, unlike Tarnów, pink shells decreased in the shaded habitat. This would appear maladaptive given expectations that darker coloration should be favoured in shaded habitats. However, pink background coloration at Jarosław is exceptionally pale compared with that at our other sites. The intensity of pink shells is determined by alleles at yet another locus (Jones *et al.*, 1977) and thus it is likely that the Jarosław site was founded by a limited gene pool of individuals that carried the faint pink allele. As a consequence, selection appears to have acted largely on banding patterns (both the banded/unbanded locus and loci controlling band number) irrespective of background colour. Banding pattern evolution has been inferred in other cases where *Cepaea nemoralis* populations lack much background colour diversity on which environmental selection might act (Arnold, 1969; Richards and Murray, 1975). However, no time frame is known for the differentiation observed in those other studies.

The results of the present study contrast with previously suggested limits to rates of evolution of shell colour and banding in *Cepaea* (e.g. Cain and Cook, 1989; Cook, 1998) and with apparent morph stability in other field studies (Goodhart, 1956, 1958; Wolda, 1969; Cain *et al.*, 1990; Arthur *et al.*, 1993; Cowie and Jones, 1998; Cameron, 2001). Although contemporary evolution is not entirely unprecedented in *Cepaea* (e.g. Clarke and Murray, 1962a, 1962b; Murray and Clarke, 1978; Stine, 1989; Cameron, 1992), directional selection appeared weaker in those studies than in the present one. The

comparative subtlety of evolution detected by prior studies may suggest an important methodological consideration in the study of contemporary evolution. Studies that quantify *divergence* across stable selective gradients [synchronic (Hendry and Kinnison, 1999)] integrate the entire time course of evolution in both lineages, including the colonization process that is especially conducive to contemporary evolution (Kinnison and Hendry, 2001; Reznick and Ghalambor, 2001). In comparison, studies of later changes within populations [allochronic (Hendry and Kinnison, 1999)] may tend to capture weaker or more variable bouts of selection. Anecdotal support for this limitation is provided by a follow-up sample collected at the open site in Tarnów in 2007 (the only site that remained unaltered). That sample did not differ statistically in any respect from the 1998 sample (M. Ozgo, unpublished data).

Other evolutionary processes may further shape the patterns of divergence we noted in this study. Snails are notoriously slow animals with an extremely high cost of locomotion (Denny, 1980). For *Cepaea nemoralis*, the estimated average movement is just 5–10 m per year (Lamotte, 1951; Goodhart, 1962) and it is generally assumed that individuals have a strong inclination to stay put (Cook, 1998). Schweiger *et al.* (2004) show that local population structuring can arise at very small scales in this species, even in the absence of apparent barriers. Hence, one may predict that strong divergent selection may overwhelm the limited homogenizing effects of gene flow in this study system. It is noteworthy that our coefficients of selection would be underestimates if homogenizing gene flow were operating. Alternatively, gene flow itself is not always random with respect to phenotypes. Recent studies on the great tit (*Parus major*) provide two examples where biased dispersal shapes trait divergence over small geographic scales (Garant *et al.*, 2005; Postma and van Noordwijk, 2005). Such biased dispersal from a source to a new site during colonization could accelerate the process of initial population divergence through a ‘favoured founders’ effect (Quinn *et al.*, 2001). Either way, gene flow and fine-scale divergence are not incompatible.

The present study shows that contemporary evolution does occur in *Cepaea nemoralis* in response to habitat type. The consistent habitat gradient between open and shaded sites likely provides for particularly strong selection, giving rise to an important element of determinism in replicate cases of local adaptive divergence. However, as pointed out in popular fashion by Gould (1990), there are limits to how much we might ‘replay the evolutionary tape of life’, because even contemporary evolution must build off chance and history. Because the inheritance of shell colour traits is well described in this species, we were able to identify some likely roles for genetic architecture and restricted genetic variation in constraining patterns of adaptive divergence. In combination, we believe this study provides an integrated view into the interaction of determinism and contingency in the earliest stages of population adaptation.

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REFERENCES

- Arnold, R.W. 1969. The effects of selection by climate on the land-snail *Cepaea nemoralis* (L.). *Evolution*, **23**: 370–378.
- Arthur, W., Phillips, D. and Mitchell, P. 1993. Long-term stability of morph frequency distribution in a sand-dune colony of *Cepaea*. *Proc. R. Soc. Lond. B*, **251**: 159–163.

- Blackledge, T.A. and Gillespie, R.G. 2004. Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. *Proc. Natl. Acad. Sci. USA*, **101**: 16228–16233.
- Cain, A.J. and Cook, L.M. 1989. Persistence and extinction in some *Cepaea* populations. *Biol. J. Linn. Soc.*, **38**: 183–190.
- Cain, A.J. and Currey, J.D. 1968. Studies on *Cepaea*. III. Ecogenetics of a population of *Cepaea nemoralis* (L.) subject to strong area effects. *Phil. Trans. R. Soc. Lond. B*, **253**: 447–482.
- Cain, A.J. and Sheppard, P.M. 1950. Selection in the polymorphic land snail *Cepaea nemoralis*. *Heredity*, **4**: 275–294.
- Cain, A.J., Cook, L.M. and Currey, J.D. 1990. Population size and morph frequency in a long-term study of *Cepaea nemoralis*. *Proc. R. Soc. Lond. B*, **240**: 231–250.
- Cameron, R.A.D. 1992. Change and stability in *Cepaea* populations over 25 years: a case of climatic selection. *Proc. R. Soc. Lond. B*, **248**: 181–187.
- Cameron, R.A.D. 2001. *Cepaea nemoralis* in a hostile environment: continuity, colonizations and morph-frequencies over time. *Biol. J. Linn. Soc.*, **74**: 255–264.
- Chang, H.-W. 1991. Activity and weight loss in relation to solar radiation in the polymorphic land snail *Cepaea nemoralis*. *J. Zool. (Lond.)*, **255**: 213–225.
- Clarke, B.C. and Murray, J.J. 1962a. Changes in gene frequency in *Cepaea nemoralis* (L.). *Heredity*, **17**: 445–465.
- Clarke, B.C. and Murray, J.J. 1962b. Changes in gene frequency in *Cepaea nemoralis* (L.): the estimation of selective values. *Heredity*, **17**: 467–476.
- Collyer, M.L., Novak, J.M. and Stockwell, C.A. 2005. Morphological divergence of native and recently established populations of White Sands pupfish (*Cyprinodon tularosa*). *Copeia*, **2005**: 1–11.
- Cook, L.M. 1998. A two-stage model for *Cepaea* polymorphism. *Phil. Trans. R. Soc. Lond. B*, **353**: 1577–1593.
- Cook, L.M. 2005. Disequilibrium in some *Cepaea* populations. *Heredity*, **94**: 497–500.
- Cook, L.M., Cowie, R.H. and Jones, J.S. 1999. Change in morph frequency in the snail *Cepaea nemoralis* on the Marlborough Downs. *Heredity*, **82**: 336–342.
- Cowie, R.H. and Jones, J.S. 1998. Gene frequency changes in *Cepaea* snails on the Marlborough Downs over twenty-five years. *Biol. J. Linn. Soc.*, **65**: 233–255.
- Denny, M. 1980. Locomotion: the cost of Gastropod crawling. *Science*, **208**: 1288–1290.
- Futuyma, D.J. 1998. *Evolutionary Biology*, 3rd edn. Sunderland, MA: Sinauer Associates.
- Garant, D., Kruuk, L.E.B., Wilkin, T.A., McCleery, R.H. and Sheldon, B.C. 2005. Evolution driven by differential dispersal within a wild bird population. *Nature*, **433**: 60–65.
- Gilchrist, G.W., Huey, R.B. and Serra, L. 2001. Rapid evolution of wing size clines in *Drosophila subobscura*. *Genetica*, **112/113**: 273–286.
- Goodhart, C.B. 1956. Genetic stability in populations of the polymorphic snail, *Cepaea nemoralis* (L.). *Proc. Linn. Soc. Lond.*, **167**: 50–67.
- Goodhart, C.B. 1958. Genetic stability in populations of the polymorphic snail, *Cepaea nemoralis* L.: a further example. *Proc. Linn. Soc. Lond.*, **169**: 163–167.
- Goodhart, C.B. 1962. Variation in a colony of the snail *Cepaea nemoralis* (L.). *J. Anim. Ecol.*, **31**: 207–237.
- Gould, S.J. 1990. *Wonderful Life: The Burgess Shale and the Nature of History*. New York: W.W. Norton.
- Grant, P.R. and Grant, B.R. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution*, **49**: 241–251.
- Grant, P.R. and Grant, B.R. 2002 Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, **296**: 707–711.
- Hairston, N.G., Jr., Ellner, S.P., Geber, M.A., Yoshida, T. and Fox, J.A. 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol. Lett.*, **8**: 1114–1127.

- Heath, D.J. 1975. Colour, sunlight and internal temperatures in the land snail *Cepaea nemoralis* (L.). *Oecologia (Berl.)*, **19**: 29–38.
- Hendry, A.P. and Kinnison, M.T. 1999. The pace of modern life: measuring rates of contemporary microevolution. *Evolution*, **53**: 1637–1653.
- Huey, R.B., Gilchrist, G.W., Carlson, M.L., Berrigan, D. and Serra, L. 2000. Rapid evolution of a geographic cline in size in an introduced fly. *Science*, **287**: 308–309.
- Jones, J.S. 1973. Ecological genetics and natural selection in molluscs. *Science*, **1182**: 546–552.
- Jones, J.S., Leith, B.H. and Rawlings, P. 1977. Polymorphism in *Cepaea*: a problem with too many solutions? *Annu. Rev. Ecol. Syst.*, **8**: 109–143.
- Jones, R., Culver, D.C. and Kane, T.C. 1992. Are parallel morphologies of cave organisms the result of similar selection pressures? *Evolution*, **46**: 353–365.
- Kerney, M.P., Cameron, R.A.D. and Jungbluth, J.H. 1983. *Die Landschnecken Nord- und Mitteleuropas*. Hamburg: Verlag Paul Parey.
- Kingsolver, J.G. 1996. Experimental manipulation of wing pigment pattern and survival in western white butterflies. *Am. Nat.*, **147**: 296–306.
- Kinnison, M.T. and Hendry, A.P. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica*, **112/113**: 145–164.
- Lamotte, M. 1951. Recherches sur la structure génétique des populations naturelles de *Cepaea nemoralis* (L.). *Bull. Biol. Fr. Suppl.*, **35**: 1–239.
- Langerhans, R.L. and DeWitt, T.J. 2004. Shared and unique features of evolutionary diversification. *Am. Nat.*, **164**: 335–349.
- Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K. and Rodriguez-Schettino, L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, **279**: 2115–2118.
- Murray, J. and Clarke, B.C. 1978. Changes of gene frequency in *Cepaea nemoralis* over fifty years. *Malacologia*, **17**: 317–330.
- Ożgo, M. 2005. *Cepaea nemoralis* (L.) in southeastern Poland: association of morph frequencies with habitat. *J. Moll. Stud.*, **71**: 93–103.
- Postma, E. and van Noordwijk, A.J. 2005. Gene flow maintains a large genetic difference in clutch size at a small spatial scale. *Nature*, **433**: 65–68.
- Quinn, T.P., Kinnison, M.T. and Unwin, M.J. 2001. Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate and process. *Genetica*, **112/113**: 493–513.
- Reznick, D.N. and Ghalambor, C.K. 2001. The population ecology of contemporary adaptations: what do empirical studies reveal about the conditions that promote adaptive evolution. *Genetica*, **112/113**: 183–198.
- Reznick, D.N., Shaw, F.H., Rodd, F.H. and Shaw, R.G. 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science*, **275**: 1934–1937.
- Richards, A.V. and Murray, J.J. 1975. The relation of phenotype to habitat in an introduced colony of *Cepaea nemoralis*. *Heredity*, **34**: 128–131.
- Richardson, A.M.M. 1974. Differential climatic selection in natural populations of the land snail *Cepaea nemoralis*. *Nature*, **247**: 572–573.
- Riedel, A. 1988. *Ślimaki lądowe. Gastropoda terrestria*. Katalog fauny polskiej. Part 36, Vol. 1. PWN Warszawa: Polska Akademia Nauk, Instytut Zoologii.
- Schweiger, O., Frenzel, M. and Durka, W. 2004. Spatial genetic structure in a metapopulation of the land snail *Cepaea nemoralis* (Gastropoda: Helicidae). *Molec. Ecol.*, **13**: 3645–3655.
- Stine, O.C. 1989. *Cepaea nemoralis* from Lexington, Virginia: the isolation and characterization of their mitochondrial DNA, the implications for their origin and climatic selection. *Malacologia*, **30**: 305–315.
- Thompson, J.N. 1998. Rapid evolution as an ecological process. *Trends Ecol. Evol.*, **13**: 329–332.
- Tomiałojć, L. and Stawarczyk, T. 2003. *Awifauna Polski: Rozmieszczenie, liczebność i zmiany (Avifauna of Poland: Distribution, Numbers and Trends)*. Wrocław: PTPP 'proNatura'.

- Travisano, M., Mongold, J.A., Bennett, A.F. and Lenski, R.E. 1995. Experimental tests of the roles of adaptation, chance, and history in evolution. *Science*, **267**: 87–90.
- Wall, S., Carter, M.A. and Clarke, B. 1980. Temporal changes of gene-frequencies in *Cepaea hortensis*. *Biol. J. Linn. Soc.*, **14**: 303–318.
- Wolda, H. 1969. Stability of a steep cline in morph frequencies of the snail *Cepaea nemoralis* (L.). *J. Anim. Ecol.*, **38**: 623–635.

