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Land snails as a model to understand the role of history and selection in the origins of biodiversity

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Abstract It is nearly 100 years since the first studies on variation in the shell patterns of land snails. Subsequently, snails have come to play an important role in our understanding of natural selection in the wild. In particular, snails have been an ideal model to understand the roles of history and selection in the origins of diversity. More recently, many studies have investigated the molecular genetic variation within snails. It is clear that snails are unusual, because some genes may vary by 10%–30% within a species. This molecular variation affords an excellent opportunity to further understand the action of natural selection in shaping the present-day phenotypic diversity. In the first part of this review, I illustrate the distinction between the historical and selective interpretations using one of the best-studied species, *Cepaea nemoralis*, and the example of "area effects." In the second part, studies that have compared patterns of morphological and molecular variation (especially DNA) are examined.

Key words Adaptation · Drift · *Euhadra* · Hybridization · Introgression · Mitochondrial DNA · *Partula*

Introduction

It is nearly 100 years since the first studies on variation in the shell patterns of land snails. In the meantime, snails have come to play a crucial role in our understanding of natural selection in the wild (Clarke 1978; Clarke et al. 1978), and the work of Cain and Sheppard (1950, 1952, 1954) has become a textbook classic.

In particular, snails are an ideal model to understand the roles of history and selection in the origins of diversity. Often, there is a clear correlation between the frequencies of shell phenotypes, the habitat, and the effects of natural selection (Cain and Sheppard 1950, 1952, 1954). In other circumstances, contrasting patterns of shell types between populations may owe more to their separate population histories compared with selection (Cain and Currey 1963; Gould and Woodruff 1990). Different populations of snails could have distinct shell types because they have colonized from a variety of sources and subsequently have been affected by population bottlenecks or other demographic factors. In this review, I illustrate the distinction between historical and selective interpretations using one of the best-studied species, *Cepaea nemoralis*, and the example of "area effects."

Recently, many studies have investigated the molecular genetic variation within and between snail species because this provides an independent account of the history of the populations, which can be compared with the shell patterns (Chiba 1999; Douris et al. 1998; Davison and Clarke 2000; Goodacre 2001). It is clear that snails are unusual because some mitochondrial DNA (mtDNA) sequences may vary by 10%–30% within a species (Thomaz et al. 1996). This enormous molecular variation, albeit unexplained, affords an excellent opportunity to further understand the action of natural selection in shaping the present-day phenotypic diversity, because it allows the history of individual genes to be mapped in detail. Therefore, studies that have compared patterns of morphological and molecular variation (especially DNA) are also reviewed. Several other authors have recently reviewed some of the same topics, but with a different emphasis (Backeljau et al. 2001; Hugall et al. 2003).

Historical perspective

It is easy to forget that the role of selection in determining frequencies of shell phenotypes was not realized in the first half of the twentieth century. The more common interpretation was that variation in the color and banding patterns of

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snails is entirely random and nonadaptive (Dobzhansky 1937; Mayr 1942; Lamotte 1951). It was not until that the 1950s that the situation was reversed. Then, Cain and Sheppard (1950, 1952, 1954) studied *Cepaea nemoralis* (L.) and reported that in some lowland areas of Britain there are clear correlations between the frequencies of shell phenotypes, the kinds of habitat in which they live, and the effects of natural selection by predators, notably the song thrush *Turdus philomelos*. This observation strongly implied that cryptic selection is important in determining shell frequencies. Soon after, similar results were obtained in other snail species, with the realization that other mechanisms, such as frequency-dependent (apostatic) selection and climatic selection, may be equally important (Cain and Sheppard 1954; Clarke 1962; Jones 1973; Heath 1975). Now, polymorphism in *Cepaea* is seen as "a problem with too many solutions?" (Jones et al. 1977) when the many different modes of selection and drift are considered together as possible explanations.

Cuban *Polymita*

Important questions remain, especially concerning the pervasiveness of natural selection in land snails. Some species, such as Cuban *Polymita*, have an astonishing phenotypic diversity that remains mostly unexplained (Torre 1950). In *Polymita*, an endangered (or possibly extinct) predatory snail-hawk *Chondrohierax wilsoni* is implicated, but there is no direct evidence. Instead, as in *Cepaea*, shell frequencies have been compared against different habitats, with lighter shells more often found in open environments, implying climatic selection (Berovides and Zamora 1986). It is unfortunate that the only way unequivocally to show natural selection experimentally is to demonstrate a clear mechanistic connection between the changes in gene frequency and the action of the selective agent (Clarke et al. 1978; Davison and Clarke 2000). Thus, climatic selection on shell color and banding in *Cepaea* is one of the few good examples (Jones 1973; Heath 1975; Clarke et al. 1978). In *Polymita*, we are more ignorant: different morphological types within the same *Polymita* species may be confined to separate regions of Cuba, but whether the explanation lies in a shared evolutionary history for snails in one region or some poorly understood aspect of the current selective regimen is not known.

Area effects in *Cepaea nemoralis*

The issue of "history versus selection" in explaining patterns of gene frequencies is best illustrated by studies on so-called area effects in *C. nemoralis*. In 1963, Cain and Currey found that on chalk downlands in England, where song thrushes are relatively rare, particular color and banding alleles predominate over large areas, apparently regardless of the habitat. Groups of similar populations are separated from other such groups by steep gradients of gene frequencies, over a few hundred meters, and often in places where the habitat seems to be uniform (Cain and Currey 1963). Subsequently, area effects have been found in several species of snails (Clarke 1968; Gould and Woodruff 1990; Johnson et al. 1993). Cain and Currey attributed these area effects to selection by cryptic features of the microclimate. Since then, other explanations have been suggested, which invoke either some aspect of the population history or recent selection: genetic drift and co-adaptation (Goodhart 1963), the selective accumulation of modifiers in morph-ratio clines (Clarke 1966), and differentiation in refugia produced by changing uses of land (Cameron et al. 1980). Importantly, the historical explanation does not exclude the effect of selection in the distant past, so it is not simply a distinction between a neutral or selective interpretation (Gould and Woodruff 1990).

Although the area effects on the downlands persist more than 25 years since they were first described (Cowie and Jones 1998; Cook et al. 1999), their origins are still a matter for debate. Some studies have looked for geographic correlations between the frequencies of allozymes and those of shell genotypes. The point with these studies is that the frequencies of molecular markers are probably not altered locally by natural selection, so give an independent account of the history of a population (but see Mitton 1997). Thus, a coincidence between allozymes and shell genotypes would immediately suggest that the two forms of variation reflect a common pattern of historical events, such as the founding of populations.

Johnson (1976; Table 1) found just that: a *C. nemoralis* area effect in Berkshire "reflects substantial genetic differentiation," supporting the historical explanation. On the other hand, Ochman et al. (1983) reported that the frequencies of allozymes in Pyrenean *C. nemoralis* correlate neither with shell genotypes nor with climate or vegetation. Similarly, Jones et al. (1980) found no correlation using snails from a sand dune in Wales. Ochman et al. (1983) suggested that the geographic patterns of allozymes in the Pyrenees reflect the isolation of snails in Pleistocene refugia, whereas the patterns of shell genotypes have become locally adjusted to the present environment.

Up to the 1980s, allozymes were the best available molecular genetic markers, but more recently, mtDNA (Thomaz et al. 1996; Chiba 1999) and latterly microsatellites have been used in snails (Davison and Clarke 2000; Arnaud et al. 2001). These advances have been complemented by increasingly sophisticated methodological approaches to investigate DNA variation (Emerson et al. 2001). DNA markers have advantages over allozymes, because many different markers can be compared, because they are more polymorphic, and because they are less likely to be influenced by selection (Mitton 1997).

Thus, Bryan Clarke and I recently used variation in microsatellites and mtDNA to attempt to understand area effects in *C. nemoralis*, using snails from the "type locality" of Cain and Currey (1963). We found that the frequencies of microsatellites were significantly associated with the frequencies of alleles for shell banding, with a less clear asso-

Table 1. Molecular studies on land snails, showing approximate maximum divergence, and the correlation (if any) between morphological and molecular markers

Study	Snail species	Morphological trait	Genetic marker	Sequence divergence (%)	Correlation?
Within species: small scale					
Jones et al. (1980)	*Cepaea nemoralis*	Color, banding	Allozymes		No
Johnson (1976)	*Cepaea nemoralis*	Color, banding	Allozymes		Yes
Davison and Clarke (2000)	*Cepaea nemoralis*	Color, banding	Microsatellites/mtDNA	6	Yes
Arnaud et al. (2001)	*Helix aspersa*		Microsatellites/Allozymes		
Goodacre (2001)	*Partula taeniata*	Color, banding	mtDNA	7	Yes
Gould and Woodruff (1990)	*Cerion* sp.	Shell morphology	Allozymes		Yes
Schilthuizen et al. (1999a)	*Albinaria hippolyti*	Shell characters, Body anatomy	rRNA/allozymes/intron	3[a]	Yes
Holland and Hadfield (2002)	*Achatinella* sp.		mtDNA	5[b]	
Within species: large scale					
Thomaz et al. (1996)	*Cepaea nemoralis*		mtDNA	13	
	Helix aspersa			13	
Guiller et al. (2001)	*Helix aspersa*		mtDNA	11	
Ochman et al. (1983)	*Cepaea nemoralis*	Color, banding	Allozymes		No
Ochman et al. (1987)	*Cepaea nemoralis*	Color	Allozymes		Yes
	Cepaea hortensis	Color	Allozymes		No
Davison (2000b)	*Cepaea nemoralis*	Color, banding	mtDNA	6	No
Goodacre and Wade (2001b)	*Partula* sp.	Morphology	mtDNA	31[c]	No
Goodacre (2001)					
Hayashi and Chiba (2000)	*Euhadra peliomphala*	Body color	mtDNA	10	Yes
Shimizu and Ueshima (2000)	*Euhadra peliomphala*		mtDNA	13[b]	
Watanabe and Chiba (2001)	*Euhadra quaesita*	Body color, shell characters	mtDNA	14	No
Guiller et al. (2001)	*Helix aspersa*	Shell characters	mtDNA/allozymes	11	Yes
Pfenninger and Magnin (2001)	*Candida unifasciata*	Quantitative shell morphology	mtDNA	21	No
Ross (1999)	*Discus macclintocki*		mtDNA	11	
Hugall et al. (2002)	*Gnarosophia bellendenkerenis*		mtDNA	12–15[d]	
Schilthuizen et al. (1999b)	*Gyliotrachela hungerfordiana*		rRNA	5[e]	
Between species					
Chiba (1998, 1999)	*Mandarina* sp.	Color, banding, genitalia, ecology	mtDNA/allozymes	19 18[f]	No
Douris et al. (1998)	*Albinaria*	Morphology	mtDNA	12	No
Between genera					
van Moorsel et al. (2000)	*Albinaria/Isabellaria/Sericata*	Shell characters	rRNA	31[e]	
Goodacre and Wade (2001a)	*Partula/Samoana* sp.	Shell thickness, tentacle length, body color, mucus	rRNA	2[e]	No
Thacker and Hadfield (2000)	*Achatinella/Partulina* sp.	Morphology	mtDNA	14	No

Only the most recent or comprehensive reference is given, where there has been more than one by the same group

All genetic distances are for mitochondrial 16S rRNA, except where indicated

[a] Calmodulin intron

[b] Cytochrome oxidase subunit I

[c] Cytochrome b

[d] Cytochrome oxidase subunit II

[e] Nuclear rRNA and ITS

[f] 12S rRNA

ciation between microsatellites and shell color, and no clear relationship with mtDNA (Davison and Clarke 2000). One explanation could be that migration and drift produced two sets of area effects, one in shell genotypes and the other in microsatellites. If so, they could show coincident clines, by chance, but this was dismissed following the suggestion of Endler (1977) that the correlations would be weak unless other factors were involved. Similarly, a coincidence due to selection on the shell types, and drift and migration on the microsatellites, was considered unsatisfactory because it multiplies hypotheses. As the magnitudes of the patterns in *Cepaea* and the correlations between them were probably too strong to have arisen by drift since the last glaciation, then invasions from refugia may have been the most important factors in forming area effects.

Importantly, although the molecular results agree with a historical explanation, they do not falsify the selective interpretation. Matching correlations in other species would significantly strengthen the historical interpretation.

Similar area effects to those in *Cepaea* have been reported in other snail species, although none have been studied so intensively (Clarke 1968; Gould and Woodruff 1990; Johnson et al. 1993; Goodacre 2001). If the patterns of shell types (and other inherited morphological variation, if the category is broadened) have a similar explanation, then a similar correlation with molecular genetic data would be predicted. One problem is that few studies on snails have investigated patterns of molecular variation on a small scale (Davison and Clarke 2000; Arnaud et al. 2001; Goodacre 2001), or if they have, then morphological variation (if any) is not reported (Ross 1999; Arnaud et al. 2001; Holland and Hadfield 2002). In addition, there is danger of an ascertainment bias. Probably, most shell variation is strongly influenced by selection most of the time, but the few exceptions stand out and thus have been studied. No one would think to directly compare patterns of molecular variation with shell variation, in the absence of any broad-scale patterns in shell type.

However, various studies have investigated aspects of the history of snail populations. Aside from the allozyme studies mentioned earlier (Johnson et al. 1976; Jones et al. 1980; Ochman et al. 1983), Goodacre (2001) has studied an area effect in greatest detail, over a relatively small scale. What is the evidence, albeit indirect, for the effects of history or selection on the shell types in that study and others? It may be useful to compare the results across different spatial scales, within a species (small scale, large scale), between species, and between genera (see Table 1).

Genetic studies in snails: within species

Previous studies of *Partula* from the Society Islands, French Polynesia, have reported striking differences in shell shape, color, and banding pattern between adjacent populations, without any obvious geographic barrier to snail dispersal or environmental gradient (Johnson et al. 1993). Goodacre (2001) found a similar pattern in the mtDNA from *P. taeniata*. The transition between the two main mitochondrial types roughly coincided with clines in some morphological characters but appeared to be unrelated to others. Goodacre (2001) suggested a primarily historic explanation – that many of the morphological differences may have accumulated while populations were isolated from one another, through the effects of random drift and selection – although conspicuous characters such as shell colors and banding patterns may also be influenced by selection.

There have also been a number of studies on *Albinaria* and *Cerion* over a relatively fine scale. Both of these genera are characterized by a high species and subspecies diversity, with each species often having a strictly local distribution, either in allopatry or parapatry. In fact, each taxon could almost be described as an area effect, because particular shell and morphological types predominate over large areas, apparently regardless of the habitat, with steep clines between them (Gould and Woodruff 1990; Schilthuizen et al. 1999a). In *Cerion*, one area effect may be caused by an earlier colonization of a part of the island of Great Inagua, where the snails are long and thin, by snails from Cuba, where the snails are flattopped (Gould and Woodruff 1990). In *Albinaria hippolyti*, the hybrid zone between subspecies is not associated with any obvious environmental gradient, with coincident clines between shell, morphological, and allozyme characteristics (Schilthuizen et al. 1999a). Interestingly, the hybrid zone in this species and others (Woodruff 1989; Chiba 1997; Schilthuizen et al. 1999a) is associated with rare alleles and novel polymorphisms, a potential source of evolutionary novelty.

Various other studies have investigated differentiation on a small scale, sometimes over only a few meters (Arnaud et al. 2001), but have not reported any differences in morphological characters, perhaps because there were none. The remainder of the studies have been over a larger scale (see Table 1). Here, the interpretation is more complicated because it is likely to be longer since populations (and their genes) had a common origin. I studied patterns of mtDNA variation across much of Britain (Davison 2000b). An East–West pattern of mitochondrial lineages in *C. nemoralis* was found, which probably reflects two separate colonization events after the last glaciation, circa 10000 years before the present. However, no correlation was noted with an earlier allozyme study (Ochman et al. 1987), nor have any East–West patterns of shell differences been reported in British *C. nemoralis*. If the founding populations did differ in their shell frequencies, then selection may have modified them to their local conditions, in a similar manner to the situation in the Pyrenees (Ochman et al. 1983).

In continental Europe, there is a cline in the shell types of *C. nemoralis* (but not in *C. hortensis*), with yellow shells more often found in Northern cooler climates (Jones et al. 1977). It is likely that this is due to climatic selection, although there is also a North–South cline in allozyme frequencies in both *Cepaea* species (Ochman et al. 1987). Similarly, in *Partula* there is no simple relationship either between genetic distance and geographic proximity or morphological characteristics. The potentially confusing effects of gene flow between islands and interspecific hybridization are also evident (Goodacre and Wade 2001b; Goodacre 2002; Johnson et al. 2000). In particular, introgression of mtDNA alleles between taxa is a problem when using a mtDNA phylogeny as a proxy for a species phylogeny (see following).

In Japan, two groups have focused on the phylogeography of the land snail *Euhadra* (Hayashi and Chiba 2000; Shimizu and Ueshima 2000; Watanabe and Chiba 2001). Hayashi and Chiba (2000) recorded variation in the shell type and body color patterns of *Euhadra peliomphala*, sampled across the Kanto region and Izu peninsula. Shell type was similar across the whole region, but three main body color types were found with distinct but overlapping distributions. Although the inheritance of body color in many snails is uncertain (Backeljau et al. 2001), so that environmental factors may have a marked effect, the pattern is consistent with the historical explanation because there are also three groups of mtDNA haplotypes with a broadly equivalent distribution (Hayashi and Chiba 2000). In contrast, in the related species *E. quaesita*, light snails with light shells tend to be found near the coast, and dark snails with dark shells in the mountains (S. Chiba, personal communication). The *E. quaesita* mtDNA phylogeny does not correspond with the patterns in shell types, but there is a correlation with some of the mtDNA patterns in *E. peliomphala*, suggesting a common historic cause (Watanabe and Chiba 2001; S. Chiba, personal communication).

One study has compared quantitative shell variation with molecular data. Pfenninger and Magnin (2001) reported no significant association between mtDNA distance and morphological distance in *Candidula unifasciata*, suggesting independent evolution of the two characters. In addition, some quantitative shell traits were correlated with environmental factors, implying that selection is important. Unfortunately, the inheritance of quantitative characters is much less certain, and local environmental conditions may have a great effect on the phenotype.

Genetic studies in snails: between species and genera

In *Anolis* lizards, there is strong evidence that morphological similarities have arisen between species because of convergent adaptation to similar habitats on different Carribean islands (Losos et al. 1998). A similar circumstance may apply in many snail species.

In *Mandarina*, an endemic land snail genus of the oceanic Bonin Islands, the mitochondrial phylogeny suggests that species with similar shell morphologies and life habits (arboreal, semiarboreal, terrestrial) appeared repeatedly and independently in different lineages and islands at different times (Chiba 1999) as a result of an adaptive radiation.

Three partulid genera – *Eua*, *Partula*, and *Samoana* – have traditionally been separated by their genital anatomy, and a recent ribosomal RNA phylogeny generally supports the previous classification. However, *Samoana* from the Marquesas Islands, where *Partula* are absent, have characters more commonly associated with *Partula* elsewhere (thick, pigmented, and banded shells, short tentacles, and less sticky mucus). In contrast, some *Partula* from the Society Islands have features more commonly associated with *Samoana*. As both the DNA and allozymes (Johnson et al. 2000; Goodacre and Wade 2001a) are consistent with the anatomic classification, the other morphological similarities may be a consequence of adaptive convergence.

Not all studies suggest such a clear, adaptive explanation (Douris et al. 1998; Thacker and Hadfield 2000), and whether the adaptive explanation is actually correct must be rigorously tested. Mitochondrial introgression through hybridization and long distance gene flow (leptokurtic dispersal; Ibrahim et al. 1996) have probably also confused the interpretation.

Hybridization

Recent hybrids are easy to detect, because the animals tend to have intermediate morphology, but even with a long history of hybridization species may remain distinct if there is selection on the morphological characters (Chiba 1998). Inevitably, however, hybridization will lead to the exchange of neutral markers, through gene flow or “molecular leakage” (Clarke et al. 1996). mtDNA is especially able to introgress (Avise 2000). For instance, Shimizu and Ueshima (2000) reported that *E. peliomphala* in Japan is polyphyletic, with at least two different mtDNA lineages. They suggest that one lineage could represent another species, *E. “peliomphala” kunoensis*. However, as the *E. peliomphala kunoensis* lineage is a sister group to another species, *E. brandtii*, their alternative explanation is that some *E. peliomphala* gained an *E. brandtii* mtDNA in the past through introgressive hybridization (Shimizu and Ueshima 2000). As they point out, distinguishing between the two will be difficult, but comparing the mtDNA sequences and morphology with multiple nuclear genes is the best approach. Introgressed genes are not always easy to detect, and the situation is more confusing because there are several other reasons why the mitochondrial phylogeny may not correspond with the species phylogeny (Nichols 2001).

Thus, a concordance between morphological and molecular characters, when comparing taxa, could result from their shared history. Alternatively, a nonconcordance could result from selection or introgression. However, the more ancient the split, then the more difficult it is to detect previous introgression, even when a range of molecular markers, such as nuclear gene sequences, are used. One major advantage of mtDNA for phylogenies is that it may not recombine (although there is some doubt, and we are especially ignorant of molluscan mtDNA) (Eyre-Walker et al. 1999). Unfortunately, working with nuclear gene sequences is technically more demanding, and the analysis requires further care, for reasons of the confusing effects of recombination (Hare 2001). Most molecular studies on land snails have realized the problem of hybridization confusing the phylogeny, even though it is difficult to show conclusively, including Goodacre and Wade (2001a,b), Chiba (1998, 1999), Thacker and Hadfield (2000), Hayashi and Chiba (2000), Shimizu and Ueshima (2000), and Douris et al. (1998).

Alternative approaches

Obviously, the foregoing method of comparing morphology with phylogeny has limitations, especially when the evolutionary history is quite ancient. An complementary technique to understanding diversity was suggested by Hugall et al. (2002, 2003). The key to their investigation is to use snails (the *Sphaerospira* lineage, including *Gnarosophia*) that are limited by habitat, the wet rain forest of northeast Australia. Thus, climate and geography govern the habitat of the snail, so that bioclimatic modeling can be used to infer the distribution under Holocene and late Pleistocene climates. In *Sphaerospira*, the spatial distribution of phylogenetic diversity is consistent across the range, suggesting no large-scale extinction of diversity. In this group of species, local peripheral (allopatric) isolation may be mostly responsible for the snail diversity (Hugall et al. 2003).

High mtDNA diversity equals high mutation rate?

Thomaz et al. (1996) were first to report on the extreme divergence of mtDNA within and between land snail species. Subsequently, most studies of land snails have reported similar results (see Table 1). Thomaz et al. suggested four explanations for the diversity*:* (1) unusually rapid mtDNA evolution; (2) ancient isolation of populations that consequently diverged; (3) selection acting to generate and maintain variability; and (4) unusually structured or exceptionally large populations. Another possibility was that pulmonate mtDNA is inherited in the doubly uniparental mode, as in *Mytilus*, allowing separate maternal and paternal lineages to coexist (Skibinski et al. 1994). In *Cepaea*, mtDNA inheritance is maternal (Davison 2000a), and heteroplasmic individuals have not been reported in any study so far.

The first explanation, that mtDNA evolves unusually rapidly, is useful because it is testable by comparison with known events, such as colonization of islands, and dated fossils. Assuming a single colonization of the Bonin Islands by *Mandarina* 1.8 million years ago and a divergence of up to 18%, then Chiba (1999) estimated the mitochondrial rRNA mutation rate at approximately 10% per million years: very fast. In contrast, the evolutionary rate for *Albinaria* may be only 1% per million years (Douris et al. 1998), and in *Gnarosophia bellendenkerensis*, similar diversities were found compared with verterbrates (Hugall et al. 2002). Of course, there is no reason to expect the mutation rate to be the same for all snails (either high or low), but in *Gnarosophia* and *Sphaerospira*, we have the most detailed estimation of their evolutionary history (Hugall et al. 2002, 2003). It is also necessary to make the distinction between a high mutation rate (explanation 1 above), and a high substitution rate, which could arise when haplotypes become "trapped" in structured subpopulations. Both could result in high mtDNA diversity.

In these kinds of analyses, acquiring precise details of geologic events is a problem and does not necessarily coincide with the coalescence of DNA lineages (Nichols 2001). Further problems remain with estimating the potential error, so it is generally not possible to use the rate in one species for another circumstance, except as a very broad tool (Swofford et al. 1996).

If land snail mtDNA does evolve fast, then it begs the question, why? and are nuclear genes affected in a similar manner? At present, the data from nuclear gene sequences are sparse and mostly confined to rRNA regions or introns. At least one study has reported relatively large divergences between rRNA internal transcribed spacer (ITS) sequences (van Moorsel et al. 2000). A useful starting point may be to note circumstances in other species that correlate with a high mutation rate, such as a fast metabolism or short generation time. Another parallel might be with studies on sexual selection that have shown genes involved with fertilization evolve very fast (Biermann 1998) (although it is difficult to understand how this could directly affect mtDNA). If selection is implicated, then hypotheses 1 and 3 (above) could be linked. Extensive phylogeographic surveys are required to begin to test hypothesis 2 (Hugall et al. 2002), and whether structured populations act to increase or even decrease diversity is dependent on the nature of the population dynamics (Slatkin 1991; Charlesworth et al. 1997; Pannell and Charlesworth 2000).

Conclusions

Interpreting patterns of phenotypes in snails, and the underlying genetic variation, is complicated by the population history, random genetic drift, selection, and hybridization. Future research may concentrate on understanding the relatively simple situation first, involving narrowly divergent types that evolved in the recent past, with thorough sampling over a fine spatial scale. Only when within-species diversity is understood may it become possible to investigate the bigger picture and address issues such as the mode of speciation (allopatric, sympatric), and the extent to which selection is involved in that process.

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