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CHAPTER 13

CONCEPTS OF DRIFT AND SELECTION IN "THE GREAT SNAIL DEBATE" OF THE 1950S AND EARLY 1960S

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INTRODUCTION

Recently, much philosophical discussion has centered on the best way to characterize the concepts of random drift[1] and natural selection, and, in particular, whether selection and drift can be conceptually distinguished (Beatty, 1984; Brandon, 2005; Hodge, 1983, 1987; Millstein, 2002, 2005; Pfeifer, 2005; Shanahan, 1992; Stephens, 2004).[2] These authors all contend, to a greater or lesser degree, that their concepts make sense of biological practice. So it should be instructive to see how the concepts of drift and selection were distinguished by the disputants in a high-profile debate; debates such as these often force biologists to take a more philosophical turn, discussing the concepts at issue in greater detail than usual. Moreover, it is important to consider a debate where the disputants are actually trying to apply the models of population genetics to natural populations; only then can their proper interpretations become fully apparent. (Indeed, I contend that some of the philosophical confusion has arisen because authors have considered only the models themselves, and not the phenomena that the models are attempting to represent). A prime candidate for just such a case study is what Provine (1986) has termed "The Great Snail Debate," that is, the debates over the highly polymorphic land snails *Cepaea nemoralis* and *C. hortensis* in the 1950s and early 1960s. These studies represent one of the best, if not *the* best, of the early attempts to demonstrate drift in natural populations.[3]

Of course, some excellent historical accounts of the changes in the usages and meanings of random drift have been written already. Some of these histories of random drift have a broad scope (Beatty, 1992; Cain & Provine, 1991; Gigerenzer et al.,

1989; Gould, 1983), whereas others focus on the views of Theodosius Dobzhansky (Beatty, 1987), the views of Sewall Wright (Provine, 1983, 1986; Skipper, 2004), the views of Ronald A. Fisher (Turner, 1987), or the debate between Wright and Fisher (Plutynski, 2005; Skipper, 2002, this volume). I am very much indebted to these works. However, to my knowledge no one has written on the concepts of drift and selection in the debates over *Cepaea* with a focus on the views of the disputants themselves.

This study reveals that much of the present-day confusion over the concepts of drift and selection is rooted in confusions of the past. Nonetheless, there are lessons that can be learned about nonadaptiveness, random sampling, and causality with respect to these two concepts.

My approach will be to analyze the published works of the major disputants: Arthur J. Cain, Philip M. Sheppard, John D. Currey, and Maxime Lamotte. Of the works of these authors, I will focus primarily on Cain and Sheppard (1950), Lamotte (1959a), and Cain and Currey (1963). These papers were chosen because they have become classics in the field. Moreover, Cain and Sheppard (1950) is the paper where the authors most thoroughly set out their selectionist arguments and their concerns with the previous studies of *Cepaea*. Lamotte (1959a) is the paper that attributes a larger role to drift, as compared to his earlier works. Finally, Cain and Curry (1963) is in large part written in response to Lamotte (1959a) and shows some interesting changes in thinking. Other works by these and other authors will be discussed where relevant, but will receive much less attention. My hope is that this approach is useful in discussing the effects that these studies may have had on subsequent researchers, i.e., later debates over neutralism and selection in molecular evolution. The limitations of focusing only on the published works are, of course, that broader contextual factors are left out of the analysis.

Background

Although the starting point for my analysis is Cain and Sheppard (1950), it is important to understand the views against which Cain and Sheppard were reacting. The principal work that they seem to be responding to—the one that is cited most often in Cain and Sheppard (1950)—is Diver (1940).

Diver (1940):[4] "The Problem of Closely Related Species Living in the Same Area"

Diver explains that the two species, *C. nemoralis* and *C. hortensis*, can be difficult to distinguish in practice, but that the interspecific differences include differences in genitalia and general proportions of the shell (1940, p. 323), as well as differences in "courtship" behavior and "chromosome structure" (1940, p. 326). Within both species, there are differences in color and banding patterns.

Much of Diver's (1940) discussion of *C. nemoralis* and *C. hortensis* seeks to establish the claim that these species exist in small subpopulations, with very little interbreeding between populations. Regarding *C. hortensis*, Diver states, "If it be assumed that the samples [which averaged 79 per population] include no more than one-quarter of the adult population, it is clear that the average discrete population is still quite small,

and some populations can certainly be counted in tens" (Diver, 1940, p. 324). Diver allows that the average population sizes of *C. nemoralis* are "somewhat larger," but concludes, "such populations are really a number of quite small though more or less adjacent subpopulations" (Diver, 1940, p. 325).

At one point, Diver asserts, "there is no indication that the different colour and band forms confer any advantage, nor that the interspecific differences are in any way adaptive" (Diver, 1940, p. 326). This comment seems to come out of nowhere; in the preceding sentence, Diver is discussing the rarity of natural hybrids between the two species. However, his reason for the claim concerning interspecific differentiation becomes somewhat clearer later in the paper. He asserts, "it seems that selective forces and adaptive values have played little direct part in these specific differentiations," nor do they seem to be due to geographical isolation (Diver, 1940, p. 327). Then, citing Wright's essay in the same volume (*The New Systematics*, edited by Julian Huxley), Diver states that the "most probable general cause [of the differences between species] is random differentiation in small isolated populations" (Diver, 1940, p. 327).

Diver's reason for thinking that color and banding (the intraspecific differences) did not confer any advantage may have had to do with results such as the following: "For instance, in a population continuously occupying a 45-yard strip, brown shells were present in all subsamples for 25 yards, forming 2.3 per cent. of a sample of 653, but absent from the next two samples (10 yards each), which totalled 552 and 346 respectively" (Diver, 1940, p. 325). Since "colonies were mostly sampled on the principle of taking every visible adult throughout the area of occupation" (Diver, 1940, p. 324), Diver may have thought that the distances between the differing colonies were too small to have had any environmental differences. Moreover, in an earlier work Diver noted that one need only "look at a few *Cepaea* colonies for it to become obvious that in one colony there may be 90 per cent banded, while in another, which comes from an ecologically similar habitat there may be only 25 per cent pinks but as many as 80 per cent banded" (Diver, 1939, p. 121).

In these quotes, we see the association of random drift ("random differentiation") not only with Wright's ideas about small, isolated populations[5] but also with "non-adaptive" differentiation between species. (Provine [1986] has documented the ways in which Wright's early writings lent themselves to this association, despite Wright's later assertions). Selection, on the other hand, is associated with adaptive differentiations between species. What is less clear is whether Diver saw interspecific differentiation in the same light as intraspecific differentiation; he states, "it is still an open question, even among geneticists, whether the small genetic differences which are the regular material of intraspecific genetic analysis are the blocks with which interspecific and generic differences can be built up" (Diver, 1940, p. 304).

The confusion is compounded because Diver uses the word "advantage" to refer to intraspecific differences, but the word "adaptive" to refer to interspecific differences (or, rather, lack of advantage and lack of adaptiveness). Did Diver distinguish between the term "advantage" (which is a term that implies that two or more things are being compared) and the term "adaptive" (which is a term that does not necessarily imply this sort of comparison)? Perhaps he is making the same distinction that Provine makes between "adaptive differences" and "adaptive to the environment." As Provine explains,

> We can speak about assessing whether or not a particular character of an organism, such as a color pattern or leaf shape or jaw structure, is adapted to the environment. Does the character enable the organism to leave more or fewer offspring than would otherwise be the case? Or we can ask whether the characters that distinguish two species or other taxonomic categories are adaptive or nonadaptive. This is not simply the earlier question applied twice but can mean that the assessment of adaptation is applied to differences, for example, in homologous characters in two different species. In this case, both characters might be highly adapted to the two different environments, but neither contributes more than the other does to reproductive fitness. The adaptive difference between them would therefore be none. In this sense, one could be an intense selectionist who believes that all characters of a species are highly adapted to the environment and still believe that many constant differences in characters between closely related species are nonadaptive. (Provine, 1986, p. 207)

Thus, there could be widespread agreement that two variants are both adapted to the environment, yet disagreement on whether there are adaptive differences between the variants. Those that believe that there are adaptive differences between the variants would believe that one is more adapted to the environment than the other (or that one has a greater capacity for reproductive success than the other), whereas those that believe that there are not adaptive differences between the variants would believe that the two variants are equally adapted to the environment (or have an equal capacity for reproductive success).[6]

It is also important to note that someone who denies that a variant is adaptive in its environment does not necessarily mean that the variant is *poorly* adapted to its environment; they might simply mean that the trait in question is neither harmful nor helpful to the organism. Rather, it is "neutral" or "functionless." If the trait could be removed, the organism's capacity for reproductive success would not change. For example, some believe that in contemporary society, human tonsils are nonadaptive, or functionless, in this sense.

It is not clear whether Diver recognized a distinction between adaptive *simpliciter* (adaptive to the environment) and advantage (adaptive differences). Nonetheless, we will see that confusion between these two meanings extends throughout much of the debate, and I will use Provine's terms to highlight these cases.

Other Authors Cited by Cain and Sheppard (1950): Haldane (1932), Robson and Richards (1936), Dobzhansky (1941), Huxley (1942), and Mayr (1942)

In addition to citing Diver's work itself, Cain and Sheppard note that Diver influenced a number of other (prominent) biologists of the day: "*Cepaea nemoralis* has been quoted by Haldane (1932), Robson and Richards (1936), Dobzhansky (1941), Huxley (1942), and Mayr (1942) on the evidence of Diver as giving an example of random distribution of varieties, the patterns of which have no selective value" (Cain & Sheppard, 1950, p. 291).[7] It is instructive to see what each of these biologists actually said (or, in some cases, did not say) about adaptiveness, drift, and Wright's and Diver's work.

Haldane, in discussing populations that are in equilibrium, notes that the "common snails, *Cepaea hortensis* and *C. nemoralis* . . . possess several varieties which differ as regards the banding on their shells. . . . Diver, in a very careful unpublished work

which he kindly allows me to quote, found no selective destruction of any type by birds" (Haldane, 1932, p. 83). Here we see the simple assertion that selection does not act on the variations. Since Diver did not invoke drift until his 1940 essay,[8] it is not surprising that Haldane's 1932 work makes no mention of drift, either. However, Haldane's comment does illustrate the important point that one can deny that selection is acting without believing that drift *is* acting.

Robson and Richards (1936) neither cite Diver nor discuss drift explicitly, as far as I can tell. However, they do critique a number of experiments that alleged to demonstrate selection in *Cepaea* (Robson & Richards, 1936, pp. 200–201, 203–204). Furthermore, one piece of evidence concerning *Cepaea* is discussed in a positive light, namely a finding by Haviland and Pitt (1919) that there was "no preference between banded and unbanded" snails in a comparison between collections from "anvils" (stones where birds take the shells to break them) and the local population (Robson & Richards, 1936, pp. 200–201). This, they say, is "clearly indicative of no selection" (Robson & Richards, 1936, p. 201). Later in the book, they state, "there is no evidence that [heterozygous] selection occurs, and in the case of land snails (*Cepaea*) there is some evidence that the attacks of birds on the different colour-forms are indiscriminate" (Robson & Richards, 1936, p. 229). So there is a denial of selection, as with Haldane, together with a claim for indiscriminate, rather than selective predation.[9]

Dobzhansky, writing in 1941 and thus having the benefit of Diver's later work, does make the connection between the snail studies, Wright's views on small and partially isolated populations, and drift. Dobzhansky states: "In recent years many acute observers have realized that segregation of species into small and partly independent colonies is a very common phenomenon. Thus, Diver (1940) finds it to be the rule not only in the snails, where it is most striking, but also in nonmarine organisms in general" (Dobzhansky, 1941, p. 172). After discussing this example (citing the discussion concerning brown snails quoted from Diver above) and many others, Dobzhansky summarizes his arguments:

> To recapitulate: restriction of the genetically effective size of natural populations is in all probability an important agent engendering differentiation of species into local groups possessing different genotypes. It must be admitted that, except in some relic species and in *Drosophila pseudoobscura*, we do not have even approximate estimates of the magnitude of population numbers. And yet, a large and rapidly growing amount of evidence pertaining to different subdivisions of the living world and secured by different methods and by different biological disciplines, attests the existence of phenomena which can most plausibly be accounted for by genetic "drift" in populations of limited sizes. Although it would certainly be premature to conclude that evolution in all groups and at all times is conditioned by the genetic drift, it is reasonable to assume that it is frequently assisted by this factor, the importance of which has only recently become appreciated. (Dobzhansky 1941, p. 185)[10]

However, even though Dobzhansky implies that drift is acting on *Cepaea*, and, more broadly, seeks to determine whether drift will "loom important" or be "negligible" as an evolutionary agent (Dobzhansky, 1941, p. 168), he does not explicitly rule out selection. He also does not deny that intraspecific differences are adaptive to

their environments or that they have adaptive differences. (Beatty [1987] argues that Dobzhansky never saw drift as a strict alternative to natural selection.)

Huxley asserts, "Diver (1939) in the snail *Cepaea* finds that the proportions of the various types of colour and banding vary from colony to colony, almost always in an arbitrary, non-graded way" (Huxley, 1942, p. 202). As noted above, differences in color and banding refer to intraspecific differences. Again, this could imply that color and banding serve no purpose in the environment (i.e., that these traits are not adaptive in their environment), or it could be that both are adaptive in their environment, meaning that there are no adaptive differences in the given environment; it is unclear which (if either) is meant here.

Mayr, similar to Haldane, denies that selection acts on the banding: "The variation in color patterns, such as bands in snails and spot patterns in lady beetles are, by themselves, obviously of very insignificant selective value" (Mayr, 1942, p. 32). However, his remarks go further:

> Ford distinguishes in a recent study (1940) (1) neutral polymorphism, (2) balanced polymorphism, and (3) transient polymorphism, relating to chances of polymorphism in time.
>
> *Neutral polymorphism* is due to the actions of alleles "approximately neutral as regards survival value." Ford (following Fisher) believes that this kind of polymorphism is relatively rare, because "the balance of advantage between a gene and its allelomorph must be extraordinarily exact in order to be effectively neutral." This reasoning may be correct in all of the cases in which one of the alternative features has a definite survival value or at least is genetically linked with one. There is, for example, no reason to believe that the presence or absence of a band on a snail shell would be a noticeable advantage or disadvantage. . . . Even more convincing proof for the selective neutrality of the alternating characters is evidenced by the constancy of the proportions of the different variants in one population. The most striking case is that of the snails *Cepaea nemoralis* and *C. hortensis*, in which Diver (1929) found that the proportions of the various forms from Pleistocene deposits agree closely with those in colonies living today. (Mayr, 1942, p. 75)[11]

So, here we see Mayr asserting that not only does selection *not* act on the banding but also the banding is "neutral" (or "approximately neutral").[12] Moreover, these neutral traits are associated with constancy of proportions over time. Here, Mayr seems to be emphasizing the lack of adaptive differences between variants, rather than the lack of adaptive fit to the environment, but again, the distinction is not expressed entirely clearly.

What picture emerges from these different authors? One point worth noting is that even though Diver was concerned with both interspecific differences and intraspecific differences, the focus of these authors is on the intraspecific differences in *Cepaea*. Some deny that selection acts on intraspecific differences in *Cepaea* (Haldane, Mayr, Robson and Richards). Only Dobzhansky ties the discussion of *Cepaea* to small, isolated populations and drift, although clearly Diver did as well. Huxley's comments could imply either that color and banding were not adaptive in the environment or that the differences were not adaptive, whereas Mayr seems to focus instead on the lack of adaptive differences (or "neutrality") among variants, but, as with Diver, these distinctions may not have been made consciously. Thus, the picture against which Cain and Sheppard are reacting is a mosaic of related ideas rather than a uniform backdrop, with some of the tiles of the mosaic being a bit blurry.

CAIN AND SHEPPARD (1950): "SELECTION IN THE POLYMORPHIC LAND SNAIL *Cepaea nemoralis*"

And yet, the brush strokes of Cain and Sheppard's own ideas bore the mark of some very prominent twentieth century thinkers. Speaking very broadly, Cain and Sheppard were influenced by R. A. Fisher and E. B. Ford. Furthermore, Cain and Sheppard were at Oxford University at the same time and both are considered to have been part of the "Oxford School of Ecological Genetics" founded by Ford. However, it should be noted that Cain considered himself to have been "preadapted" to Ford's ideas as a result of his early interest in natural history, rather than having been influenced by them (Provine, 1986). And as John Turner (1987) has argued, Fisher himself had a close, but complex, relationship with the Oxford School. Indeed, Cain and Sheppard's disagreements with Lamotte are not the same as Fisher's disagreements with Wright over the shifting balance theory; they are much narrower in scope, dealing only with drift and selection, and only with the populations of *Cepaea nemoralis*. These complexities would suggest that Cain and Sheppard are more in Ford's tradition than in Fisher's, the Oxford school approach not having fully been a vindication of the Fisherian approach.

But why study *Cepaea nemoralis*? First, polymorphism had long been of evolutionary interest (Provine, 1986),[13] and the snail is highly polymorphic. The snails show obvious differences (in other words, they manifest a "conspicuous polymorphism") both in color (yellow, pink, or brown) and in the number of bands (from zero to five). Interestingly enough, however, persistence of the polymorphism (which was of great interest to much of the rest of the Oxford School) was at best an afterthought for Cain and Sheppard.

Rather, the issue of adaptiveness loomed more important. In an interview with Provine, Cain recounted a conversation with Philip Sheppard:

> When Philip was in my room one day . . . I poured out on the table in front of him a sample of *Cepaea nemoralis* shells . . . and we decided then and there (a) that it was impossible that such striking variation could be wholly neutral, and (b) that we would work on it. (quoted in Provine, 1986, pp. 440–441)

And yet, as described above, the variations in *Cepaea nemoralis* had often been cited as the primary example of *nonadaptive* variations, going back to the work of Diver. So, Cain and Sheppard were motivated to set the record straight on that score; they sought to explain the way in which the different forms were adaptive. (However, we will see again that it is not always clear whether "adaptive differences" or "adaptiveness to the environment" were at stake.)

Moreover, the distributions among the snail populations were very striking. In some populations, banded shells predominated; in others, unbanded were the most common. Similarly, the relative proportions of shell *colors* varied from population to population. Thus, one of Cain and Sheppard's primary goals was to explain the observed distributions—in other words, to state which evolutionary processes, or "factors," had caused the distributions to be as they were.

Cain and Sheppard begin their 1950 paper as follows:

The structure of natural populations of animals and plants and of variation both within and between colonies needs more study as Diver (1940) has pointed out. Research along these lines is of particular importance because of the evidence he has obtained that many, apparently continuous, natural populations are broken up into small breeding-communities, giving the conditions in which genetic drift, as suggested by Sewall Wright (e.g., 1940), might be expected to occur if it were operative. Diver has stated that from his observations on populations of *Cepaea nemoralis* (L.) and *C. hortensis* (Müll.) he obtained no indications that the variations in shell colour and banding have any selective value. He considers that these small breeding-communities show definite divergences from each other because of nonrandom mating, but expresses surprise (1940, p. 312) that such divergences have not proceeded further by means of genetical drift. (Cain & Sheppard, 1950, p. 275)

Note the many qualifications surrounding drift: Wright has outlined the *conditions* in which drift *might* be expected to occur *if* it were operative. (Below, we will see that their remarks concerning drift are even more qualified, if that is possible.)

Here is the paragraph from Diver to which Cain and Sheppard are reacting:

The fact that these conditions, which result in breaking up specific assemblages into a great number of numerically small, discrete population units, are so widespread has a highly important bearing on evolutionary mechanics (Wright, 1939). In such a distributional structure it is most unsafe to assume any wide degree of random mating. In those few cases where some evidence is available (e.g., *Cepaea*) there is obviously a large amount of inbreeding; and in a great many populations the migration rate must be extremely low. The need for carefully planned attempts to measure this is pressing. The problem almost seems not one of why local races are formed but rather why such differentiation is not proceeding more prevalently and at a faster rate than it apparently is. (Diver, 1940, pp. 311–312)

So, indeed, Diver is citing Wrightian drift as an explanation for "local races"—what I have been calling intraspecific differences—in many populations (namely, populations which are broken up into small, isolated interbreeding groups). However, the reference to *Cepaea* here is just made in passing. As I noted above, Diver does not go into very much detail anywhere in his essay about the color and banding differences within the two species, stating only that there is "no indication" that they "confer any advantage," and noting that communities located very close to one another vary in their distributions. So, when Cain and Sheppard state that, according to Diver, there is "no indication" that the variations in shell color and banding "have any selective value," presumably they are equating "no advantage" with "no selective value." What exactly Cain and Sheppard mean by "no selective value" will become clearer as we explore the rest of their essay.

In response to these assertions of "drift" and "no selective value," Cain and Sheppard set out to

describe an investigation into this problem of the relative importance of selection and drift in determining the distribution of different colour and banding patterns in *C. nemoralis*. We find, on the contrary, that they have definite selective values, related to the environment, determining the general aspect of different populations and therefore of their gene ratios. Although small inbreeding communities within each population may

diverge from one another in colour and banding patterns, this random divergence cannot proceed far, because of the effects of natural selection. (Cain & Sheppard, 1950, p. 275)

Note that Cain and Sheppard have departed completely from the interspecific analysis that Diver was engaging in; they study only *C. nemoralis.* It is interesting to see Cain and Sheppard's departure from interspecific analysis because many authors (e.g., Gould, 1983; Provine, 1986; Turner, 1987) have traced contemporary debates over nonadaptiveness back to the earlier debates that tried to use nonadaptive characters to differentiate among species. It may be true that the earliest debates over nonadaptive characters focused on nonadaptive differences among species, but if so, Cain and Sheppard represent a departure from that tradition. This is a third way that Cain and Sheppard's concerns are narrower than those of their predecessors (the other two being their relative lack of interest in the persistence of polymorphism and the decoupling of their debate from the Fisher-Wright debate over shifting balance theory, respectively). Future work might profitably reveal the origins of this narrowing.

Moreover, the debate is cashed out in terms of "the relative importance of selection and drift." As Beatty (1984, 1997) has argued, debates over the relative significance of various factors are common in biology, and indeed, this one will exhibit some of the characteristics that Beatty identifies: Cain and Sheppard do not rule out drift entirely, but it is relegated to an insignificant role.

Thus, Cain and Sheppard set out to argue that the variations in color and banding in the snails are due to selection and do have "definite selective value." Their method was as follows. They collected all of the *C. nemoralis* shells that they could find in each of 25 different areas in southern England. These areas were categorized into six habitat types, plus a seventh "other" category. The snails were identified as being one of three main color types (yellow, pink, or brown), with pink being further subdivided into fawn, pink, and red, yielding five color types altogether. They were also identified by a banding system that specified which of five bands, if any, were present.[14] However, most of the time Cain and Sheppard classify these as "unbanded," "one band," and "other," even though the data that they collected were more specific. Cain and Sheppard give a detailed analysis of which color types and which band types were most prevalent in each area, which they subsequently summarize as follows:

> There is a definite relationship between the proportions of different varieties in any colony, and the background on which they live. The more uniform the background (e.g., a continuous leaf-carpet, or an expanse of very closely grazed turf) the higher is the number of unbanded shells. Pink, fawn, red and brown shells vary in numbers and exact shade according to the general colour of the background. The proportion of yellow shells increases as the amount of green vegetation at ground level increases. (Cain & Sheppard, 1950)

In other words, Cain and Sheppard are claiming that there are *correlations* between habitat-types and color-types, and between habitat-types and band-types. The more uniform habitats tend to have more unbanded (i.e., more uniform) shells. The predominant shell color in any habitat tends to be similar to the general color of the habitat; in particular, the more green vegetation there is, the greater the proportion of yellow snails. And these correlations, Cain and Sheppard argue, are "good evidence

that the general appearance of any colony is determined by natural selection" (Cain & Sheppard, 1950, p. 292).

They state that a "nonrandom distribution" was also what Diver found, i.e., "particular patterns . . . found only within one . . . community, or in a few close together" (Cain & Sheppard, 1950, p. 291). (Presumably, then, a "random distribution" would be one where types were distributed equally in different populations.) But what is significant about the nonrandom distribution that Cain and Sheppard found are the correlations between habitat and shell type, and "it is exceedingly improbable that if the colonies visited by us were all showing random divergence, all the beechwood colonies, for example, should have reached by chance such a remarkable similarity in stations often so many miles apart, especially while differing from those in other types of locality, which also show great similarities within the same locality-class" (Cain & Sheppard, 1950, p. 287). In other words, such correlations would be exceedingly unlikely to be the result of chance; and "the only other explanation which will account for this correspondence is natural selection acting upon genetic variation" (Cain & Sheppard, 1950, p. 287).

Furthermore, they assert, "an explanation of the correspondence between background and colour-pattern of shell must be found" (Cain & Sheppard, 1950, p. 286). Having ruled out direct action of the environment and drift, they argue that selection by predators must be the reason for the correlations. They found "plentiful evidence of predation by thrushes, grey squirrels, rats, small field rodents, and rabbits," and although "no complete investigation has so far been made into the different intensities and kinds of selection by these animals," "experiments are in progress," even though (citing Fisher) the amount of selection may be undetectable (Cain & Sheppard, 1950, p. 288). And, citing Cott, they state that it is "unnecessary to demonstrate that these predators have colour vision since tone is as important as colour" (Cain & Sheppard, 1950, p. 288). They conclude that the "close correspondence between the general appearance of each colony and its background suggests that predators hunting by sight are the agents of selection" (Cain & Sheppard, 1950, p. 292).

Although they do not state so explicitly, one wonders if this conclusion was not reached in part as a result of their own experience in collecting: "heavily banded shells are more conspicuous than unbanded ones in uniform localities, whereas unbanded ones tend to be conspicuous in hedgerows and similar places" (Cain & Sheppard, 1950, p. 285). However, even if this were true initially, Sheppard subsequently sought to confirm the hypothesis of selection by predator by looking at the changes in frequencies of snails killed over time, as correlated with environmental changes (Sheppard, 1951).

Even though explaining the observed distributions was Cain and Sheppard's primary focus, the fact that *C. nemoralis* exhibits a stable polymorphism must still be explained, and this they attribute to the "physiological advantage of certain gene-combinations" (what they call "physiological selection"). So, there are two types of selection acting on these populations, physiological selection and selection by predators. The physiological selection produces a "balance of different genetic forms in each population," a balance which is then altered by the selective actions of predators. The types that are at a physiological advantage might be different in different climates, yielding a different initial balance, but "one would expect to find the relative proportions in different types of localities to be much as in the district investigated

by us" (Cain & Sheppard, 1950, p. 287). Thus, given the action of these two types of selection, "whatever genetical drift may occur cannot act against natural selection, and is severely limited by it" (Cain & Sheppard, 1950, p. 292). Drift's "relative significance" is insignificant.

They further conclude that in light of their results, overturning Diver's conclusions, as well as other deficiencies in the studies of purported cases of drift, "all such cases of polymorphic species showing apparently random variation should be reinvestigated. No useful conclusions on this matter can be drawn merely from a knowledge of the distribution of varieties without a study of their habitats" (Cain & Sheppard, 1950, p. 292).

I would argue that this last quote, echoing the above-discussed comment that Diver observed the nonrandom *distributions* of types but not the *correlations* of types to habitat, is central to understanding Cain and Sheppard's views of drift and selection. Clearly, knowing the details about different types of habit is the linchpin of their arguments. But again, merely establishing that different habit-types were associated with different color-types and band-types was not sufficient; Cain and Sheppard identified two causal factors within the habitats—what Darden and Cain (1989) call the "critical factor" in the environment (see also Skipper, 1999), i.e., the factor that affects the interaction between individuals and their environment—that could account for the observed distributions, corresponding to the two types of selection that they identified. In the first case, the critical factor is the climate; Cain and Sheppard hypothesize that it is the climate that is responsible for the polymorphism, and that a different climate would produce a different distribution (again, the so-called "physiological selection"). In the second case, the critical factors are the predators, and they are responsible for the distributions of color-types and band-types in the various habitat-types. Of course, the critical factors do not act alone; there is an *interaction* between the organisms and their environment. Thus, in the first case, the climate acts on the "physiological advantage" produced by "certain gene-combinations." And in the second case, the predators act on the relative conspicuousness of some of the snails—because of their color or banding pattern, or both—against the background of their habitats. Thus, the physical traits of the organisms are causal factors in selection as well, a point emphasized by Hodge (1983, 1987) and Millstein (2002, 2005). In short, selection for Cain and Sheppard is not merely a matter of a certain distribution pattern, but crucially involves identifying the causal factors at work.

Therefore, when Cain and Sheppard speak of the varieties[15] having "selective value," that is, that the variations in shell color and banding have "definite selective values, related to the environment, determining the general aspect of different populations and therefore of their gene ratios" (Cain & Sheppard, 1950, p. 275), the claim seems to be that the different shell color and banding patterns confer different survival abilities in a given environment. In other words, certain types of shells may have an "advantage" over other types in a given environment.

This very language (of "advantage") is used in a subsequent paper by Sheppard: "it is possible to say not only that the selective advantage of yellow was changing but also that it was at a disadvantage during most of April, becoming neutral in value some time in late April or early May, and that by the middle of May it was actually an advantage . . . it is certain that the selective value will alter markedly from season to season, year to year, and locality to locality" (Sheppard,

1951, p. 132).[16] Thus, it would appear that to have "no selective value" (which is, apparently, the same thing as being "neutral") means simply that different types are equally suited to their environments. Sheppard was asserting that there were no adaptive differences; he does not seem to be claiming that the types were not adaptive in their environments. Moreover, note that "advantage," or lack of advantage, is conferred at the *phenotypic level* (as opposed to, say, the allelic level. I will return to this point in the conclusion). Thus, it is as a result of the different physical traits of the organisms that selection is occurring—or not, if the differences fail to confer an advantage over one another in the given environment.

Cain and Sheppard's views on drift are less clear, but I think the following can be reasonably inferred. If I am right in thinking that for varieties to have selective value means that the differences confer different abilities to survive in a given environment, then for them to have "no selective value," as is asserted for Diver and the other authors mentioned above, is for the differences to fail to confer different abilities to survive in a given environment. Put another way, certain types fail to have an "advantage" over other types in a given environment; there are no adaptive differences. This reading seems to be supported by the following passage:

> Diver (1940) has claimed that variations in shell colour and banding in the snail *Cepaea nemoralis* (L.) have no selective value, and occur at random in different colonies. He ascribes the differences between colonies to genetical drift. These contentions cannot be sustained. There is a definite relationship between the proportions of different varieties in any colony, and the background on which they live. (Cain & Sheppard, 1950, p. 292)

This quote introduces the idea that the variations "occur at random." It is not entirely clear what that means, or how it relates to the idea of there being "no selective value," but clearly both ideas, and drift itself, stand in contradistinction to the existence of a "definite relationship" between the proportions of varieties in a colony and their habitat.

However, looking at some of their other works muddies the picture a bit—in particular, Cain's reply to Carter (1951). Regarding *Cepaea*, Carter had asserted, "there is no evidence that any of the [banding] arrangements have adaptive value; none of them are cryptic and it is difficult to suggest any other adaptive use that they could serve" (Carter, 1951, p. 262). In response, Cain asserts,

> This is the real basis for every postulate of random variation or (more recently) genetical drift. The investigator finds that he, personally, cannot see any correlations in a given example of variation, and concludes that, therefore, there is [*sic*] none. (Cain, 1951, p. 424)

Cain does acknowledge that "one must agree that some characters have no value in themselves," a concession he immediately weakens by asserting, "those characters or variation patterns that have been described as nonadaptive or random should properly be described as uninvestigated" (Cain, 1951, p. 424). Here, then, we see drift associated with characters that are "nonadaptive"—characters that have "no value in themselves." Rather than concerning the relative advantage of one type over another, these passages suggest that the trait is simply of no use to the organism in the environment.

Rather than simply denying adaptive differences among organisms, these passages imply that there may be cases (associated with drift) where the organisms are *not* adaptive in their environment. (Recall that this does not necessarily mean that the variants are *poorly* adapted to their environments; it might simply mean that the traits in question are neither harmful nor helpful to the organism.) This is, presumably, a stronger and more contentious claim. Thus drift, at least according to Cain (or, at least, on my reading of Cain), is associated with *both* senses of nonadaptiveness.[17]

However, the concept of drift itself receives no further elaboration in Cain and Sheppard (1950) beyond the discussion of the lack of selective value of variants other than, as mentioned previously, to note the conditions that "may" occur "if" it is operative (small breeding communities). Nonetheless, even with this brief treatment confusion arises. Is nonadaptiveness evidence that drift has acted, or that drift will act, or both? A further confusion arises because Cain and Sheppard, as noted above, do not rule out the action of drift entirely. So, what is it that may be operating, if only at extremely insignificant levels? Is it a process that is acting on some *other* variations that have no selective value? Or is it a consequence of small population sizes? Or a consequence of inbreeding and the lack of random mating? There is no way to determine this from the text alone, and so a contemporary reader might easily infer any or all of these. As we will see, Lamotte (1959a) is somewhat clearer in his use of the term drift, but some ambiguities remain even with Lamotte's explanation.

Lamotte (1959a): "Polymorphism of Natural Populations of *Cepaea nemoralis*"

Maxime Lamotte was the product of a very different tradition than that of Cain and Sheppard; instead of having the influences of Fisher and Ford, Lamotte was influenced by his colleague Gustave Malécot and also Sewall Wright. Moreover, in contrast to Cain and Sheppard's association with the Oxford School of Ecological Genetics, Lamotte was a student of Georges Tessier at l'École Normale Supérieure in Paris, an experimental school heavily influenced by Wright (Gayon & Veuille, 2000). Tessier encouraged Lamotte to perform an experimental study of Wright's models during the time when France was occupied by Nazi Germany and laboratories were in disarray, and so Lamotte picked an organism—*Cepaea nemoralis*—that was found in large numbers throughout Europe (Gayon, 1998). In addition, the snails were an ideal case for those either trying to prove or disprove the efficacy of drift; one of the striking properties of the snails was that, both in England and in France, they lived in numerous populations, of varying sizes, with very little migration between populations. These are precisely the conditions required for drift in Wright's shifting balance model. When Lamotte published his first study of *Cepaea* in 1951 (a massive study of over 900 populations or "colonies"), he was unaware of Cain and Sheppard's work (Provine, 1986). However, that condition quickly changed.

Lamotte (1959a) is, in part, written as a response to Cain and Sheppard (1954).[18] The occasion for Lamotte's paper was a Cold Spring Harbor Symposium on quantitative biology, held to celebrate the centenary of Darwin's *Origin of Species*. According to Provine, Lamotte read his paper in French; the published English translation is from Dobzhansky (Provine, 1986, pp. 446–447).

The primary focus of Lamotte's study was also on the single species, *Cepaea nemoralis*. Lamotte gives a detailed analysis on the question of selection, looking at his own data on *C. nemoralis* in France (Cain and Sheppard's data are from Great Britain). For the most part, Lamotte concurs with, and uses, the same methods that Cain and Sheppard did: he looks for correlations between habitat-types and color- and banding-types, and he sought to determine the kind of selection (physiological, or predatory, or both). The following passage summarizes his views on selection in *C. nemoralis*:

> We have attempted to investigate the factors which impinge on populations and their roles in the determination of the differences in the composition of the populations. Some environmental facts are effective in determining the equilibrium levels of the variable genes in the populations. As shown by experimental studies microclimatic conditions are doubtless effective factors determining the genetic equilibrium. Selection by predation is also effective, at least in some cases. However, when one attempts to assess the cumulative action of these factors in the course of time, there always remains some unexplained residual diversity. (Lamotte, 1959a, p. 83)

Lamotte, in effect, acknowledges that both physiological selection and selection by predator occur to some extent, as Cain and Sheppard assert, but not to the extent claimed by Cain and Sheppard.[19] Furthermore, throughout the paper he notes that there is always quite a bit of variation among the populations, even when there is a correlation on average. For example, he states, "Considering populations living in apparently similar environments, one nevertheless finds that their genetic compositions may be quite diverse. Conversely, populations of the same phenotype composition may be found in apparently different biotypes" (Lamotte, 1959a, p. 80).

This is the "unexplained residual diversity" that must be explained. Thus, given that "the genetic composition of a population inhabiting a biotope cannot be predicted with any degree of precision from the known environmental characteristics of their biotope, nor can the characteristics of a biotope be deduced from the characteristics of a population which is found in it," Lamotte seeks to "inquire into the causes of this apparent indeterminacy" (Lamotte, 1959a, p. 80). The next section of the paper, "Variations in the environment," begins with the assertion: "The first cause of the non-uniformity of the genetic constitution of populations is the variation of the environment in the latter" (Lamotte, 1959a, p. 80). The section following is entitled, "The role of random fluctuations."

By "variations in the environment," Lamotte is referring to "recent changes which make the genetic composition of the population of a colony discordant with its environment," where "the amplitude of certain changes is too great to be compatible with the life of *Cepaea*" (Lamotte, 1959a, p. 80). As a result, there may be "rapid large variations in the size of the populations, or even total disappearance" (Lamotte, 1959a, p. 80). Lamotte, citing Fisher, notes that these are the conditions under which one would expect "some random charges [*sic*] of the gene frequencies," producing deviations from the "ideal equilibrium composition" of a population, "as determined by the various factors of the environment" (Lamotte, 1959a, p. 80). Moreover, he asserts: "These fortuitous fluctuations around the levels of equilibria correspond at least in part to random genetic drift as defined by Sewall Wright" (Lamotte, 1959a, p. 80). It is unclear what Lamotte means by "at least in part"; he does not elaborate.

In the same section ("Variations in the environment"), Lamotte also mentions a separate chance phenomenon: "The first stages of the origin of colonies are of considerable importance because of the chance variations in the composition of the first colonizers" (Lamotte, 1959a, p. 80). In discussion, Dobzhansky includes the former phenomenon—fluctuations in gene frequencies in "populations which periodically expanded and contracted to make the effective sizes small"—under the umbrella of "classical genetic drift" (Dobzhansky, 1959, p. 85). (Today, this phenomenon is usually referred to as a "bottleneck" or the "bottleneck effect," and it is often, although not always, considered a form of drift—Millstein [2002]). On the other hand, Dobzhansky asserts that the latter phenomenon, the "founder principle," is "closely related" to classical genetic drift while "different enough to make some distinction useful," although he subsequently refers to "classical drift" and "drift in colonies descended from small numbers of founders" (Dobzhansky, 1959, p. 85). Lamotte, in response, agrees

> that it may be useful to examine as a special aspect of random genetic drift, the so-called "founder principle." But it must be pointed out that this "founder principle" is included in the principle of "effective size" as defined by Sewall Wright. (Lamotte, 1959b, p. 86)

Wright agrees with Lamotte, stating: "From the standpoint of mathematical theory, the founder principle in its random aspect is merely one form of random drift and it happens that it is the form that is most effective in contributing to evolution," and indeed, Wright thought that Lamotte had shown that random drift plays an "important role" in *Cepaea nemoralis*, although he maintained that "the importance of random drift in evolution does not come from cases of this sort in which there is merely local fluctuation about equilibrium for a single pair of alleles" (Wright, 1959, p. 86).[20] Thus, Lamotte considers two causes of the "residual diversity" (that which selection could not account for) to be the founder principle and bottlenecks, both of which can (more or less) be considered kinds of random drift.

In the section entitled "The role of random fluctuations," Lamotte asserts that the problem with trying to determine the role of random fluctuations is that it is far more difficult to provide experimental evidence for them than it is for natural selection: "To do so one would need to demonstrate the absence of factors other than chance" and the necessary conditions to do this are "impossible to realize in practice" (Lamotte, 1959a, p. 81). Instead, he attempts to analyze "the role of a factor which is capable of producing fluctuations, namely the size of the populations" (Lamotte, 1959a, p. 81). In brief, he compares the amount of variance in frequencies in small populations to the amount of variance in frequencies in large populations, for both shell color and banding pattern. He finds that in both cases, the amount of variance is greater for small populations than it is for large populations, exactly what you would expect under the conditions of drift (or, as he usually says, "random fluctuations").[21] Thus, Lamotte concludes that despite the existence of selection in the populations of *C. nemoralis*, drift also plays a significant role. Note that, once again, we see the signs of a relative significance debate. However, whereas for Cain and Sheppard, the goal was to establish selection as the overwhelming cause of the observed variation, Lamotte

seeks only to establish that drift is a *significant* cause, and he seems willing to attribute more of a role to selection than Cain and Sheppard were willing to attribute to drift.

Toward the end of the section, it becomes clear that Lamotte thinks that these results (greater variance in small populations than among large) apply to *three* kinds of drift—the two previously mentioned (founder principle and bottlenecks) and the effect of population structure (small, isolated populations, as with Diver):

> The existence and the amplitude of these fluctuations are imposed by the very structure of the natural populations of the species, which are broken up into islands with limited population sizes, and even more limited effective population sizes. Even if the systematic pressures tending to produce definite equilibria, such as selection coefficients, are strong, effective population sizes of even a few hundred individuals result in considerable fluctuations. These fluctuations will be even greater if one takes into account the variations of the populations sizes [i.e., bottlenecks], and the recent origin of some of the colonies [i.e., founder principle]. The theory underlying these inferences was worked out in the mathematical studies of Sewall Wright and of G. Malécot. (Lamotte, 1959a, pp. 82–83)

Lamotte's essay is less explicit than Cain and Sheppard's about the concepts of selection and drift, but even with the little that Lamotte says, there seems to be a disconnect with respect to his concept of drift, but not his concept of selection, as compared to theirs. With respect to selection, Lamotte does speak of one type having an advantage over another type (Lamotte, 1959a, pp. 75, 76), as Cain and Sheppard do. Furthermore, as noted above, Lamotte agrees with Cain and Sheppard about the way to demonstrate selection; the disagreement lies over whether that is sufficient to determine all of the observed frequencies. Thus for Lamotte, as for Cain and Sheppard, selection is a causal interaction between organisms and their environment.

However, with respect to drift, Lamotte never claims (as Diver did) that the colors or banding patterns were nonadaptive in either of the two senses that we have discussed. In fact, he is acknowledging that in certain cases, these traits do confer an advantage, but again, the issue for Lamotte is that this advantage does not account for all of the variance in the populations. Of course, one might reasonably infer that the random fluctuations that Lamotte proposes are taking the population in nonadaptive directions. But that seems to be a different claim than the claim that the physical traits in question are nonadaptive; it suggests a less-than-optimal distribution of traits that do in fact differ in the advantages that they confer in the given environment. To get to a claim that the existing traits are nonadaptive, one must extrapolate that process further (i.e., drift acting repeatedly over many generations, producing nonadaptive variation), an extrapolation that Lamotte does not make (or does not make explicitly).

As discussed above, Lamotte seems to think there are at least three sources of "random fluctuations": (a) fluctuations that "are related to the isolation of the colonies and to their limited population size"; (b) "chance variations in the composition of the first colonizers," which, as we saw above, Lamotte asserts is also related to effective population size (this is the founder principle), and (c) "variations in population size" (these are bottlenecks). All three, it should be noted, are related to small population size. So, then, did Lamotte consider small population size to be the ultimate cause of the observed diversity? Perhaps so. He did speak of it as a "factor that is capable of producing fluctuations" (Lamotte, 1959a, p. 81).

And yet, if it is a cause, small population size is an odd sort of cause. Or, at least, it is not a cause that acts alone. A silly example will illustrate this point: a small population of jellybeans will not change in frequency, let alone fluctuate in frequency over time. So, what is it that allows population size to affect fluctuations and frequency? The answer, unfortunately, is not to be had directly within Lamotte's essay (1959a) itself, but there is an answer within Wright's work, which Lamotte cites (see quotes above): random sampling. Three papers of Wright's are included in the references: 1931, 1937, and 1948.

Looking at these three papers in turn, Wright's 1931 paper speaks of a population's size as a "factor of the greatest importance in understanding the evolution of a Mendelian system," but in giving an example of its importance, Wright asserts that the change in the population is "merely as a result of random sampling among the gametes" (Wright, 1931, p. 106). In his 1937 paper, Wright asserts: "If the population is not indefinitely large, random changes occur in gene frequencies merely as a result of the accidents of sampling among the gametes" (Wright, 1937, p. 310). And in 1948, Wright compares "the amount of random drifting of gene frequency expected in small populations merely from accidents of sampling and that expected in large ones from variations in degree and direction of selection or in amount and character of immigration" (Wright, 1948, p. 279). What these three quotes show is that, *given* "random" or "accidental" sampling, small population size is expected to produce fluctuations in gene frequencies. Small population size does not act alone. To use the case of gamete sampling, which Wright adverts to, many of the gametes that are produced are not joined in zygotes, and so those that *are* joined are a "sample" of the whole—and if they are a small sample, they may not be a representative sample, just as a small sample from my jellybean jar may not be representative (see Beatty, 1984 for further discussion). Although I cannot state definitively that Lamotte meant to attribute the observed diversity to random sampling—whether of gametes, as in the case of small isolated populations, or of organisms, as in the case of bottlenecks and the founder principle—it is possible that he simply assumed that this would be understood by his audience (and given the background of the audience at the Cold Spring Harbor Symposium, that would have been a reasonable assumption).

However, even if I am right that Lamotte did mean to attribute his results to random sampling, a terminological question remains; namely, what is Lamotte's conception of "drift"? Is "drift" (a) random sampling, (b) random sampling when the population size is small, (c) the change in *one* generation as a result of random sampling in a small populations, (d) the *fluctuations* in gene frequency from one generation to the next that result from random sampling in small populations, (e) the observed diversity in a small population, or (f) the pattern that we expect when we compare small populations to large: greater deviations among the smaller populations than among the large? Lamotte may have meant several of these, or all. It is simply not clear which is meant, and the fact that his 1959a paper is Dobzhansky's translation from the French does not help. His 1952 paper, which equates "dérive génétique" (genetic drift) with "fluctuations fortuite" (fortuitous fluctuations) (Lamotte, 1952, p. 341), suggests that it is the fourth of these possibilities. Even then, the term still encompasses random sampling, else why would the fluctuations be fortuitous? Moreover, it is odd to speak of *fluctuations* as having produced genetic diversity at a given point in time; the gene frequencies at any point in time are more properly a function

of the gene frequency of the preceding generation together with whatever processes are operating in the population (thus, drift is often characterized as a Markov process); this suggests the third possibility. And if Lamotte's goal really was to answer the question, "what factors are responsible for this diversity [i.e., the 'diversity in the distribution of the various local populations']?" then the factors at work are more properly random sampling (the first or second possibility). And if all one is concerned about is "random fluctuations," then why differentiate between the different causes of random fluctuation (gamete sampling, founder principle, and bottlenecks)? In short, it is unclear as to how to answer the question of what "drift" is for Lamotte, particularly if drift is supposed to be providing an alternative means through which genetic diversity can be produced. However, the issue of sampling will arise again in Cain and Currey (1963).

Cain and Currey (1963): "Area Effects in *Cepaea*"

Cain and Currey's 1963 essay represents a large shift in thinking from Cain and Sheppard's papers from 1950 and 1954, both in their approach to selection and in their approach to drift (not to mention their conclusions), as the following discussion shows.

One of the points of contention between Cain and Sheppard on the one hand and Lamotte on the other hand was a methodological one: should the habitats chosen for study be heterogeneous or homogenous? Lamotte asserted: "Contrary to Cain and Sheppard, who have studied for preference colonies living in well defined biotopes, we have done our best to study the populations in all possible environments. But in France, *C. nemoralis* are living in heterogeneous biotopes" (Lamotte, 1959a, pp. 70–72). Whether in response to this or not, Cain and Currey state,

> The present investigations were begun in order to sample colonies close to Sharpridge 2 which was discovered [by Currey] in 1958 and recognized as having remarkably few genotypes; it was desired to know how close were the nearest occurrences of the genotypes that might be expected. It quickly became apparent that gene frequencies on the whole scarpland nearby were highly abnormal compared with previously recorded English colonies, and several collecting trips were made to find colonies over the whole district. Subsequently, special visits have been made to ensure a fairly uniform coverage, and to obtain as many samples as possible from the rarer habitats, such as mixed deciduous woods. (Cain & Currey, 1963, p. 3)

These anomalous populations presented Cain and Currey with a problem: the usual correlations between habitat-type and color- and banding-type either were not observed in many of the colonies, or were greater or less than expected. In particular, they found that for a number of the colonies, one type was predominant—and not the type that would be expected based on the habitat. Thus, they could no longer invoke visual selection by a predator, at least to the same extent as Cain and Sheppard did previously. How to explain these anomalies? Cain and Currey invoke the idea of *area effects*: "Such phenomena as these just described, in which, throughout an area large compared with the area occupied by a panmictic population of *Cepaea*, one color or banding variety is predominant, or at an unusually high frequency throughout

without regard to habitat, we refer to as *area effects* (Cain & Currey, 1963, p. 14). Throughout much of the paper it is difficult to determine exactly what an "area effect" is. The text often reads as though an area effect is any effect that cannot be explained by visual selection, and exactly how the area is producing the effect is not specified. For example,

> Moreover, at least in the non-five-banded area woodlands do tend to have less yellows than do other habitats [as would be expected from visual predation]. But some of them, at least, have few yellows because that is characteristic of their area. The area effects cannot therefore be explained by visual selection. (Cain & Currey, 1963, pp. 17–18)

A second example is no more clear: "the discovery of excess browns at Overton Down 2, Fyfield Down 2 and Clatford Down 5 made it clear that there was a strong area effect producing an excess of browns, and the low proportions of yellows in the beechwood and mixed deciduous wood (Wroughton Copse) were typical of the area, and need not be of their habitats" (Cain & Currey, 1963, p. 24).

At one point, Cain and Currey refer to the "fortuitous result of area effects," (Cain & Currey, 1963, p. 22), which sounds like a form of drift. But they make it very clear that whatever area effects are, they are not drift. In a section entitled "Probable causes of the area effects," Cain and Currey rule out visual selection, for reasons I have described above. However, if drift were operating "one would expect to find not whole areas sharply characterized by absence or excess of particular phenotypes, but a random scatter of colonies with an excess interspersed with others with a deficiency" (Cain & Currey, 1963, p. 39). Furthermore, based on the testimony of Dr. E. L. Jones (whose statement is included in the paper), Cain and Currey conclude, "there is no reason to believe that in the last few hundred years there has been a catastrophe sufficient to destroy the *C. nemoralis* populations on the Marlborough Downs on such a scale as to leave only a few widely separated and tiny groups, in which sampling drift could occur" (Cain & Currey, 1963, p. 39). Competitive exclusion by *C. hortensis*, is, they argue, unlikely. With these alternatives ruled out, they conclude, "the most likely hypothesis is that the area effects are produced largely by selection, and have been stable over a very long period" (Cain & Currey, 1963, p. 40). With the qualification that "it is usually much easier to show that selection of some sort is acting in the wild than to identify the agent responsible for it, still less the details of its action" (Cain & Currey, 1963, p. 40), Cain and Currey offer the explanation that very localized variations in climate—"over distances of sometimes only a few yards because of local topographical features"—are the probable cause of the distributions (Cain & Currey, 1963, p. 42). These variations in climate can, Cain and Currey assert, account for the distributions of *C. nemoralis* as compared to *C. hortensis*, as well as the distributions of browns in *C. nemoralis*. They offer various hypotheses for banding, but do not commit to any of them.

One might think that this willingness to assert selection without a full understanding of the environmental factors and other relevant causal factors represents a shift in thinking from Cain and Sheppard (1950, 1953) to Cain and Currey (1963). However, Cain and Currey begin the paper with this proclamation:

It is impossible to determine the relative importance of natural selection, genetic drift . . . and the founder effect in producing differences between populations in the wild, merely by inspecting the variation in proportions of given genotypes in different colonies and the differences in the size of the colonies. This may well be sufficient in the laboratory, if the environment can be considered identical for all populations; but this is probably never so in the wild, and can certainly never be safely assumed. Features of the environment that may affect gene frequencies must also be examined. (Cain & Currey, 1963, p. 3)

Thus, it seems as though the commitment to the importance of the "causal crux" (Skipper, 1999) of selection has not changed; what has changed, therefore, is the confidence in our ability to determine it. Of course, there has also been a change in what is considered the relative importance of selection by predation versus physiological selection in *C. nemoralis*. What most assuredly has *not* changed is the commitment to providing explanations in terms of selection rather than drift. (They assert: "Even when some selective forces have been demonstrated and their strength determined and effects estimated, it is rash to assume that the residual genetic variation can only be due to random effects. In the wild it is far more likely that all the selective influences have not been identified" [Cain & Currey, 1963, p. 61].) And, to the extent that they still invoke visual selection by predator as an explanation for distributions in *C. nemoralis*, they still speak in terms of the relative advantages and disadvantages of different types in a given environment.

The most radical shifts in thinking can be seen in the discussions of drift. The emphasis on drift as invoking nonadaptive explanations (in either sense) is almost entirely gone.[22] This is striking, given Cain and Sheppard's extensive focus on these concepts. Instead, what has caught Cain and Currey's attention is what they see as a shift in the way that Sewall Wright characterizes random drift (or "genetic drift"). In his earlier work, they assert, he gave the impression that random drift was the result of "accidents of sampling" in small populations. However, Cain and Currey note, correctly, that in his later papers Wright claims that phenomena such as fluctuations in mutation rate, fluctuations in migration, and fluctuations in selection should be considered random drift. Cain and Currey object to this because "whatever may be the conveniences for mathematical geneticists of considering together all processes regarded as random, irrespective of their biological significance, the worker on actual examples must classify processes according to their biological significance" (Cain & Currey, 1963, p. 59). Furthermore, they assert, "in practice the lumping of 'random' processes prevents the proper analysis of actual situations. . . . Such confusions can only lead to erroneous general conclusions about the relative importance of selection, sampling error, mutation and other factors" (Cain & Currey, 1963, p. 59). Because "sampling error is biologically a very different phenomenon from selection, and as Wright has declared that 'genetic drift' must have a wider connotation, we propose to refer to the effects of sampling error as *sampling drift*" (Cain & Currey, 1963, p. 59). (Wright appears to have agreed, at least in part; for example, he uses the term in his 1978 magnum opus, *Evolution and the Genetics of Populations*.)

Thus, Cain and Currey once again emphasize the importance of understanding the biological processes and causal factors at work, deemphasizing the merely statistical. What is odd about their way of describing drift, however, is that sampling drift is characterized as an effect. Yet it is precisely the point that the *effects* of random

sampling cannot be distinguished from fluctuations in selection; this is what enables them to be treated together mathematically. So, Cain and Currey's proposal really amounts to highlighting the importance of distinguishing between selection and random sampling.

Having clarified the use of the term drift, Cain and Currey proceed to argue that Lamotte (1959a) has not succeeded in making the case for sampling drift. The problem with his arguments, according to Cain and Currey, is

> the comparison that Lamotte makes between variances in large and small colonies is carried out absolutely irrespective of the circumstances of these colonies. He says himself . . . that "the large populations are more often found in well-defined biotopes, such as woods or large meadows. The small colonies are more often in intermediate environments such as hedges and gardens." But hedges and gardens are more likely to be disturbed than large woods or meadows, and it is quite possible that what Lamotte has shown is merely that in disturbed habitats populations tend to be small, and not at all that smallness of the populations is the factor allowing random effects to produce greater variance. A mere comparison of the genetic variance of populations of different sizes irrespective of their circumstances is valueless for determining the relative roles of sampling drift and selection of any type. With respect to visual selection, this had been already pointed out by Cain & Sheppard. (Cain & Currey, 1963, p. 60)

Once again, the environment must be attended to; statistics alone cannot determine the biological factors at work in the population. Of course, as we saw above, Lamotte also thought that it was important to attend the interactions between organisms and their environments; he did not take a "statistics alone" approach. So, where the two camps differ is over how finely the environment must be drawn. Lamotte delineated habitats broadly; he let the geographical distribution of the different populations determine where to draw the boundaries. When the selective interactions based on those environmental delineations were not sufficient to account for the observed distributions, Lamotte turned to statistical analysis. Cain and Currey, on the other hand, thought that biologists must attend to much smaller-grained variations within habitats—as small-grained as a few yards, as mentioned in a previous quote. Their assertion, then, was that a microhabitat analysis was required.

Instead of using a statistical analysis, sampling drift could be demonstrated in wild populations,

> if the history of several adjacent colonies was followed over a period of years and it could be shown that the gene frequency in one of them, but not the others (which act as the controls), had altered as the result of nonselective events. These could be, for example, repeated local burnings or ploughing-up which are certainly not related to the composition of the colony and are observed to leave each time survivors that form unrepresentative genetic samples of the colony as it was just before each event. If the resulting changes happened to be cumulative there would be no reason for thinking of them as being other than sampling drift. (Cain & Currey, 1963, p. 62)

This passage is revealing, and not only because it seems to demand more of the proponent of sampling drift than it does the proponent of selection. For one, sampling drift is still characterized as "nonselective," hearkening back to Cain and Sheppard's

earlier concerns. Second, and relatedly, the sampling (as a result of repeated local burnings or "ploughing-up") is *not related to the composition of the colony*—an implication that the sampling is indiscriminate. This supports my claim above that, for Cain and Currey, drift is a matter of indiscriminate sampling, in spite of their references to it as an "effect."

Conclusion

The "Great Snail Debate" of the 1950s and early 1960s was both subtle and messy—subtle, because it was not an "either-or" debate of drift versus selection, and messy, because different interpretations of key concepts were in play. With regard to the former, as I suggest above, the debate is best viewed as an example of what Beatty (1984, 1997) has called a relative significance debate. Those who were in what has often been called the "selectionist" camp in fact took the position that drift does occur, but that its role is insignificant as compared to that of selection. (Here "role" should be understood as "effect" or "outcome"; in other words, the claim is that drift, although occurring, contributed very little to the distributions of *Cepaea nemoralis.*) Similarly, the so-called "neutralist" camp did not deny that selection occurred, and in fact, Lamotte ascribed a fairly large role to selection. (This term is a particularly misleading one for Lamotte since, as discussed above, he did not explicitly claim that the colors and bandings of the snails were nonadaptive.) However, he thought that drift must also be ascribed a significant role, not only because selection could not fully account for the observed distributions, but also because the distinctive pattern where there was greater variance among smaller populations than among large could only be produced by drift. Thus, the two camps did indeed differ over the relative roles of selection and drift, a fact that the labels "selectionist" and "neutralist"—if not carefully spelled out—can obscure. (I will use these labels for the sake of convenience, but the reader should be certain to infer the more nuanced meanings that I have described here.)

The debate was also messy; disputants were forced to turn philosophical and define their terms. The messiness is encountered in at least three areas:

1. Is drift associated with nonadaptiveness? Is the denial that a particular variant is adaptive a denial that the variant is adaptive in its environment (that is, a denial that the character in question benefits or harms the individual in its environment), or simply a denial that the differences among variants confer any advantage or disadvantage?
2. Can disputes concerning selection and drift be settled by statistics alone, or is causal information essential?
3. What is meant by drift—is it purely mathematical or is it a phenomenon in nature? If it is a phenomenon, what kind of phenomenon—or rather, phenomena—does it encompass? Does the term refer to a process or the outcome of a process?

These three areas are still under lively philosophical debate today, but perhaps we can learn something from the early attempts to address them. (Other conceptual debates are revealed here—for example, the question of whether the selective environment is "fine-grained" or "coarse-grained," which is also a topic that has engaged philosophers in the present day—but I will focus on these three.)

With regard to the first area, early accounts did indeed associate drift with nonadaptiveness—in fact, refuting nonadaptiveness seemed to be one of the primary motivations of the selectionist camp—and yet, as I have emphasized throughout this chapter, the definition of adaptiveness that was at stake was not always clear. Indeed, the two meanings of the term persist in today's debates concerning the neutral theory of molecular evolution. When authors refer to a "neutral" molecular substitution, in some cases they are referring to substitutions that are functionless (witness the discussions of "junk" DNA). Thus, the substitution is neither harmful nor beneficial to the organism in its environment. In other cases, they mean simply to deny that the substitution makes an adaptive difference; the claim is that the same protein, or an equivalent protein, is produced. In still other cases (in many cases), it is not clear which of these two meanings is meant (see Dietrich & Millstein, forthcoming, for discussion). And yet, it is hard not to think that much of the vehemence of these debates (both past and present) has to do with concerns over nonadaptiveness. Many people seem to be discomfited by the idea of nonadaptiveness, whether because it seems to be an abdication of our responsibility to explain the world or for some other (psychological, religious, cultural?) reason. Thus, it is all the more surprising that nonadaptiveness plays less of a role—or, at least, less of an *explicit* role—in the later discussions of drift in the period under examination.

The proper role of statistics in determining the relative effects of drift and selection plays a large role in this debate. However, even though the two camps disagreed on this issue, there is agreement on the necessity of determining the causal factors at play. More specifically, both camps sought to determine the critical factors in the environment that determined which variant properties of the organisms were relevant to surviving and reproducing (to use the apt terminology of Darden & J. Cain, 1989). Simple correlations were not sufficient; specific selection mechanisms, such as selection by predator or climatic selection, that identified the causal factors at work had to be proposed (ideally, with evidence). Causality was at the heart of this debate, and at the heart of the concept of selection as understood by the disputants. By considering a case where biologists were trying to apply the abstract models of population genetics to populations in nature, the causal nature of selection is highlighted. In contrast, examination of the models alone has a tendency to obscure this causal aspect, leading to the misapprehension that selection is purely statistical (Matthen & Ariew, 2002; Walsh, Lewens, & Ariew, 2002). Such accounts would have difficulty making sense of much of what was under debate in this historical episode; the accounts of Bouchard and Rosenberg (2004) and Millstein (2006) are more amenable.

Similarly, the concept of drift, although clearly in flux during this time period, emerges as more than a merely mathematical concept (Hodge, 1987 emphasizes the point that drift is not merely mathematical). Many present-day accounts would have us think of drift as a purely mathematical side effect of finite population size; if we think of natural selection as the achievement of fitness expectations, then any deviation from expectations (which would be expected mathematically if the population size is finite) is called drift. Such accounts have forgotten the *biological phenomena* that the concept of drift was originally intended to cover. The neutralist camp sought to distinguish among three different biological phenomena, all of which, after some discussion among the participants in the 1959 Cold Spring Harbor Symposium on Quantitative Biology, were seen to come under the umbrella of drift: the indiscriminate sampling of gametes that occurs in every generation (since far more gametes are produced than organisms), the sampling that

can occur as a population passes through a "bottleneck," and the sampling that occurs as a subset of a population becomes founders of a new population. On the other hand, when Wright tried to extend the concept of drift to cover more than sampling—to cover phenomena such as fluctuating selection, which can mimic the effects of drift—it was the selectionist camp who objected, arguing that "the worker on actual examples must classify processes according to their biological significance." Such lumping would lead to erroneous conclusions about the relative roles of the different causal factors acting on a population (Cain & Currey, 1963, p. 59)—the very heart of this debate. This exchange highlights not only the importance of attending to the biological phenomena, which the concept of drift is intended to cover, but also the importance of distinguishing between process and outcome in discussions of drift and selection (Millstein, 2002, 2005), since the outcomes of fluctuating processes and drift can be the same.

Although this examination of the Great Snail Debate cannot completely settle our present-day philosophical debates over the concepts of drift and selection, it can certainly help us locate the roots of our disagreements, and, in some instances, point us in directions of resolution.

Acknowledgments

Notes

1. Authors refer variously to "drift," "genetic drift," "random drift," and "random genetic drift"; these terms are interchangeable.
2. Note that the question of how to distinguish the *concepts* of drift and selection is different from the question of how one determines *empirically* whether a given population is undergoing drift or selection. Here I discuss only the former question; see Millstein (2008) for discussion of the latter.
3. Lamotte's studies of drift in natural populations were preceded by at least two others in the 1940s: Wright's study of *Linanthus parryae* (desert snow) and Wright's study of *Panaxia dominula* (scarlet tiger moth). However, subpopulations of *Linanthus parryae* are continuous, rather than discrete as are the subpopulations of *Cepaea nemoralis*, and so it is harder to make a strong case for drift, and Wright's analysis of *Panaxia dominula* is more of a response to Fisher and Ford than it is an attempt to provide positive evidence for drift.
4. According to Provine, Diver did not incorporate drift into his thinking until Huxley sent Wright's manuscript (the one that would appear in *The New Systematics*) to Diver in 1938 (Provine, 1986, p. 483). Thus, since this is the first essay where Diver invokes drift, and since it is the essay that Cain and Sheppard are primarily responding to, I begin with Diver's 1940 essay rather than his earlier works.
5. I will follow Diver in not describing these as *partially* isolated subpopulations. Wright later complained when Fisher and Ford left out the word "partially" in describing Wright's views on drift (Wright, 1948, p. 280).
6. See Turner (1987) for a discussion of other possible ambiguities relating to the term "adaptive."
7. Cain and Sheppard also bemoan the lack of access to Diver's data: "It is regrettable that most of the evidence from which widely quoted conclusions on this species were originally drawn remains unpublished and therefore inaccessible to zoologists in general" (1950, p. 291).

8. According to Provine, Diver did not incorporate drift into his thinking until Huxley sent Wright's manuscript (the one that would appear in *The New Systematics*) to Diver in 1938 (Provine, 1986, p. 483).

9. And yet they present a number of objections to Elton's theory "of the multiplication of non-adaptive mutations," a theory they refer to as "chance survival," concluding that it may account for "some measure of local diversification within a species" but that it does not "[account] for the main evolutionary tendencies" (Robson & Richards, 1936, pp. 318–323).

10. Although there is no explicit mention of Wright in this quote, Wright's views are discussed extensively earlier in the chapter.

11. Contrast Mayr's 1942 claim that there is no reason to believe that the presence or absence of a band on a snail shell would be a noticeable advantage or disadvantage with his later assertion that only after all attempts to explain biological processes through natural selection have failed is a biologist "justified in designating the unexplained residue tentatively as a product of chance" (Mayr, 1942, p. 326). This change in Mayr's views in an adaptationist direction is perhaps an example of what Gould calls the "hardening of the synthesis" (Gould, 1983).

12. It is hard for the present-day reader not to hear precursors of the neutral and nearly-neutral theories here. Whether these ideas are indeed historically related is, however, a topic for another paper.

13. After all, directional selection in a population would seem to lead to the prevalence, and ultimately, the omnipresence, of the most advantageous type. How, then, to explain the fact that many populations consist of multiple forms and persist in that state for many generations?

14. Cain and Sheppard state that work needs to be done on the genetics of *Cepaea*, but it appears they are dealing with two sets of genes (one controlling color and one controlling banding), with linkages of "varying degrees of closeness." They assert that the shell pattern having one band in the center position seems to be distinct from the other patterns (Cain & Sheppard, 1950, p. 287).

15. This is the term that Cain and Sheppard used to describe the differently colored and banded snails; the reader should not infer the contemporary technical meaning of the term.

16. Sheppard is able to support his claim here by noting, "Changes in selective values have been demonstrated in a high proportion of recent investigations into natural selection" (1951, p. 133), with citations to Ford and Dobzhansky, among others.

17. Interestingly, the distinction between the two types of nonadaptiveness (nonadaptive differences and nonadaptiveness to an environment) is implied by Cain and Sheppard in another context—discussing whether polymorphism is itself adaptive. They state, "Because yellow shells are at a disadvantage to others in beechwoods, it does not in the least follow that an entirely yellow population could not persist in a beechwood (in the absence of pinks)" (Cain & Sheppard, 1954, p. 114). That is, just because yellow snails are at a disadvantage to pink snails in an environment of beechwoods, does not mean that yellow is not adapted to that environment. It is also interesting to note that nonadaptive differences have an implicit role to play in Cain and Sheppard's account; even though Cain and Sheppard collected data that identified the number of bands for each snail shell, they usually grouped these as "unbanded," "one band," and "other." This seems to be an implicit acknowledgment that there were few or no adaptive differences between, say, two bands and three bands. Whether they would have been willing to concede that these variants were undergoing drift with respect to one another is a different matter entirely.

18. Note that there is a mistake in the references; Cain and Sheppard (1950) is included in the references but not cited in Lamotte's paper, whereas Cain and Sheppard (1954) is not included in the references but is cited in the paper. The conclusions of Cain and Sheppard's 1954 paper are essentially the same as their 1950 paper; they provide additional data in support of their claims and argue against Lamotte (1951) and other works published in the intervening years. However, one difference between the 1950 paper and the 1954 paper is the relative lack of emphasis on the issue of nonadaptiveness in the latter; presumably, this shift in strategy was in response to Lamotte's own lack of emphasis on the issue. In fact, Lamotte's work is spoken

of in very positive terms; Lamotte's paper is "the most important single paper on *Cepaea* that has yet appeared," his work on "population-size, panmictic units, homogamy, and migration is the best yet produced," he has quantitatively applied Wright's equations to an actual population, and his study of over 800 French colonies is "careful" (Cain & Sheppard, 1954, p. 106). Of course, in spite of their stated respect for his work, their own conclusions were "diametrically opposed" (Cain & Sheppard, 1954, p. 106).

19. This seems to be a shift from his earlier position, which was that (with regard to banding, the primary focus of this earlier study) "on the whole, the selection which can be attributed to predators is exceedingly small" (Lamotte, 1951, p. 234).

20. This lukewarm support represents a change of position for Wright; in an essay published in 1951, Wright had endorsed Cain and Sheppard's conclusions concerning *Cepaea nemoralis.* By the time the fourth volume of *Evolution and the Genetics of Populations* was published in 1978, Wright seems to have warmed up to the idea again; he was using *Cepaea nemoralis* as one of two primary examples of conspicuous polymorphism—the other being *Linanthus parryae*, which he had studied himself—and was attributing a large, although not exclusive, role to "sampling drift" in *Cepaea.*

21. Cavalli-Sforza (1969) uses a similar method to demonstrate drift in human blood groups.

22. Nonadaptiveness is mentioned only once, in the discussion portion of the paper, where the implication seems to be that the issue is of historical interest. With the phrase, "on the other hand," the discussion turns to Lamotte (Cain & Currey, 1963, p. 59). This would appear to be Cain and Currey's recognition that Lamotte (1959a) does not use nonadaptiveness as the basis for his claims concerning drift.

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