Distinguishing Drift and Selection Empirically:
"The Great Snail Debate" of the 1950s

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Abstract: Biologists and philosophers have been extremely pessimistic about the possibility of demonstrating random drift in nature, particularly when it comes to distinguishing random drift from natural selection. However, examination of a historical case - Maxime Lamotte's study of natural populations of the land snail, *Cepaea nemoralis* in the 1950s - shows that while some pessimism is warranted, it has been overstated. Indeed, by describing a unique signature for drift and showing that this signature obtained in the populations under study, Lamotte was able to make a good case for a significant role for drift. It may be difficult to disentangle the causes of drift and selection acting in a population, but it is not (always) impossible.

Pessimistic Introduction

The process known as "random drift"[1] is often considered to be one of the most important chance elements in evolution. Yet, over the years, biologists and philosophers have expressed pessimism about the possibility of demonstrating random drift in nature. The following is just a sampling.

In 1951, Arthur Cain argued:

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[1] Authors refer to this phenomenon variously as "random drift," "genetic drift," "random genetic drift," or simply "drift," without any apparent shift in meaning.

"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 [are] none."[2]

Cain elaborated on his views concerning drift in a second paper, published in the same year:

"...it is doubtful whether any example of variation in Nature can be so completely analysed that, after selective effects have been estimated, the residual variation can be ascribed with confidence to genetic drift. There is always the possibility, indeed the likelihood, that the analysis of selective effects was not complete."[3]

In 1983, Ernst Mayr declared:

"When one attempts to determine for a given trait whether it is the result of natural selection or of chance (the incidental byproduct of stochastic processes), one is faced by an epistemological dilemma. Almost any change in the course of evolution might have resulted by chance. Can one ever prove this? Probably never. By contrast, can one deduce the probability of causation by selection? Yes, by showing that possession of the respective feature would be favored by selection. It is this consideration which determines the approach of the evolutionist. He must first attempt to explain biological

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[2] Cain, 1951a, p. 424.
[3] Cain, 1951b, p. 1049.

phenomena and processes as the product of natural selection. Only after all attempts to

do so have failed, is he justified in designating the unexplained residue tentatively as a

product of chance."[4]

Recently, historian of biology and Sewall Wright biographer William Provine asserted:

"I think that Wright's concept of random drift is hopeless both in theory and in the

experimental basis provided in the mid-1950s, and I have offered a prize (a pristine copy

of Wright's famous paper, "Evolution in Mendelian Populations") to anyone who can

furnish proof of random genetic drift in a natural or experimental population."[5]

I, too, have been guilty of some degree of pessimism:

"...as a conceptual matter, natural selection and random drift are distinct, but... as an

empirical matter, their outcomes are difficult to distinguish."[6]

Inferring from these quotes, we can see that demonstrations of random drift in nature have been

said to be one or more of the following: 1) difficult, 2) questionable – the investigator is most

likely ignorant of the real selective story, 3) nonexistent – e.g., Provine's claim that random drift

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[4] Mayr, 1983, p. 326.
[5] Provine, 2001, p. 201.

has never been demonstrated, or 4) impossible in principle – it has been suggested that positive evidence can be given for selection, but not for drift (drift is only what is concluded when selection is not found).

Is this pessimism warranted? Is it true that in natural populations, we cannot provide positive evidence for drift at the phenotypic level?[7] One obvious way to begin to answer these questions is to take a closer look at a purported demonstration of drift in nature, with an emphasis on the methods of study and analysis used, and here, I will do just that. My focus will be on Maxime Lamotte's study of natural populations of the land snail *Cepaea nemoralis* in the 1950s. His snail work is among the best, if not the best, of the early attempts to demonstrate drift and selection in natural populations. 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, the subpopulations of *Linanthus parryae* were continuous, rather than discrete as were the subpopulations of *Cepaea nemoralis*, and so it was harder to make a strong case for drift. Furthermore, Wright's analysis of *Panaxia dominula* was more of a response to Fisher and Ford than it was an attempt to provide positive evidence for drift, as Lamotte's was.[8] And yet, it is not uncommon for authors to cite only the selectionist studies of *Cepaea nemoralis*, failing to cite Lamotte altogether or

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[6] Millstein, 2002, p. 47. Although the quoted paper was focused on the question of how to distinguish natural selection from random drift conceptually, the present paper addresses the possibility of distinguishing them empirically.

[7] Here, I specify "phenotypic level" to contrast with studies of drift at the molecular level. For a discussion of the ways in which claims for drift at the molecular level have been substantiated, see Dietrich, forthcoming, and Dietrich and Millstein, forthcoming.

[8] Also, in addition to the study of drift in natural populations in the 1950s, there was experimental work on drift during the same decade; see, e.g., Merrell, 1953; Kerr and Wright, 1954ab; Wright and Kerr, 1954; Dobzhansky and Pavlovsky, 1957. The present paper is focused on studies of natural populations.

citing only his earliest work.[9] Although one case study cannot be definitive, my claim is that it

is suggestive: suggestive that the pessimism concerning random drift has been overstated.

Origins of the 1950s debate over the land snail, *Cepaea nemoralis*

In discussing Lamotte's study of *Cepaea nemoralis*, it is important to recognize that he

represented one of two camps who were studying this common land snail in the 1950s. The

other camp was represented by Arthur Cain and Philip Sheppard. The debate between these two

camps, dubbed "The Great Snail Debate" by William Provine, is perhaps less well known than

the (sometimes acrimonious) debate between Sewall Wright and Ronald A. Fisher.[10] Although

there are some connections between the two debates, they are not the same; the studies I will

discuss in this essay are focused almost exclusively on the question of which evolutionary

processes were operating in the populations of *Cepaea nemoralis*, rather than (for example) more

general questions about the shifting balance model or the mass selection model. In a paper

published in 1950, Cain and Sheppard argued that the snails were undergoing selection, which,

they maintained, limited the role for drift. The next year, unaware of Cain and Sheppard's

work,[11] Maxime Lamotte published *his* first snail study, coming to the opposite conclusion;

Lamotte concluded that even though selection *did* act on the snails, as did the processes of

mutation and migration, drift played a significant role.

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[9] Dawkins, 1999 is an example of the former; Davison and Clarke, 2000 are an example of the latter. However, I do not wish to give the impression that Lamotte's later work is never cited by biologists; rather, the general pattern seems to be that his role is downplayed by selectionists and highlighted by those arguing for a substantial role for drift.

[10] For discussion of these debates, see Provine, 1985, 1986; Skipper, 2002, forthcoming a.

[11] Provine, 1986.

These two conclusions were the product of two very different schools of thought. Speaking very broadly, Cain and Sheppard were influenced by the selectionists R. A. Fisher and E. B. Ford; in fact, Sheppard was Ford's student. Furthermore, Cain and Sheppard were at Oxford University at the same time and are both considered to have been part of the "Oxford School of Ecological Genetics" founded by Ford. However, it should be noted that Cain considers 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.[12] And as John Turner has argued, Fisher himself had a close (if complex) relationship with the Oxford School.[13] The complexity would suggest that Cain and Sheppard are more in Ford's tradition than in Fisher's, since the Oxford school approach did not completely vindicate the Fisherian approach. Lamotte, on the other hand, was a student of Georges Teissier at l'École Normale Supérieure in Paris, an experimental school heavily influenced by the work of Sewall Wright.[14] (Wright is considered one of the founders of population genetics, and he did much to articulate the mathematical consequences of drift). Lamotte was also influenced by his colleague, Gustave Malécot, a French mathematician who is perhaps best known for his extensions to Wright's population genetics models. So, even though the debate over *Cepaea nemoralis* was not the same as "Fisher-Wright" debate, it was, in a broad sense, influenced by that debate.

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[12] Provine, 1986.

[13] Turner, 1987.

[14] Gayon, 1998; Gayon and Veuille, 2000

But why would groups from these two different traditions both want to study *Cepaea nemoralis*?

First, *Cepaea nemoralis* is highly polymorphic (the snails show obvious differences – in other words, they manifest a "conspicuous polymorphism" – both in color and in the number of bands) and polymorphism had long been of evolutionary interest. After all, directional selection in a population would seem to lead to the prevalence, and ultimately, the omnipresence, of the most advantageous type. However, fossil records indicated that the species had been polymorphic since at least the Pleistocene. How, then, to explain the fact that the *Cepaea nemoralis* populations consisted of multiple forms and had persisted in that state for many generations?

However, explaining the maintenance of polymorphism was not the primary reason that these individuals were interested in studying *Cepaea*. 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."[15]

And yet, as Cain and Sheppard noted later in their published works, the variations in *Cepaea nemoralis* had often been cited as the primary example of *nonadaptive* variations. Cain and

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[15] Quoted in Provine, 1986, pp. 440-441. This conversation would have taken place in the late 1940s, around the same time that David Lack was also coming to believe that small differences previously considered to be insignificant were actually adaptive; see Borrello, 2003, for discussion. Thanks to an anonymous reviewer for noticing the connection.

Sheppard suggested that in the late 1930s and early 1940s biologists such as J. B. S. Haldane, G. C. Robson, O. W. Richards, Theodosius Dobzhansky, Julian Huxley, and Ernst Mayr[16] had foolishly accepted Cyril Diver's analysis of *Cepaea nemoralis* (performed during the same time period) as "an example of random distribution of varieties, the patterns of which have no selective value."[17] (However, it should be noted that the actual influence of Diver on these authors is somewhat complex).[18] These biologists were writing during a time period just prior to what Gould termed the "hardening of the synthesis" of the late 1940s;[19] in this earlier period, many such small differences were thought to be nonadaptive, but with the "hardening," nonadaptive and nonselectionist explanations came to be excluded from evolutionary accounts (and Cain and Sheppard were a part of, as well as instrumental in, that change). With all of these prominent biologists championing nonadaptive differences in *Cepaea nemoralis*, Cain and Sheppard were motivated to set the record straight.

Lamotte's particular reasons for studying *Cepaea* were perhaps a bit more pragmatic; having been encouraged by Teissier to perform an experimental study of Wright's models during the time when France was occupied by Nazi Germany and laboratories were in disarray, he picked an organism that was found in large numbers throughout Europe.[20] Lamotte seemed less

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[16] Obviously, this early view of Mayr's was later to change, as the quote presented at the outset of this paper illustrates. By 1952, Mayr was praising Lamotte for having "brought new methods and new viewpoints to the ever fascinating problem of the banded snails," but he questioned Lamotte's conclusions, especially concerning drift.

[17] Cain and Sheppard, 1950, p. 291.

[18] See Millstein, forthcoming, for discussion of these views.

[19] Gould, 1983.

[20] Gayon, 1998.

concerned with the adaptiveness – or nonadaptiveness – of the different snail forms than Cain and Sheppard were.[21]

Although the motives of the two camps were different, they sought to explain essentially the same biological phenomena. The population structure of the snails was quite striking; 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 – making the snail an ideal case for those either trying to prove or disprove the efficacy of drift.

However, even more striking than the small, partially isolated populations were the *distributions* among the populations. 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 the primary goals of both camps 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. For Cain and Sheppard, that factor was *selection*.

Arthur Cain and Philip Sheppard: Selection in *Cepaea nemoralis*

In their initial paper, published in 1950, Cain and Sheppard described a very simple technique. Seeking to determine "the relative importance of selection and drift,"[22] they collected all of the

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[21] See Millstein, forthcoming, for discussion.
[22] Cain and Sheppard, 1950, p. 275.

C. nemoralis shells that they could find (live or dead, whole or broken, mostly adults) in several small areas within each of 25 different localities in southern England, chosen for the "diversity of vegetation." These localities were categorized into six habitat types, plus a seventh "other" category. The snails, on the other hand, were identified as being one of three main color types: pink, brown, or yellow. Sometimes pink was further subdivided into fawn, pink, and red. The snails were also identified by a banding system that specified which of five bands, if any, were present. However, most of the time Cain and Sheppard classified these as "unbanded," "one band," and "other." Snails that could not be classified were discarded.

Cain and Sheppard stated that work needed to be done on the genetics of *Cepaea*, but that it appeared that they were dealing with two sets of genes (one controlling color and one controlling banding), with linkages of "varying degrees of closeness." They asserted that the shell pattern having one band in the center position seemed to be distinct from the other patterns.[23] Later work showed that yellow was recessive to pink and brown, and bandless was dominant, with close linkage between bandless and pink or yellow.[24] (The genetic basis of the traits was not a point of contention between the two camps).

After collecting the shells, Cain and Sheppard simply tabulated their results, and then gave a detailed analysis of which color types and which band types were most prevalent in each locality. They summarized their results as follows:

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[23] Cain and Sheppard, 1950, p. 287.
[24] Lamotte, 1959.

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.[25]

In other words, Cain and Sheppard claimed that there were *correlations* between habitat-types

and color-types, and between habitat-types and band-types. The more uniform habitats tended to

have more unbanded (i.e., more uniform) shells. The predominant shell color in any habitat

tended to be similar to the general color of the habitat; in particular, the more green vegetation,

the greater the proportion of yellow snails. These correlations were confirmed with additional

studies published by Sheppard in 1952 and by Cain and Sheppard in 1952 and 1954. However,

my primary focus will be on the 1950 essay where they set out their main arguments; the other

papers, which elaborate on that basic position, will only be mentioned briefly where relevant.

Cain and Sheppard insisted that these correlations must be explained. They considered three

candidate explanations: 1) the differences in shell coloration and banding were due to differences

in diet, 2) the differences between the colonies were due to drift, or 3) the differences were due

to selection. Diet was rejected as a cause; as far as could be determined, both color and banding

were under genetic control, and changing a snail's diet did not cause newly formed bands to be

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[25] Cain and Sheppard, 1950, p. 292.

of a different color.[26] As for drift, they asserted that it was "exceedingly improbable" that distant

colonies within the same habitat-type should be so similar to one another – and so different from

those living in different habitat-types – as a result of chance.[27] Thus, they concluded, "the only

other explanation which will account for this correspondence is natural selection acting upon

genetic variation"[28]

In addition to this "deduction by elimination" for selection and against drift, Cain and Sheppard

also sought positive evidence for their selectionist claims. They proposed that their results were

due to a specific type of selection: selection by predators, namely, thrushes, which prey on the

snails by dropping them against stone "anvils" and breaking their shells. Cain and Sheppard

were suggesting that when the color of a snail was similar to the color of its background, the

thrushes would have more difficulty spotting it, providing a selective advantage to the

camouflaged snails over other snails in that environment. Sheppard attempted to confirm their

claim of selection by predators by tracking the proportions of each form among the broken shells

through seasonal changes of habitat color. He determined that there were fewer broken yellow

shells during the greener periods, indicating that the yellow snails were indeed at a selective

advantage with respect to predation in greener habitats.[29] This was an important piece of

evidence for Cain and Sheppard; it provided additional support for their correlation-based

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[26] Additional studies to rule out environmental influence on shell color are discussed in Cain and Sheppard, 1952.

[27] Cain and Sheppard, 1950, p. 287.

[28] Cain and Sheppard, 1950, p. 287.

[29] Sheppard, 1951. Other hypotheses were ruled out. For example, by marking the shells, Sheppard determined that thrushes were not carrying them to other areas. And by periodically sampling live shells, Sheppard determined that the overall proportion of yellows was not declining.

hypothesis, providing reason to think that the proposed causal mechanism (selection by predators) was really at work.[30]

But what about the stable polymorphism – what was *maintaining* the variation in the snail populations? This was attributed to what Cain and Sheppard called the "physiological advantage of certain gene-combinations," i.e., selection where the heterozygote has a physiological advantage in the given climate. So, according to Cain and Sheppard, there were two types of selection acting on the snail populations, physiological selection and selection by predators. The physiological selection produced a "balance of different genetic forms in each population," a balance which was then altered by the selective actions of predators. The types that were at a physiological advantage might be different in different climates, yielding a different initial balance, but, Cain and Sheppard stated, "one would expect to find the relative proportions in different types of localities to be much as in the district investigated by us."[31]

Nonetheless, I think it is fair to say that Cain and Sheppard's primary focus was not on physiological selection. It is certainly the case that far more of their study was devoted to establishing the correlations between habitat-types and band and color types, and thus to establishing selection by predator; the discussion of physiological selection was much briefer and more speculative. Their lack of emphasis on explaining polymorphism is a bit surprising, given the general emphasis placed on it by other ecological geneticists of the time.[32] Instead, Cain and

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[30] See Millstein, forthcoming, for a discussion of the important role that causality played in Cain and Sheppard's conception of natural selection.

[31] Cain and Sheppard, 1950, p. 287.

[32] See Wade, 2005, for a discussion of ecological geneticists' studies of polymorphism.

Sheppard were focused on the type of selection (selection by predator) that would support their initial intuitions that the colors and banding of the snail shells were adaptive. Two short polemics by Cain – in the initial section of this paper, I quote from both of these articles – support my claim that adaptationism was a central focus for Cain and Sheppard during the 1950s. Cain pointed out the "error in reasoning" of those who would claim that features were not adaptive; according to Cain, they did so only because they couldn't see any adaptive purpose. Cain insisted that all claims for drift should be reinvestigated,[33] and these two papers were cited in Cain and Sheppard's later works.[34] Again, Cain and Sheppard's beliefs seem to fit Gould's characterization of the "hardening of the synthesis." (As we will see below, Lamotte, in advocating a strong role for drift, went against the general "hardening" trend of this time period.)

Given the action of the two types of selection, selection by predator and physiological selection, Cain and Sheppard concluded: "Whatever genetical drift may occur cannot act against natural selection, and is severely limited by it."[35] In other words, drift's "relative significance" was insignificant. Here we seem to have an example of what John Beatty has called a "relative significance" claim.[36] Rather than making a claim that selection is "the" correct explanation, Cain and Sheppard made a claim about the degree to which the outcome is due to drift. In this

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[33] Cain, 1951ab.

[34] See, e.g., Cain and Sheppard, 1954.

[35] Cain and Sheppard, 1950, p. 292.

[36] Beatty, 1997, p. S433 explicitly mentions the example of selection and drift. He implies that the scope of his account extends to cases where multiple theories compete, rather than to cases where there are multiple causes within one theory, as with selection and drift. However, it seems to me that selection and drift can be equally well construed as competing causes within one theory (of evolution, or population genetics more specifically) or as competing theories. In any case, the distinction does not seem important here, as everything that Beatty has said about competing theories applies to competing causes within one theory. Indeed, Beatty cites Darwin's claim that, "Natural selection has been the main but not the exclusive means of modification," which Darwin later changed to

case, drift was not ruled out entirely, but it was severely downplayed; as Beatty notes, disputants in relative significance debates often take highly polarized positions.[37]

It is also important to note that Cain and Sheppard's claim concerned the relative *effect* of drift. They did not deny that the *process* of drift was occurring in the populations; what they denied was that it made any significant contribution to the "outcome," i.e., to the observed distributions in the populations.[38] (As I have argued elsewhere, it is important to distinguish the process of drift from its possible outcomes[39]). This last point is significant because it has become commonplace for biologists to criticize studies that were performed during this time period. The criticism goes as follows: there was no need to argue about drift vs. selection because, as we all now know, both drift and selection occur in all, real, finite populations. Such critiques miss the point; it is possible to acknowledge that the processes of drift and selection are both occurring in a population, and yet *not* think that, say, drift, has made a significant contribution to the outcome.

By seeking out correlations between habitat-types and snail-types, as well as a selection mechanism to connect the two, Cain and Sheppard were able to reach a conclusion that many biologists of the day found convincing. In particular, Sewall Wright was convinced that Cain

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"the most important, but not the exclusive means of modification," as an example of a (changing, and fairly ambiguous) relative significance claim. See Beatty, 1997, p. S438.

[37] Beatty, 1997, p. S438.

[38] Williams would later make a similar claim with respect to group selection; he stated that there was "no sane doubt about the reality of the process," and instead focused his criticism on "the importance of the process and its adequacy in explaining the phenomena attributed to it" (Williams, 1966, p. 109). Thanks to an anonymous reviewer for the suggestion.

[39] Millstein, 2002, 2005.

and Sheppard had made their case.[40] (We will see, however, that Wright did not remain convinced on this score). Unlike the previous studies that had been done on *Panaxia dominula*, studies that sought only to provide evidence that drift was not responsible for the observed gene frequency fluctuations,[41] Cain and Sheppard provided *positive* evidence for the causal efficacy of selection in *Cepaea nemoralis*. Furthermore, by picking a species where multiple populations could be studied (again, an improvement over the studies of *Panaxia dominula*), Cain and Sheppard were able to add weight to their conclusions by being able to point to *persistent* correlations. Nonetheless, Cain, at least, was skeptical that positive evidence could be provided for *drift*; in a letter to Wright, he remarked: "I have been trying to work out a suitable experiment to *demonstrate* drift, but it seems very difficult."[42] What Cain did not realize at the time was that Maxime Lamotte in France had been attempting to do just that, and for the same species, *Cepaea nemoralis*.

Maxime Lamotte: Selection *and* Drift in *Cepaea nemoralis*

With regard to providing evidence for selection, Lamotte for the most part concurred with, and used, the same methods that Cain and Sheppard did: he looked for correlations between habitat-types and color- and banding-types, he compared the proportions of different types among the broken shells to the proportions of different types among living snails, and he also sought to determine the type of selection processes (physiological, predatory, or both) that were acting to produce the correlations. In his earliest work, published in 1951 – a massive study, it should be

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[40] Wright, 1951; see also Provine, 1986 for discussion.
[41] Fisher and Ford, 1947.

noted, of over 900 populations or "colonies" – Lamotte focused on the "bandless" vs. "banded"

snails, and concluded that "the selection which can be attributed to predators is exceedingly

small."[43] Lamotte's reasoned that even though the proportions of broken shells indicated some

advantage for the banded snails, under many conditions the bands were buried in the soil and

thus not visible to predators. He did acknowledge, however, that other forms of selection were

likely to be involved.

By 1959, however, Lamotte had modified his views on selection in *Cepaea* somewhat. His later

work gave greater discussion to the color-types, and described a somewhat larger role for

selection. (Because of this change in position, the rest of my essay will focus less on the 1951

essay than on the 1959 essay; the former is a far more detailed study overall, but the latter is

more detailed with respect to the issues at hand).[44] Nonetheless, even though Lamotte used many

of the same methods as Cain and Sheppard, and even though he acknowledged a relatively large

role for selection, Lamotte diverged from Cain and Sheppard in two important ways.

First, Lamotte attributed a much smaller role to selection by predators than Cain and Sheppard

did, as compared to other forms of selection. This conclusion involved the use of two additional

methods: 1) He compared gene frequencies of *Cepaea nemoralis* to gene frequencies of the

virtually indistinguishable *Cepaea hortensis* in a given locality. Frequently, these diverged

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[42] Cain, 1951; quoted in Provine, 1986, p. 442.

[43] Lamotte, 1951, p. 234.

[44] In addition to the argument for drift that will be presented here, the earlier (1951) work used Wright's equations, with enhancements from Lamotte's colleague Gustave Malécot, to show that Lamotte's results fit the predicted curves when all factors – selection, drift, migration, and mutation – were included. However, Wright later argued that the values that Lamotte used to achieve this fit were "hardly acceptable" (Wright, 1978, p. 229).

considerably; on this basis, Lamotte concluded that selection by predator could not have been the primary cause of the distributions, because the predator would not have been able to distinguish between the two species. (He did not deny that selection by predator had occurred, only that it had had much of an effect.) 2) He performed laboratory experiments on the snails, exposing them to the heat of a light bulb to approximate the effects of the sun. His results showed an advantage for yellow snails, especially bandless yellow snails, which taken together with correlational data, led Lamotte to conclude that there had been a greater effect from microclimatic selection than from selection by predator.

Second (and more importantly for the discussion at hand), unlike Cain and Sheppard, Lamotte believed that after the methods for detecting selection had been applied, the distributions among the populations were still not completely explained: "when one attempts to assess the cumulative action of these [selective] factors in the course of time, there always remains some *unexplained residual diversity*."[45] But what was the unexplained residual diversity? "Considering populations living in apparently similar environments, one nevertheless finds that their genetic compositions may be quite diverse. Conversely, populations of the same phenotypic composition may be found in apparently different biotopes."[46]

Lamotte had found correlations between the environment and color-types and the environment and banding-types, as Cain and Sheppard did; however, the correlations were weak overall and not consistent across the colonies. For example, in the Parisian district, Lamotte found that dry

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[45] Lamotte, 1959, p. 83; emphasis added.
[46] Lamotte, 1959, p. 80.

sunny meadows contained 80% yellows on average, whereas humid shaded woods contained only 47% yellows on average. And yet, in the former habitat, the range was from 49%-100%, and in the latter, the range was from 22%-95%. That is, the correlations were only on average, with considerable variation among colonies.[47] 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 sought to "inquire into the causes of this apparent indeterminacy."[48]

That is, he tried to determine what other causal factor could explain the deviations from selective expectations. Note that, unlike many contemporary accounts,[49] deviation from selective expectations was not sufficient in itself to invoke drift; it was *suggestive* of drift, but additional evidence was needed. Indeed, Lamotte also considered the possibility that fluctuations in the environment could be the cause of the residual diversity. However, although Lamotte believed that these fluctuations were responsible for some of the variability, they could not be responsible for all of it, because some of the environments had been stable recently. Thus, he explored the question of whether drift could be responsible for the residual diversity.

Recall that one of the goals of Lamotte's study was to provide a demonstration of Sewall Wright's views. Indeed, as noted earlier, Lamotte had found almost the perfect conditions for doing so: Wright had analyzed the dynamics of small, partially isolated subpopulations (so-

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[47] Lamotte, 1959, p. 72.
[48] Lamotte, 1959, p. 80.

called "island populations"), and the subpopulations (or "colonies") that Lamotte studied were exactly that. The colonies were separated by anywhere from one hundred meters to several kilometers. Most of them were small in numbers. Furthermore, there was some migration between colonies, but in most cases, only a very limited amount: "In the gaps between the colonies practically no *Cepaea* are found, or else only a few individuals or little groups of them, here and there, along the hedges running along the field boundaries, or upon shaded banks."[50]

What Wright's equations show is that the expected *outcome* of drift – the expected size of the fluctuations in gene frequencies from one generation to the next – is greater in small populations than it is in large populations. To see why, we must understand (what I see as the core idea in) Wright's conception of drift: indiscriminate sampling.[51] Random drift, I have argued, is an *indiscriminate sampling process*, meaning that it is a process where heritable physical differences between entities (e.g., organisms, gametes) are causally irrelevant to differences in reproductive success.[52] This contrasts with natural selection, which is a *discriminate* sampling process, meaning that it is a process where heritable physical differences between entities (e.g., organisms, gametes) are causally relevant to differences in reproductive success. Lamotte subsumed three kinds of phenomena – sampling of gametes, founder principle, bottlenecks – under the broad category of "drift," [53] as have many others, including Wright and Dobzhansky. All three can exhibit indiscriminate sampling, as follows. In the sampling of gametes, gametes

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[49] See, e.g., Sober, 1984; Brandon and Carson, 1996.
[50] Lamotte, 1959, p. 66.
[51] Beatty, 1984.
[52] Millstein 2002, 2005.
[53] See Millstein, forthcoming, for a more detailed discussion of Lamotte's views on drift.

that are joined are an indiscriminate sample of the whole gamete "pool" if heritable differences between gametes are causally irrelevant to which gametes are successfully joined (i.e., which gametes participate in successful fertilizations that yield zygotes). (According to Wright, "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."[54]) Under the founder principle, organisms founding a new population are an indiscriminate sample of the original population if heritable differences between organisms are causally irrelevant to which organisms are founders of the new population. In a bottleneck, organisms surviving a drastic reduction in population size are an indiscriminate sample of the original population if heritable differences between organisms are causally irrelevant to which organisms survive the reduction in population size.

When sampling indiscriminately, the smaller the sample, the less likely the sample will be representative, just as a small handful of jellybeans from a large jar is less likely to be representative than a large scoopful from a large jar. That is, frequencies of the sample may increase or decrease relative to the frequencies in the original population. If indiscriminate sampling occurs in every generation (as is generally expected with indiscriminate gamete sampling, and may occur in the other two types of drift as well), a given gene may experience increases in some generations and decreases in others (a possible outcome of the process of drift). Thus, drift can produce fluctuations in gene frequencies from one generation to the next. The smaller the population, the smaller the samples, and the greater the expected fluctuations (since, again, the samples are less likely to be representative).

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[54] Wright, 1937, p. 310.

However, even though the random sampling of gametes alone would lead us to expect fluctuations in gene frequencies from one generation to the next, Lamotte stated that following a single population through time would be difficult: one would have to observe many generations, and one would need constant environmental conditions to exclude the possibility of fluctuating selection, which can produce similar gene frequency fluctuations. In *Cepaea nemoralis* in particular, Lamotte stated that "generation time is at least two years,"[55] so that following numerous generations would be quite a lengthy project indeed. Lamotte proposed, instead, to compare the gene frequencies of many populations at one time. But what do Wright's equations predict when we consider a number of populations? As we just discussed, we would expect that all of the populations would experience fluctuations in gene frequencies from one generation to the next. However, there would be no reason to expect them to experience the *same* fluctuations; they would likely experience different fluctuations. Thus, if we were to take a snapshot at one point in time, a given gene might predominate in some populations, and yet be relatively rare in others. That is, the populations would differ from one another. In particular, the small populations would tend to experience *larger* fluctuations; thus, we would expect them to exhibit a greater divergence from each other than the larger populations would from each other. This distinctive outcome provides evidence that drift processes are occurring in the populations.

And indeed, these are exactly the results that Lamotte found. Using population sizes estimated by the method of mark, release, and recapture (or in some cases, simple enumeration), his data showed that the inter-colonial diversity among the smaller colonies (500-1000) was greater than the inter-colonial diversity among the large colonies (3000-10,000), with respect to both yellow

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[55] Lamotte, 1959, p. 81.

snails and bandless snails. (See Figures 1 and 2; I have included only the yellow snail data here.)

[Figures 1 and 2 about here] In other words, the large populations were more similar to one

another than the small populations, which is what Wright's model predicts.

In the 1959 paper, Lamotte provided only the table (Figure 1) and the bar graph (Figure 2); in his

earlier 1952 paper, Lamotte provided the same data in the same table and bar graph and, in

addition, presented the variances (presumably, the average of the squared deviation of each value

from the overall mean) for the small and large populations: 53×10^{-3} and 29×10^{-3}, respectively.

Unfortunately, Lamotte did not provide specific enough data to replicate his calculations; he

asserted that the variances were calculated directly starting from the frequencies observed in the

populations, rather than from the groupings shown in the table, which would obviously introduce

inaccuracies.[56]

One would not expect these kinds of results for selection, Lamotte argued, because "if the

diversity of the populations were due only to the diverse effects of the environments acting

through natural selection, it would be independent of the population sizes of the colonies."[57] In

other words, Lamotte claimed, there is no reason for selection alone to produce a greater

divergence among small populations than among large, whereas this is precisely what a drift

model predicts. Lamotte also pointed out that there were more monomorphic populations among

the small populations than among the large (7 as compared to 2; Lamotte indicated the

monomorphic populations by the numbers within parentheses in the table of Figure 1 and by

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[56] Lamotte, 1952, pp. 334-335.

[57] Lamotte, 1959, p. 81.

shading areas of the bar graph in Figure 2). He found this fact to be particularly significant, because, once again, there is no reason we should expect this under selection. With drift, however, the larger fluctuations of the smaller populations may cause a population to become monomorphic; once monomorphic, only a mutation would change its monomorphic state (i.e., the population has gone to "fixation"). Lamotte concluded:

> "The increase of diversity thus observed among the small colonies demonstrates the existence of other factors than the variable selective influences of the environment. It agrees with the expectation of fluctuation 'at random'... One need not feel surprised, let alone shocked, by the important role which the random fluctuations seem to play in producing the diversity of the genetic compositions of *Cepaea nemoralis*. The existence and the amplitude of these fluctuations are imposed by the very structure of the natural populations of these species."[58]

More generally, then, we can characterize Lamotte's style of argument as follows: if multiple causes are operating in a population, and if one of those causes is known to produce a distinctive type of outcome that we would not expect the other causes to produce – and if we observe that distinctive outcome – then we have evidence that the cause in question (in this case, random drift) contributed to the effect. In this instance, he was able to invoke qualitatively different types of outcomes for selection and drift in order to bolster his case.

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[58] Lamotte, 1959, p. 82.

Thus, just as Cain and Sheppard's methods for detecting selection were more advanced than those used during earlier debates (i.e., the debates over *Panaxia dominula*), Lamotte also succeeded in advancing the analysis of drift in natural populations by describing statistical methods through which positive evidence for drift could be given. That is, he had done what Cain had thought would be "very difficult" to do. (Of course, as we saw, Lamotte's approach was not *purely* statistical; establishing the causal role of selection was also an important part of his analysis).

Based on his selection results together with his statistical analysis of drift, Lamotte concluded that even though selection by predator and microclimatic selection were both partially responsible for the observed distributions, drift was clearly playing a significant role as well. In other words, like Cain and Sheppard, Lamotte was making a claim about the relative significance of drift and selection,[59] but unlike Cain and Sheppard, the position he took was not a polarized one. Again, it should be emphasized that Lamotte's "relative significance" conclusion was a claim about which processes were *effective*, not about which processes were *occurring*; Lamotte was very explicit about this point:

> We find enough evidence to convince us that certain factors do influence the genetic composition of populations, but does it follow that the observed differences between the local colonies and populations are explicable as consequences of these factors? Should

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[59] This raises a question about whether one can *quantify* the relative contributions of drift and selection. Lamotte did not try to do this in his 1959 paper, but he did in his 1952 paper, where he argued that drift was responsible for half of the banded/unbanded variation in the large populations and 5/6 of the banded/unbanded variation in the small

one not raise the question whether this factor is sufficient to bring about the results which one wishes to ascribe to it?[60]

Lamotte raised the question, and given the data that showed greater divergence among small populations than among large, denied that selection was sufficient to bring about the observed results.

Lamotte had presented the research that became his 1959 paper at a Cold Spring Harbor Symposium on Quantitative Biology, held to celebrate the centenary of Darwin's *Origin of Species*. Some of the post-presentation discussion – almost universally positive – was published as well, including, notably, comments from Wright and Dobzhansky. The formerly skeptical Wright stated, "it seems to me that Dr. Lamotte's results indicate strongly that random drift is playing an important role in the variations of gene frequency in the populations of *Cepaea* species," although he qualified that claim by saying that "the importance of random drift in evolution does not come from cases of this sort"[61] (the latter remark reflects the fact that this case did not provide much support for Wright's shifting balance model). Dobzhansky, on the other hand, asserted, "It seems probable that both the classical drift and the drift in colonies descended from small numbers of founders may be effective in the snail populations studied by Dr. Lamotte."[62]

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populations. Lamotte's calculations, together with the general question about whether such quantification is possible, bear further analysis.

[60] Lamotte, 1959, p. 84.

[61] Wright, 1959, p. 86.

However, Cain and Sheppard, perhaps unsurprisingly, were not convinced.[63] Part of their objection, outlined in a paper published in 1961, stemmed from a claim that there might be important differences between the English populations and the French populations (e.g., with respect to their response to climate) a possibility that Lamotte himself had admitted.[64] (Elsewhere, Cain and Sheppard seemed to deny any difference between English populations and French populations; they asserted that "[Lamotte's] data are in no way incompatible with ours,"[65] and they repeatedly critiqued the conclusions that Lamotte had drawn about his own data[66]). Nevertheless, it is unclear that a Lamotte-style analysis of Cain and Sheppard's data would lead to significantly different conclusions about the effects of drift. For example, Cain and Sheppard noted that hedgerow habitats were greener than beech habitats, which in turn, were greener than oakwood habitats, and that these corresponded to the average proportion of yellows in each habitat. Tabulating the numbers, these are 38% yellows, 22% yellows, and 6% yellows, respectively. However, computing the average for each locality shows that the range for hedgerow habitats was 17%-67%, the range for beechwood habitats was 0%-27%, and the range for oakwoods was 4%-13%. Cain and Sheppard would have attributed these ranges to differences within the habitat-types (e.g., they noted the habitat with 17% yellow "had been

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[62] Dobzhansky, 1959.

[63] Van Valen, 1960, claimed that Sheppard, who was also in the audience when Lamotte presented his paper in 1959, had verbally agreed with Lamotte's conclusions, but Cain and Sheppard stated that Van Valen's remarks were "a fantastic misrepresentation" that could "only be given an unqualified contradiction" (Cain and Sheppard, 1961, p. 61). Instead, they contended that Sheppard had remarked that Lamotte had misunderstood their position and that the editor had deleted those remarks from the Discussion. Regardless of who said what, the claim that Lamotte had misunderstood Cain and Sheppard is a bit suspect; they attributed to Lamotte a claim that *he* did not make (that physiological selection and selection by predators was an either-or proposition) and claimed that they had always held that physiological selection was more important than selection by predator (a claim that is not supported by the published evidence).

[64] Lamotte, 1959.

[65] Cain and Sheppard, 1954, 112.

neglected and had a thick outgrowth of brambles, beneath which there was little green vegetation"[67]). Still, the ranges do show considerable overlap. Although they are not as striking as the ranges that Lamotte had found in France, it should also be kept in mind that Lamotte's data were far more extensive than Cain and Sheppard's (over 900 populations, as compared to 25; Cain and Sheppard's 1954 paper analyzed 115 populations, including some that had been analyzed previously), and took into account population sizes, which Cain and Sheppard did not estimate.[68] Moreover, when Cain and John D. Currey performed more extensive studies of English populations of *Cepaea nemoralis* in 1963, the correlations that Cain and Sheppard had found previously did not hold up. So, the claim that the English snails were different from the French snails – at least, with respect to the effects of drift – does not seem to be supported.

Mildly Optimistic Conclusions

We can now return to the pessimistic remarks concerning drift that I discussed at the outset of my paper and re-examine them in the light of Lamotte's study of *Cepaea nemoralis*.[69] Cain, for example, had asserted that the real basis for claims of drift is that the investigator simply does not see any evidence for selection, and concludes on that basis alone that drift is occurring. Clearly, this accusation does not apply to Lamotte; not only was lack of evidence for selection *not* the basis for his claims, but also, he in fact acknowledged a significant role for selection.

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[66] Cain and Sheppard, 1952, 1954, 1961.

[67] Cain and Sheppard, 1950, p. 282.

[68] Lamotte notes these differences in method in his 1952 paper.

Mayr, similarly, had asserted that whereas one *could* obtain positive evidence for selection, one could *not* obtain positive evidence for drift; drift could only be asserted (and then, only "tentatively") after all attempts at a selectionist explanation had failed. On the contrary, what I find most significant about Lamotte's approach is that it *does* suggest a way to provide positive evidence for drift.

One key to that approach is to examine many populations at once, rather than a single population.[70] We expect drift to leave a (purportedly) distinctive signature; the variance among small populations is greater than the variance among large populations. If the observed signature fits with the expected signature, then we have evidence for drift. Other researchers, most notably Luigi Luca Cavalli-Sforza in his examination of human blood groups, used precisely the same line of reasoning to argue for the effects of drift. (Cavalli-Sforza's studies began in the mid-1950s; thus, Lamotte's studies began a little earlier[71]). More recently, Patrick Phillips, Michael Whitlock, and Kevin Fowler sought to distinguish the effects of drift from the effects of selection by using a more sophisticated statistical analysis that takes into account the evolution of many traits and their genetic associations (via pleiotropy and/or linkage), stemming from models

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[69] With the exception of Provine's. Although his comment is most intriguing, he has yet to present his argument for it in print. However, John Gillespie credited Provine with stimulating him to think about genetic draft as a substitute for much of what was previously thought to be genetic drift; see Skipper, forthcoming b, for discussion.

[70] Sober seemingly endorsed this general approach: "To compare the relative importance of selection and drift, it is useful to shift from a single population to an ensemble of populations that begin with the same initial gene frequency and are subject to identical selection pressures and have identical effective population sizes." (Sober, 1987, p. 111.) However, it is not clear from his discussion whether he would extend his reasoning to natural populations, where we do not have identical initial gene frequencies or identical selection pressures or identical effective population sizes. Indeed, in this case, Lamotte postulated significant founder effects, which is another way of saying that the initial gene frequencies were not identical; the selection pressures clearly differed from one population to the next, since the habitats differed; and it is the very fact that population sizes *differ* that Lamotte exploited in his reasoning.

[71] See Millstein, 1997, and Richardson, forthcoming for discussion of the Cavalli-Sforza studies.

developed by Russell Lande.[72] Notably, the basis of their reasoning is similar to that of

Lamotte's: "In addition to causing an average reduction in genetic variance within populations,

genetic drift also tends to increase the genetic variance among populations."[73] And note that, as

with Lamotte, Phillips et al. consider effects across populations rather than within a single

population. Thus, the issues raised by Lamotte's approach are of continuing importance.

However, Lamotte does not quell all of the pessimism. Cain had suggested that any "residual

variation" left over after selective analysis could simply be more, as yet undiscovered,

selection.[74] It might be tempting to dismiss this attitude as rampant selectionism (or, if you

prefer, rampant adaptationism); this seems to be the sort of adaptationist reasoning strategy that

Gould and Lewontin would later lampoon: "In the absence of a good adaptive argument in the

first place, attribute failure to imperfect understanding of where an organism lives and what it

does."[75] To an extent, the lampooning is appropriate, but I think the general point that we should

not assume that our analyses have identified all of the relevant causal factors is well taken. This

is especially true in the case at hand. Lamotte's approach would have us infer from distribution

pattern among populations back to its cause (drift), and as we all know, different causes can

produce similar effects. No other evolutionary factor is affected by population size in the above

described way (as far as I know) – there is, of course, frequency dependent selection and density

dependent selection, but strictly speaking, these do not depend on population size per se – and so

the evidence for drift is strong. However, just because evidence for drift has been given, does

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[72] Lande, 1979.

[73] Phillips, Whitlock, and Fowler, 2001, p. 1138. Thanks to an anonymous reviewer for this reference.

[74] See Beatty (1987) for an analysis of this type of reasoning, and for a discussion of testing selection hypotheses against drift hypotheses in general.

not mean that other factors can be ruled out as having contributed to the gene frequency distributions among populations, any more than a demonstration of selection rules out drift. Indeed, subsequent study of *Cepaea nemoralis* has borne out the likelihood that many evolutionary processes are active in these populations; Jones, Leith, and Rawlings, for example, argued for the occurrence of no less than eight such processes, drift among them.[76] The point that multiple causal factors are almost always at work in natural populations – a point stressed by Lamotte himself[77] – cannot be emphasized strongly enough.

Richard Lewontin has raised a different sort of concern about Lamotte's study of *Cepaea nemoralis* specifically. Lewontin stated that Lamotte's study was "successful" in comparison to what he sees as the "unsatisfactory result" obtained from the earlier studies of the evolution of the peppered moth.[78] However, Lewontin argued that the very factors that permitted Lamotte's study to be successful means that his success will be difficult to replicate in the study of other organisms. Referring to *Cepaea* as one of only a handful of "model systems," Lewontin asserted:

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[75] Gould and Lewontin, 1979, p. 152.

[76] Leith, Jones, and Rawlings, 1977. The eight processes are: 1) visual selection by predator, 2) climatic selection, 3) frequency-dependent selection, 4) disruptive selection, 5) density-dependent selection, 6) heterozygote advantage and stabilizing selection, 7) random drift (including gamete sampling, bottlenecks, and founder effect), and 8) linkage disequilibrium and coadaptation.

[77] Lamotte stated: "…the real effectiveness of selection by predators is not demonstrated, let alone measured, by the fact that it exists in some cases. The same is true of selection by microclimatic conditions. Such things could be determined only by taking into account the total situation in the populations. This applies with even greater force to the random fluctuations which are not denied by anybody in populations of limited effective size, but the importance of which cannot be evaluated without statistical analysis. Only such statistical analysis may eventually permit us to know the effective roles of each of the elementary factors, such as mutation, selection, migration, random fluctuation, and even more of their interactions." (Lamotte, 1959, p. 84.)

[78] Lewontin, 2002.

"The advantages of this system for a case study are that the presence or absence of bands is determined by a single allelic difference that is easily scored without disturbing the animals, that snails can be captured, marked, and released for migration studies and estimates of population size, that snails have low dispersal rates, that deposits of shells of dead snails leave a record of previous populations, and most important, that such shells can be scored as broken or intact, differentiating those that have been preyed upon by thrushes from those which have not."[79]

Indeed, Lewontin claimed, the snails were "carefully chosen" for their biological characteristics: "It would not be possible, for example, to carry out such studies in any small mammal or any species of Drosophila" and furthermore, these studies are "extremely labor intensive."[80]

Lewontin's points are well taken;[81] the study of selection and drift in natural populations is indeed difficult. And yet, even granting Lewontin's claim that there are aspects of the snail case that make it particularly amenable to study, perhaps further such model systems can be found (even if they are a bit *less* ideal than the snails). For example, we have seen that the key to Lamotte's analysis was that the snails were found in numerous populations (or "colonies"), of varying sizes, with very little migration between populations. These populations, taken together, fall under Alan Hastings and Susan Harrison's broad definition of a *metapopulation*, i.e., "any

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[79] Lewontin, 2002, p. 8.

[80] Lewontin, 2002, p. 9.

[81] His points described above, that is; Lewontin also suggests that there was "some influence of prior theoretical commitment in the choice of the system and the design of the study," in particular that "the snail study would not have allowed a complete study of components of natural selection, but was optimally designed to detect genetic drift." (Lewontin, 2002, p. 9.) As we have seen, selection was not excluded from the studies of *Cepaea nemoralis*.

set of conspecific populations linked by dispersal."[82] Hastings and Harrison cited studies of

many metapopulations in nature, including, e.g., metapopulations of spruce grouse, the bay

checkerspot butterfly, water voles, and orb spiders; they maintain that metapopulations can be

the result of "natural differences in habitat size or quality, or even by human fragmentation of

natural habitats."[83] If metapopulations are common in nature, then it may be possible to look for

the same variance pattern that Lamotte looked for in other species, even if the species are a bit

harder to study than *Cepaea*.

To be clear, I am not claiming that Lamotte's method is the only method of demonstrating drift;

there may be other ways of providing positive evidence of phenotypic drift in natural

populations. For example, the method of Phillips et al. (mentioned above) may prove fruitful;

Ackermann and Cheverud's comparison across seven fossil taxa of hominoid within-group facial

variation to hominin between-group patterns of variation is a study that is consistent with this

general approach. [84] And it need not necessarily be the case that one studies a metapopulation; as

Lamotte noted, it is possible (if difficult and expensive) to follow a population through time.

Rosemary and Peter Grant's 30-year study of finches in the Galapagos (primarily known as a

demonstration of selection), in which periodic bottlenecks were observed, is an example of this

approach. [85] Of course, there also are numerous methods for demonstrating drift at a molecular

level; work needs to be done to show the connections between drift at molecular and phenotypic

levels, if any. Future examinations of random drift might profitably explore these and other

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[82] Hastings and Harrison, 1994, p. 168.

[83] Hastings and Harrison, 1994, p. 169.

[84] Ackermann and Cheverud, 2004.

possible methods of demonstrating phenotypic drift in nature.

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[85] Grant and Grant, 1989.

Acknowledgments

Fig. 1. Lamotte's data as he presented it in tabular form; see fig. 2 for corresponding bar graph. (From Lamotte, 1959, p. 81.)

Fig. 2. Lamotte's data as he presented it in bar graph form; see fig 1 for corresponding tabulated data. (From Lamotte, 1959, p. 81.)

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TABLE 17. FREQUENCY DISTRIBUTION OF THE YELLOW GENE IN THE SMALL AND IN THE LARGE POPULATIONS OF C. *nemoralis*

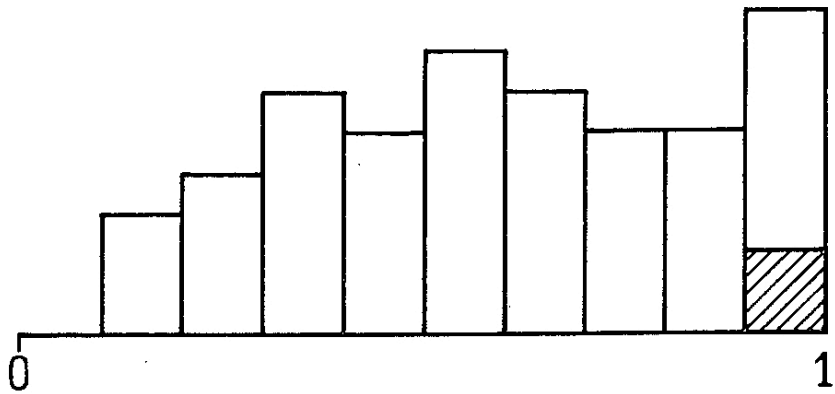| Frequency of the yellow gene	0.–0.10	0.10–0.20	0.20–0.30	0.30–0.40	0.40–0.50	0.50–0.60	0.60–0.70	0.70–0.80	0.80–0.90	0.90–1
Colonies of 500 to 1000 individuals	6 (2)	2	3	5	7	8	7	8	9	7 (5)
Colonies of 3000 to 1000 individuals	0	3	4	6	5	7	6	5	5	8 (2)
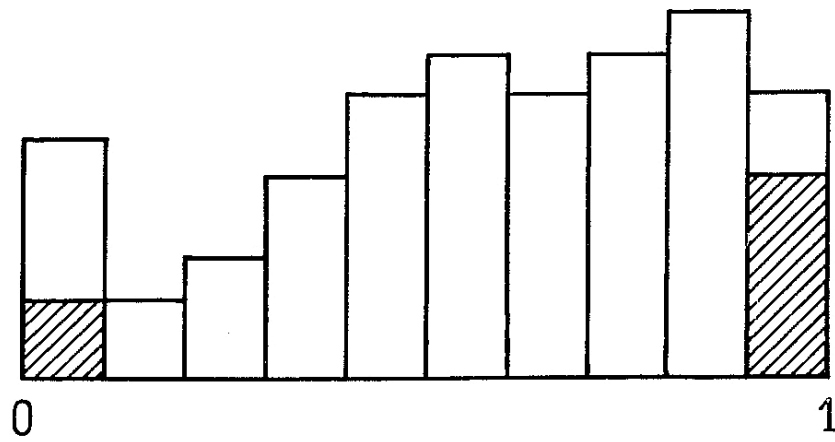
FIGURE 19. Frequency distributions of the yellow gene in small and large populations.