

Sewall Wright, shifting balance theory, and the hardening of the modern synthesis



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ARTICLE INFO

Article history:

Received 31 December 2015

Received in revised form

7 November 2016

Available online 29 November 2016

Keywords:

Sewall Wright

Shifting balance theory

Modern synthesis

Natural selection

Genetic drift

Population structure

ABSTRACT

The period between the 1940s and 1960s saw the hardening of the modern synthesis in evolutionary biology. Gould and Provine argue that Wright's shifting balance theory of evolution hardened during this period. But their account does not do justice to Wright, who always regarded selection as acting together with drift. This paper presents a more adequate account of the development of Wright's shifting balance theory, paying particular attention to his application of the theory to the geographical distribution of flower color dimorphism in *Linanthus parryae*. The account shows that even in the heyday of the hardened synthesis, the balance or interaction of evolutionary factors, such as drift, selection, and migration, occupied pride of place in Wright's theory, and that between the 1940s and 1970s, Wright developed the theory of isolation by distance to quantitatively represent the structure of the *Linanthus* population, which he argued had the kind of structure posited by his shifting balance theory. In the end, Wright arrived at a sophisticated description of the structure of the *Linanthus* population, where the interaction between drift and selection varied spatially.

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"The problem presented by distribution of blue and white flowered plants [in the population of *Linanthus parryae*] is not as simple as a decision between two sharply distinct alternative[s]: control by selection or by random drift. Selection may be involved in diverse ways, there are different sorts of random drift to be considered, and selection and random [drift] may be combined in any degrees and may conceivably interact to produce a more heterogeneous pattern than either by itself."

Sewall Wright, an unpublished manuscript on *Linanthus parryae* (1960) (Sewall Wright Papers, American Philosophical Society, Series IIa, Folder 29)

1. Introduction

Stephen Jay Gould (1980, 1982, 1983, 2002) has famously argued that the modern synthesis in evolutionary biology hardened over time. In the 1930s, evolutionary biologists were pluralistic in the sense that they accepted both adaptive and nonadaptive evolutionary processes as important in nature, but in the next three

decades, they moved toward the hard-line selectionist view that natural selection is the most important (and prevalent) process in evolution.¹ One of Gould's prime cases of the hardening is the development of Sewall Wright's shifting balance theory of evolution.²

Following Gould, William Provine argues that Wright's theory hardened (Provine, 1983; 1986, pp. 287–291, 361–362, 420–435). According to Provine, in the 1930s Wright claimed that taxonomic differences above the species level were largely nonadaptive, thereby making genetic drift not only important at the level of a small local population but also at the levels of species and genera (e.g., Wright, 1932, pp. 363–364). In saying this Wright was following the systematists' view that taxonomic differences are nonadaptive. By the 1950s, however, systematists argued that supposedly nonadaptive taxonomic differences turned out to be adaptive. Wright thus held that only local differences within a species were nonadaptive, suggesting that drift plays an important role *only* at the level of subpopulations of a species (e.g., Wright,

¹ For a review and analysis of the debates over the relative importance of drift and selection, see Beatty (1984).

² Gould's other cases are the works of Theodosius Dobzhansky, Julian Huxley, Ernst Mayr, and G. G. Simpson, and Gould's thesis has been analyzed by other scholars (e.g., Beatty, 1987; Provine, 1983, 1986; Smocovitis, 1999; Turner, 1987).

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1948). Gould and Provine interprets this change in Wright's view as indicating that natural selection became more important in Wright's theory.

Gould's and Provine's interpretation of Wright may sound counterintuitive, for Wright always maintained that subdivision of a population into small, partially isolated demes provides the balance between random genetic drift and natural selection that is most favorable for rapid adaptive evolution. On this view, drift and selection act together in adaptive evolution: drift provides a continuous supply of intraspecific variations on which natural selection may act. In fact, Provine acknowledges this point:

In one sense, Wright's theory has never changed substantially since he first conceived it in 1925. He has always argued that a certain "balance" among the various factors affecting the evolutionary process exists and that generally all the factors are acting in the balance. Thus, to say that natural selection or random drift is the primary determinant of the evolutionary process, makes no sense in Wright's scheme. Both are working, and it is the balance of their interaction that (along with all the other factors, of course) determines the course of evolution. Wright has never veered from emphasizing the "balance" of his shifting balance theory (Provine, 1986, pp. 361–362).

Nonetheless, Provine argues that Wright's theory hardened because Wright came to restrict the role of drift to the subpopulation level. For Provine, the "balance" of Wright's theory tilted toward selection.³

Even if we grant that Wright changed his view about the nonadaptive taxonomic differences, Gould's and Provine's hardening interpretation of the development of Wright's evolutionary theory is misleading in two ways. First, Wright's theory did not fit nicely with what Gould describes as pluralism in the 1930s. For Gould, an evolutionary theory would be pluralistic if it simply recognized drift and selection as important, alternative processes in evolution, and his pluralism does not require that evolutionary phenomena be explained by appeal to the balance between drift and selection. In Wright's theory, however, drift and selection are cooperating rather than alternative factors, and his theory appeals to the balance of factors (Wright, 1931, 1932). Thus, to say that Wright's theory was pluralistic in Gould's sense does not capture the nature of the relationship between drift and selection in Wright's theory. Second, Wright's theory was opposed to hard-line selectionism. As Provine noted, Wright always emphasized the interaction of different evolutionary factors, that is, the balance of the shifting balance theory. In this theory, no single factor can be given preeminent importance. Wright appealed to this point to distinguish his view from hard-line selectionism of Fisher and Ford (Fisher & Ford, 1947, 1950; Wright, 1948, 1951).⁴

Thus, although the hardening story seems to represent an influential trend in evolutionary theory between the 1940s and the 1960s, it fails to do justice to Wright's shifting balance theory. My aim in this paper is to provide a more adequate account of the development of Wright's theory during the hardening of the modern synthesis. My account has two parts, both of which occur in the context of Wright's work on the geographical distribution of

flower color dimorphism in *Linanthus parryae*, a population of desert plants that Wright regarded as an example of his shifting balance theory.⁵ The first part concerns Wright's criticism of the selectionist explanation of dimorphism in *Linanthus* and his analysis of the balance of factors in the *Linanthus* population (Sections 2 and 3). This part shows that even in the heyday of the hardened synthesis, the balance or interaction of factors occupied pride of place in Wright's theory, a fact obscured by the hardening story. The second part concerns the development of Wright's theory of isolation by distance and his application of it to *Linanthus* (Sections 4 and 5). Wright used the theory of isolation by distance to quantitatively describe how drift, selection, and migration interact with each other in the *Linanthus* population, and it underpinned his criticism of the selectionist explanation of dimorphism in *Linanthus*. This was Wright's major theoretical and empirical work in the 1940s and 50s, which is neglected in the hardening story. Taken together, my account shows that while the community of evolutionary biologists hardened, Wright not only criticized hard-line selectionism but also provided an increasingly sophisticated, quantitative analysis of the balance of drift and selection in a subdivided population. Furthermore, my account suggests ways in which the development of Wright's shifting balance theory is relevant to broader issues in evolutionary biology and philosophy of biology (Section 6).

2. Balance of factors in *Linanthus parryae*

Linanthus parryae is a diminutive desert annual in the Mojave Desert in California. It has blue and white flower color morphs, the former being dominant to the latter (Epling, Lewis, & Ball, 1960, p. 238). It is pollinated exclusively by a species of soft-winged flower beetles, whose flight distance is one to ten feet, and seeds are dispersed passively (Epling et al., 1960, p. 240, p. 243; Schemske & Bierzychudek, 2001, p. 1270). The life cycle of *Linanthus* shows two patterns. In wet years, when there is enough rainfall in winter, seed germination occurs, and plants flower in early to late April, shedding seeds in late May to early June. In dry years, no seed germination occurs, although seeds can remain dormant in the soil for seven years or longer (Epling et al., 1960, p. 240, p. 250; Schemske & Bierzychudek, 2001, p. 1270). In a favorable wet year, thousands of plants bloom and cover the desert as if snow has fallen: hence the common name "desert snow" (Epling & Dobzhansky, 1942, p. 318).

In April 1941, a population of 10–100 billion blooming *Linanthus* plants covered an 840-square-mile region of the Mojave Desert (Epling & Dobzhansky, 1942, pp. 329–330; Wright, 1943a, p. 141). The distribution of flower color exhibited interesting patterns. Overall, white flowers were most abundant, and in some areas there were only white flowers. But in three separate areas—referred to as the "variable areas" (Epling & Dobzhansky, 1942, p. 323, p. 323)—blue and white flowers coexisted (Fig. 1). There were no obvious geographical barriers that might have been responsible for these patterns. This striking dimorphism caught the attention of the UCLA botanist Carl Epling, and after he told Theodosius Dobzhansky about the *Linanthus* population, Dobzhansky saw that its conspicuous dimorphism seemed to facilitate a study of population structure, which he had been working on. At Dobzhansky's urging,

³ Wright does not seem to think that his view has hardened (Wright, 1988, p. 121).

⁴ Provine (1986, pp. 429, 435) acknowledges this point too but argues that Wright's view became more selectionist.

⁵ Wright's work on *Linanthus* is relevant to contemporary biology, as the empirical test of Wright's shifting balance theory is an ongoing problem (Coyne, Barton, & Turelli, 2000, 1997; Goodnight & Wade, 2000; Peck, Ellner, & Gould, 1998; Plutynski, 2005; Skipper, 2002; Wade & Goodnight, 1998) and the recent studies of the *Linanthus* population challenge his work (Schemske & Bierzychudek, 2001, 2007; Turelli, Schemske, & Bierzychudek, 2001).

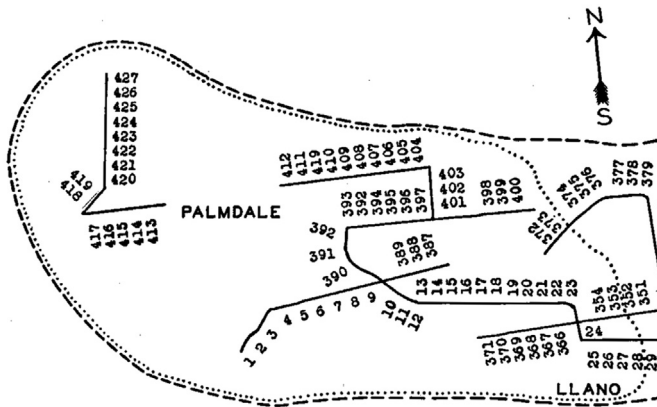


Fig. 1. A portion of Epling and Dobzhansky's map of stations. Solid lines indicate the roads traveled during the survey. The broken line marks the geographical limit of the occurrence of *Linanthus*. Inside the dotted line is the variable area, where blue and white flowers coexisted. Reproduced from Epling and Dobzhansky (1942, p. 320) with permission from the Genetics Society of America.

Epling and his students immediately started an extensive survey (Provine, 1986, p. 371), and between May and October 1941, Epling and Dobzhansky analyzed the data and wrote a manuscript.⁶

In October 1941, Dobzhansky sent Wright the manuscript on *Linanthus* (Dobzhansky to Wright, October 30, 1941).⁷ Epling and Dobzhansky suggested that the patterns of flower color distribution in the variable areas were likely to be due to subdivision of a population into small sizes. For they showed that the statistical distribution of samples containing various proportions of blues resembled the U-shaped distribution of gene frequencies, which, according to Wright (1931, pp. 122–128), was expected if the effective population size and mutation and migration rates were so small that change in gene frequency in each generation was dominated by stochastic factors, such as genetic drift (Epling & Dobzhansky, 1942, pp. 331–332).

In November, Wright wrote a detailed response, arguing that in addition to population subdivision, migration and selection may also be contributing to the observed patterns of flower color distribution (Wright to Dobzhansky, November 1941).⁸ Wright calculated the mean frequency $\bar{q}$ of a gene for blue and standard deviation σ_q of the frequencies of q in the samples.⁹ He presented the results in the first two rows of Table 1 (Wright to Dobzhansky, November 1941). From $\bar{q}$ and σ_q , Wright calculated the product Nm of population size N and migration rate m . But since no separate measurement of N or m was available, Wright had to constrain the value of at least one of these parameters and calculate the value of

Table 1

Wright's 1941 analysis of the *Linanthus* data. $\bar{q}$ is the mean gene frequency in the total population, σ_q the standard deviation in the gene frequency q among smaller territories within the total population, N the effective population size, and m the migration rate. The expression $\sigma_q/\sqrt{\bar{q}(1-\bar{q})}$ indicates the variability of gene frequencies in smaller territories relative to the total population. Redrawn from Wright to Dobzhansky, November 1941 with permission from the American Philosophical Society.

Blue recessive	White recessive
$\bar{q} = .1291$	$\bar{q} = .0718$ (blues give)
$\sigma_q = .2823$	$\sigma_q = .2056$
$\frac{\sigma_q}{\sqrt{\bar{q}(1-\bar{q})}} = .8420$	$\frac{\sigma_q}{\sqrt{\bar{q}(1-\bar{q})}} = .7962$
$Nm = \frac{1}{4} \left[\frac{\bar{q}(1-\bar{q})}{\sigma_q^2} - 1 \right] = .1026$	$Nm = .1443$
If $N = 100$, $m = .001026$	If $N = 100$, $m = .001443$
If $N = 10$, $m = .01026$	If $N = 10$, $m = .01443$

the other. In the bottom two rows of Table 1, Wright considered two possible values of N , 10 and 100, and calculated the corresponding values of m . These values of N refer to the effective size of a local population of breeding individuals rather than the total population size, which was estimated to be 10 to 100 billion.

By considering the effective size of a local population that is much smaller than the total size, Wright was assuming that the total *Linanthus* population was not a single population of billions of randomly mating individuals but was composed of numerous, partially isolated local populations. The assumption was reasonable for the population of insect-pollinated plants distributed over 840 sq mi.

Wright then calculated the distribution of gene frequencies without selection and mutation by substituting the parameter values given in Table 1 into the following equation (Wright to Dobzhansky, November 1941):

$$\varphi(\bar{q}) = C\bar{q}^{4Nm\bar{q}-1}(1-\bar{q})^{4Nm(1-\bar{q})-1} \quad (1)$$

where C is a constant guaranteeing that the area under the curve is one.¹⁰ Equation (1) represents a balance of two factors—migration and random drift due to population subdivision—but it did not fit with Epling and Dobzhansky's data well.¹¹ Thus, Wright suggested that adding a slight selection for the heterozygotes to the equation would make the theoretical distribution exhibit a pattern similar to the observed (Wright to Dobzhansky, November 1941). In short, Wright explained the observed pattern of gene frequencies in *Linanthus* as the result of an interaction—a balance—between three factors: drift, migration, and selection.

3. Epling, Wright, and the hardening of the modern synthesis

3.1. Epling and the hardening of the modern synthesis

After his 1941 survey, Epling launched what would become more than twenty years of observational and experimental studies

⁶ Epling and his students collected samples as follows. They created a station every half-mile along the roads forming a rough grid in the desert and ran, at each station, a transect at approximately right angles to the road. Along each transect, they made four equally spaced sampling points, at each of which, when there were plants, they counted plants until 100 and recorded the numbers of blue and white. Epling and his students made 1261 sampling points, counting a total of 113,955 whites and 12,145 blues (Epling & Dobzhansky, 1942, pp. 322–325).

⁷ Wright's correspondence cited in this paper is available in Sewall Wright Papers, Series I, American Philosophical Society, and each citation refers to the correspondent and date.

⁸ This letter, the handwritten copy of which has survived, is dated "November 1941." Dobzhansky replied on November 29 (Dobzhansky to Wright, November 29, 1941); for a discussion of this exchange, see Provine (1986, pp. 372–373).

⁹ In 1941, Epling was not able to germinate seeds of *Linanthus* and determine the mode of inheritance of the flower color (Epling & Dobzhansky, 1942, p. 332; Dobzhansky to Wright, October 3, 1941; Dobzhansky to Wright, October 30, 1941). Wright thus made different assumptions about which flower color is dominant and inferred distributions of gene frequencies from Epling and Dobzhansky's data (Wright to Dobzhansky, November 1941).

¹⁰ Equation (1) is a special case of Wright's general equation for the distribution of gene frequencies, which takes into account many other evolutionary factors. For the general equation that Wright had arrived at by the time of his letter to Dobzhansky, see Wright's 1941 Josiah Willard Gibbs Lecture (Wright, 1942, pp. 231–234).

¹¹ This was not a direct comparison, because the unit of the distribution was the mean gene frequencies $\bar{q}$, but the unit of Epling and Dobzhansky's data was phenotype frequencies. To overcome this problem, Wright constructed a frequency distribution of number of samples in Epling and Dobzhansky's table. One dimension of this distribution was percentages of blue divided into 12 classes, and the other dimension was the number of samples out of 1261 whose percentages of blue correspond to each class. Wright then converted the theoretical distribution of gene frequencies into the theoretical distribution of number of samples (Wright to Dobzhansky, November 1941).

of *Linanthus*. In the spring of 1944 Epling and his associates set up a permanently marked transect in the area where both blue and white had coexisted at least since the 1941 survey. They collected the data every year from 1944 on except when there were no or too few plants to count (1950, 1951, 1955, 1956, and 1958).¹²

In 1959, the year of the Darwin Centennial, Epling and his collaborators Harlan Lewis and Francis Ball submitted to *Evolution* a manuscript on their long-term study of *Linanthus*. Contrary to the conclusion reached by Epling, Dobzhansky, and Wright in the early 1940s, Epling and colleagues presented two arguments for the thesis that selection, rather than genetic drift, is the primary cause of the observed patterns of distribution of flower colors (Epling et al., 1960, p. 254). The first argument was based on Epling and colleagues' finding that the mean frequencies for the entire transect in the period 1944–1947 and in the period 1953–1957 (excluding 1955 and 1956 as no counts were made in these years) showed a stable cline (Epling et al., 1960, p. 245). A cline, introduced by Huxley (1938), refers to a spatial gradient of the distribution of phenotypes or genotypes. For Epling and colleagues, the stability of the cline of phenotype frequencies suggested that “if genetic drift has played a role, it has been of only local consequence and not persistent in its effects” (Epling et al., 1960, p. 254). “Conversely,” they claimed, the stability of the cline suggests “an intense local selection because the blues are concentrated in certain areas and because persisting clines of blue and white frequencies have been found” (Epling et al., 1960, p. 254; emphasis mine).

The second argument was based on Epling and colleagues' finding that seeds of *Linanthus* could remain dormant at least seven years in the soil.¹³ Since the seed storage should increase the effective population size, Epling and colleagues said:

The conclusion seems warranted, *therefore*, that the frequencies of blue and white flowered plants are in the long run the product of selection operating at an intensity we have been unable to measure; and that the large size of the effective population, and the localized dispersion of pollen and seeds, has precluded significant changes in pattern during 15 seasons (Epling et al., 1960, p. 254; emphasis mine).

Although Epling and colleagues acknowledged local dispersal, which would make the effective population size smaller, they argued that the phenotype distribution in *Linanthus* is the product of natural selection.

These arguments follow the same pattern of inference that reflects Epling and colleagues' hard-line selectionism. According to Epling and colleagues, the stability of the cline suggests that drift is not an important factor, and it “conversely” suggests that selection must be the most important factor. Similarly, the seed storage increases the effective population size, making drift unimportant. “*Therefore*,” selection must be the most important factor, although its intensity is too small to be detected. The stability of the cline and the seed storage surely suggest that selection can be a factor in the *Linanthus* population, but Epling and colleagues' arguments were

different. Their arguments went from the evidence that the influence of random drift is not strong in a population to the conclusion that natural selection must be *the most important* factor in that population. This form of inference is licensed by hard-line selectionism.

3.2. Wright's response

In response to Epling and colleagues' paper, Wright wrote two manuscripts, one in 1960 and the other in 1962.¹⁴ In the introduction of the 1960 manuscript, Wright explicitly noted that Epling and colleagues argued for selection only by elimination of random drift:

They [Epling, Lewis, and Ball] conclude that the frequencies of blue and white flowered plants are in the long run the product of selection. This conclusion was however arrived at *only by elimination* since studies of topography, soil samples, and of associated vegetation in areas in which one or the other color predominates have given no indication of any basis for differential selection. (Sewall Wright Papers, Series IIa, Folder 29; emphasis mine).

Wright's point was that Epling and colleagues did not find any positive evidence for the importance of selection in the *Linanthus* population. As indicated by the passage quoted in the epigraph, he believed that neither selection nor drift *alone* would adequately explain the geographical pattern of the dimorphism in *Linanthus*. In other words, he did not think that selection could be so important that other evolutionary factors became irrelevant (see also Wright, 1948, p. 281). His view was plausible since, as mentioned in Section 2, the *Linanthus* flowers were pollinated by beetles whose flight distance is only one to ten feet. Wright further argued that the hypothesis of the interaction between drift and migration explained the 1941 *Linanthus* data better than the selection hypothesis now favored by Epling and colleagues.¹⁵

In a different line of response to Epling and colleagues, Wright paid special attention to the clinal selection hypothesis and contrasted it with the balance-of-factors hypothesis involving drift and migration. Wright considered two forms of a cline: plane cline (uniform gradient in one direction) and conical cline (gradient falling off uniformly in all directions from a point). Wright tested how well the balance-of-factors hypothesis, the plane cline hypothesis, and the conical cline hypothesis fit the 1941 *Linanthus* data. The balance-of-factors hypothesis turned out to fit the data better than either of the clinal selection hypotheses. Moreover, Wright argued that it would be surprising if there were fine-grained clinal selection in the areas where blue and white were mixed:

To account for the observed distribution of blue on a largely selective basis would require a distribution of selective values, favorable and unfavorable to blue, in a fine-grained pattern that happens to simulate very closely that expected from random drift and dispersion. This would be a surprising pattern of

¹² In addition to this transect study, Epling and his associates did the following: In 1944, they established three stations in the area where blue and white coexisted. Every year from 1944 on, they recorded the frequencies of blue and white in these plots. In 1948, they established two new plots for the elimination experiment where plants of *Linanthus* were removed before they left seeds in each year so that the next year's plants had to grow from whatever seeds were dormant underground. In November 1954, they transplanted the seeds obtained from blue flowered plants living in an all-blue area to an all-white area in order to test the viability of seeds in different areas. The results of all these studies were reported in Epling et al. (1960).

¹³ This was found in the elimination experiments (see footnote 12).

¹⁴ Provine (1986, pp. 487–488) mentions in passing the typescript of the 1962 manuscript.

¹⁵ Other responses include: (i) Contrary to Epling and colleagues' claim that the cline of phenotype frequencies remained stable over the years, their data, after Wright's analysis, indicated temporal variation in the percentages of blue that cannot be attributed to sampling error alone. (ii) Wright's analysis of Epling and colleagues' data also showed that the variance of the frequencies of blue increased from 1944 to 1957, suggesting random drift within local populations. The variance quickly decreased at some time between 1957 and 1962.

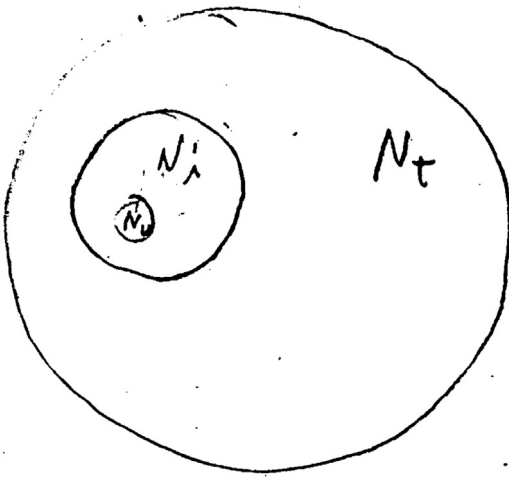


Fig. 2. Wright's diagram of hierarchical population structure. N_t is the size of the total population, and N_u is the size of a random breeding unit. N_i is the size of an intermediate population within the total and containing certain number of random breeding units. Reproduced from [Wright to Dobzhansky, November 1941](#) with permission from the American Philosophical Society.

selection to find in an apparently uniform environment since it requires such a delicate balance between opposed selective advantages that there is reversal an enormous number of times within any mixed area. The evidence... thus points strongly toward the joint effects of random drift and dispersion as the principal explanation of the pattern (Sewall Wright Papers, Series II, Box 2).

Clinal selection is directional (for or against blue), so in order for it to maintain dimorphism within a small area, its direction needs to change from time to time. Since in the 1941 data there were many such mixed areas in an apparently uniform environment, Wright argued that a kind of selection that could maintain dimorphism in these areas would be a surprising form of selection.¹⁶

As noted in Section 2, in the 1940s, Wright argued that the observed pattern of dimorphism in *Linanthus* is best explained as a result of the balance between drift, migration, and selection. The account presented thus far shows that even in the heyday of the hardened modern synthesis, Wright was opposed to hard-line selectionism and continued to pursue a balance-of-factors hypothesis that would explain the observed pattern of dimorphism in *Linanthus*.

4. Theory of isolation by distance

We have seen that while the community of evolutionary biologists hardened, Wright kept the balance of factors at the center stage. In this and the next sections, I show that Wright's work on *Linanthus* provided a theoretical and empirical underpinning for his pursuit of the balance-of-factors hypothesis. Between the 1940s and 1970s, Wright developed his theory of isolation by distance and used it to characterize the balance between drift, selection, and

migration in the *Linanthus* population. The theory of isolation by distance was thus Wright's major addition to his shifting balance theory, but as we shall see, its application to natural populations required an unrealistic assumption about population structure.

4.1. Isolation by distance

Recall that Wright's shifting balance theory posits a population that is subdivided into partially isolated demes. Suppose that a population occupies a large area in which there are no geographical barriers. In such a population, the structure posited by the shifting balance theory would arise if individuals tend to disperse over short distances and mate with their neighbors. When this occurs, a population is under isolation by distance in Wright's sense of the term ([Ishida, 2009](#)). According to Wright, in a population under isolation by distance,

there is complete continuity of distribution [of individuals], but interbreeding is restricted to small distances by the occurrence of only short range means of dispersal. Remote populations may become differentiated merely from *isolation by distance* ([Wright, 1943b](#), p. 117, p. 117).

There are two assumptions here: (1) Individuals in a population are uniformly distributed over a large territory, and (2) individuals disperse over relatively short distances from their birthplaces to locations where they produce offspring (see also [Wright, 1940](#), p. 245).

To quantitatively describe the structure of population under isolation by distance, Wright proposed the concept of random breeding unit, the smallest subpopulation within which there is random mating. In his 1941 letter to Dobzhansky, Wright explained this concept using a diagram ([Fig. 2](#)):

Let N_t be the size of the total population and suppose this to be subdivided into K territories of effective size $N_i = N_t/K$ and these into territories of size N_u within which there is random mating. Then the amount of variability of gene frequency calculated for the territories of size N_i is a function of the unknown size of the random breeding unit (actually the number of individuals from which the mate of any single individual is drawn). ([Wright to Dobzhansky, November 1941](#)).

Wright's idea is that as long as the geographical range of the population is greater than the area over which individuals disperse, parents of a given individual are drawn from a smaller area around that individual. Thus, there is a "unit" population whose effective size is smaller than the total population size. In 1941, there were 10–100 billion *Linanthus* flowers, but if the *Linanthus* population is under isolation by distance, there will be a large number of small random breeding units.

The concept of random breeding unit enabled Wright to apply Equation (1) to a population under isolation by distance. With the key assumption to be discussed below, Wright could simply substitute the size of a random breeding unit for the effective population size in Equation (1).

4.2. Wright's F_{ST}

In the passage from his 1943 paper quoted above, Wright also noted the connection between population structure and variability of gene frequency. The last sentence of the above passage refers to the results that Wright had given in his earlier papers. Wright showed that if the size of random breeding unit is small, say, 100 or

¹⁶ This was not the first time Wright considered the hypothesis of local environmental selection with regard to *Linanthus*. The hypothesis was suggested by William Hovanitz in 1942 after he saw Epling and Dobzhansky's paper (Hovanitz to Wright, May 28, 1942; Wright to Hovanitz, June 11, 1942; see also [Provine, 1986](#), pp. 375–376). Wright acknowledged Hovanitz' suggestion in his 1943 paper on *Linanthus* ([Wright, 1943a](#), p. 155). [Schemske and Bierzychudek \(2001, 2007\)](#) report evidence for temporally varying selection at a small locality.

less, frequencies of a gene in random breeding units can exhibit considerable random fluctuations (e.g., a gene may be fixed in some unit populations, lost in some, and in intermediate frequencies in others) (Wright, 1938, 1940).

In his 1943 paper on isolation by distance, Wright showed that isolation by distance has significant evolutionary consequences. For example, heterozygosity will decrease in a population under isolation by distance because local individuals become more and more genetically related and thus tend to be homozygous at a given locus. This means that the degree of inbreeding, as measured by the inbreeding coefficient F , increases in a population under isolation by distance. Yet, in this case, the reduction in heterozygosity is a result of random mating in a subdivided population rather than any systematic breeding between relatives. Wright clearly contrasted inbreeding with random mating, and identified two components of F : one is inbreeding and the other isolation by distance. He said:

The inbreeding, measured by F , may be of either of two extreme sorts: sporadic mating of close relatives with no tendency to break the population into subgroups, and division into partially isolated subgroups, within each of which there is random mating. The latter is the case in which we are primarily interested here (Wright, 1943b, p. 116, p. 116).

Of course, random mating in a finite population eventually leads to a population of relatives so that random mating becomes mating between relatives. But as a system of mating, there is an ecological difference between inbreeding (e.g., self-fertilization, brother-sister mating, etc.) and random mating in a finite population.¹⁷

Wright developed F_{ST} as a measure the effect of isolation by distance on gene and genotype frequencies, especially on the extent of local genetic differentiation. F_{ST} is defined as follows (Wright, 1943b, p. 116):

$$F_{ST} = \frac{\sigma_x}{\sqrt{q_y(1 - q_y)}} \quad (2)$$

where σ_x is the standard deviation of the frequencies of a gene of interest (say, A) among subgroups x 's in a population. The total population or any subpopulation that contains x 's is referred to as population y . q_y is the frequency of A in y . $1 - q_y$ is the frequency of the other allele (say, B) at the same locus.

The concept of random breeding unit introduced above (see Fig. 2) is related to F_{ST} . For a given size N_u of a random breeding unit, F_{ST} decreases as the size N_i of a subpopulation increases, and for a given value of N_i , F_{ST} increases as N_u decreases (Fig. 3).

Greater F_{ST} values mean greater amount of local genetic differentiation: random breeding units have widely different frequencies of a given gene, including fixation in one unit and loss in another.¹⁸

Wright calculated the values of F_{ST} for a variety of subpopulations in *Linanthus*, including random breeding units, sampling stations (collections of random breeding units), and higher divisions. He concluded that the size of a random breeding unit is

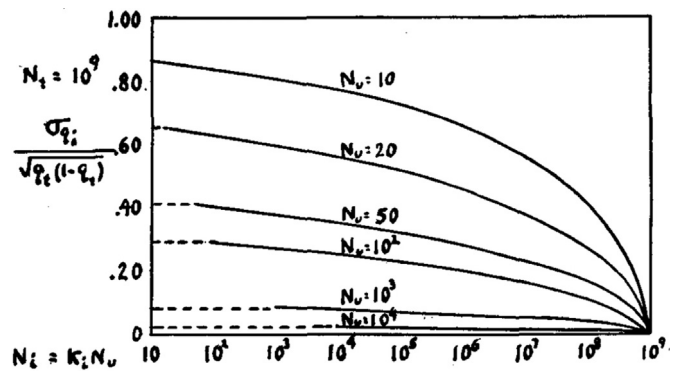


Fig. 3. Theoretical curves of F_{ST} . F_{ST} (the vertical axis) is defined according to Equation (2). The size N_i of the subpopulation under consideration (the horizontal axis) is equal to K random breeding units of size N_u . The total population N_t is constant. Reproduced from Wright (1943b, p. 122) with permission from the Genetics Society of America.

between 14 and 27. Such small size in turn implied that changes in gene frequency among random breeding units and possibly among stations (a lower level of the hierarchy) are random. Therefore, he argued that random changes in gene frequency in local populations could explain the local patterns of the distribution of flower color (e.g., the fact that two adjacent stations had widely different frequencies of blue). However, Wright also found it difficult to explain the global pattern of the distribution (e.g., the fact that there is a large area of all whites) by appealing solely to random drift. He thus suggested that the cumulative effect of mutation between blue and white, occasional long-distance migration, and slight selection for white could explain the global pattern (Wright, 1943a, p. 155).

4.3. Uniformity of population structure

Once the size of a random breeding unit is found, Wright could substitute it for N in Equation (1). This substitution was licensed by a key assumption, which can be formulated as follows:

The uniform structure assumption: There is no variation in the kinds and magnitudes of evolutionary factors from one random breeding unit to another.

The assumption implies that all parameter values in Equation (1) are constant throughout the geographical region occupied by the population in question. This is of course an idealization, but it allows one to use Equation (1) with a single set of parameter values to describe the distribution of gene frequencies in a population as a whole. Thus, Wright assumed that all random breeding units have the same effective population size N and the migration rate m (see Table 1) and substituted these values into Equation (1). In practice, this is a significant convenience, and indeed, in the early 1940s, Wright made the uniform structure assumption because of its convenience, even though he was aware that in reality it was almost certainly false (Dobzhansky & Wright, 1941, p. 35). As we shall see, Wright would find evidence that this assumption is false in the *Linanthus* population.

5. Spatially varying balance between drift and selection in *Linanthus*

Recall that in 1941 Wright found that the theoretical distribution of gene frequencies did not fit well with the *Linanthus* data. In the 1970s, Wright improved the fit by relaxing the uniform structure assumption (Wright, 1978a, pp. 209–211). This new

¹⁷ For the “parallelism” between drift (due to population structure) and inbreeding, see Hartl & Clark (1997, pp. 283–289).

¹⁸ Wright’s shifting balance theory was originally motivated by his theory of optimal animal breeding, which emphasizes the importance of the cooperation of inbreeding and selection (see Wright, 1978b; Provine, 1986, p. 236; Hodge, 1992, 2011). Wright’s inbreeding coefficient F comes from his animal breeding theory, but in his theory of evolution, Wright used F to represent the effect of both inbreeding and random drift. Provine (2015) thus claims that Wright confused inbreeding and drift and argues that drift does not exist independently of inbreeding, because drift just is inbreeding. I think Provine fails to appreciate that Wright understood inbreeding and random mating as different systems of mating.

development began in 1972 while Wright was preparing to include the *Linanthus* case in his 1978 book (see Wright, 1978a, pp. 194–223).

5.1. Wright's 1972 analysis

In September and October 1972, Wright reanalyzed the 1941 *Linanthus* data, referring back to his notes from 1942 (Sewall Wright Papers, Series IIa, Folder 40). On September 16, he wrote a new note on the table of F values he produced in 1942 (Fig. 4).

Various statistics derived from the table, written on the right hand side of the page, were published in Wright's 1943 paper on *Linanthus* (Wright, 1943a, p. 145). Fig. 4 lists sampling stations (the first column from the left) in the ascending order of frequencies of blue (the second column) together with the values of F (the third column). Wright's note on the bottom of the page, dated September 16, 1972, reads (Fig. 5):

9-16-1972
More blue when F is high: could imply that selection favors white slightly and that only when effective N is very small (F high) can blue rise to high frequencies.

Fig. 5. Close-up of Fig. 4. Reproduced from Sewall Wright Papers, Series IIa, Folder 11 with permission from the American Philosophical Society.

More blue when F is high: could imply that selection favors white slightly and that only when effective N is very small (F high) can blue rise to high frequencies. (Sewall Wright Papers, Series IIa, Folder 11).

Stn	Blue	F	Stn	Blue	F
359	.102	.051	412	.861	.818
154	.111	.1310	409	.661	.901
135	.119	.180	371	.667	.586
178	.127	.124	411	.737	.658
185	.143	.358	182	.788	.209
354	.147	.232	418	.853	.354
12	.153	.392	181	.861	.733
419	.170	.787	(47)	17.869	17.850
400	.191	.210		.380, 1514	13797624
397	.203	.229		2122556	
396	.216	.133		8.717385	9.847390
405	.232	.236		6.783642	6.779202
403	.244	.330		1.923743	3.068188
291	.269	.217		.040931	.0652806
13	.285	.245			
423	.289	.1341		8.135714	
398	.292	.145		6.786418	
388	.294	.226		1.849296	
422	.299	.660			
14	.306	.106			
390	.314	.197			
402	.331	.195			
11	.332	.298			
406	.336	.380			
288	.337	.412			
401	.341	.164			
152	.345	.221			
404	.348	.155			
395	.349	.051			
407	.352	.163			
387	.366	.233			
20	.372	.604			
410	.476	.766			
389	.493	.293			
180	.507	.397			
8	.515	.484			
416	.515	.752			
26	.534	.213			
27	.633	.850			
54	.653	.441			

Blue Deviation

$\bar{F} = .3802$ $\bar{F} = .3758$

$\sigma_F^2 = .04093$ $\sigma_F^2 = .06528$

$\sigma_F = .2023$ $\sigma_F = .2555$

$r = .028708$ $r = .5554 \pm .102$

$\sigma_F = .05169$ 5.458

$1 - r^2 = .69153$

$\sigma_F^2 = .4782 = .0104$

$\sigma_F = .102$

$b = .7014 \pm .1526$ 4.55

$T_b^2 = \frac{1.5545 \times .69153}{45} = .02451$

$\sigma_b = .1566$

$\bar{F}^2 = .1442$

$\sigma_F^2 = .0653$

$F = .2085$

$(.2086)$

9-16-1972

More blue when F is high: could imply that selection favors white slightly and that only when effective N is very small (F high) can blue rise to high frequencies.

Fig. 4. A page from Wright's analysis of the *Linanthus* data. The page is dated September 19, 1942 (upper right). Reproduced from Sewall Wright Papers, Series IIa, Folder 11 with permission from the American Philosophical Society.

Wright discovered a pattern in the 1941 data: the frequency of blue is correlated with the value of F . He then inferred that blue may be slightly selected against and that its frequency can increase only when the effective population size is so small that selection is ineffective.

Wright's inference seems to be based on the following consideration. As can be seen in Equation (2), F is greater when the standard deviation σ_x of gene frequency q in a subgroup x is greater. Greater σ_x implies that change in q is predominantly random, because σ_x represents random, as opposed to directional, change in q . Now if random change is due primarily to accidents of sampling and directional change to selection, and if selection pressure is constant throughout the geographical range of the population in question, then greater F for a given subgroup implies that the effective population size N of that group is smaller. Smaller F , in turn, implies larger N , making selection more effective. So the correlation between the frequency of blue and the value of F suggested to Wright that N may vary from one locality to another in the *Linanthus* population.

Thus Wright's notes suggest that he came to realize the importance of non-uniform population structure in *Linanthus* when he was going over his original notes taken in 1942. After September 16, Wright worked steadily. By September 29, he produced the table and graphs that would appear in his last published analysis of the *Linanthus* data (Sewall Wright Papers, Series IIa, Folder 40; Wright, 1978a, pp. 207–212).

5.2. Spatial variation in effective population size

Wright's final analysis, which addressed both the 1941 survey and Epling's long-term study, was published in the fourth volume of his treatise in 1978 (Wright, 1978a, 194–223).¹⁹ As in 1941, Wright compared the theoretical and the observed distributions of gene frequencies, but this time he did not require the parameter values to be constant throughout the geographical range of *Linanthus*. Instead, he allowed the effective population size to vary from one locality to another. With this relaxation of the uniform structure assumption, he was able to improve the fit between the theoretical and the observed distributions of gene frequencies (Wright, 1978a, pp. 209–211).

Wright began his new analysis by reproducing his 1941 result, using Equation (1) (Wright, 1978a, p. 209). He compared the theoretical and the observed distributions of gene frequencies under the uniform structure assumption, failing to obtain a good fit between the two distributions (Fig. 6; Wright, 1978a, pp. 207–209). However, in this analysis, by dividing the total population into western and eastern regions, he was able to find that the theoretical and the observed distributions fit relatively well for the eastern region but that they do not fit well for the western region. He then argued that such difference in the goodness of fit “could come about if the population is heterogeneous with respect to the parameters” (Wright, 1978a, p. 209). The geographical difference in the goodness of fit indicated the non-uniformity of population structure. Referring to Epling and Dobzhansky's map of the relative frequencies of blue and white in sample stations (Epling & Dobzhansky, 1942, p. 326; Wright, 1978a, p. 198), Wright argued that the data from the western region can be divided into two components, western central, W_C , and western peripheral, W_P . The frequency of blue was intermediate in sample stations in W_C (that is, the variance in q and hence F were low), whereas it was either high or low in those in W_P (that is, the variance in q and F were

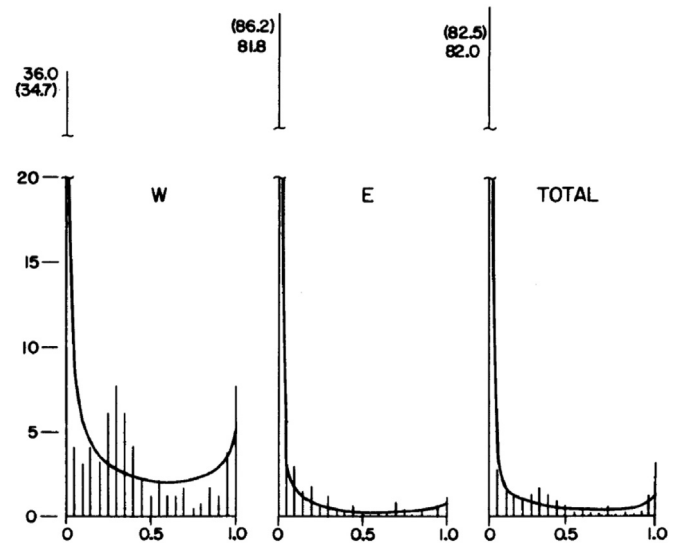


Fig. 6. The theoretical and observed distributions of gene frequencies in *Linanthus* under the assumption of uniform population structure. The x-axis is the frequencies of genes for blue (assumed to be dominant), and the y-axis shows the percentages of samples in western, eastern, and the total populations. Reproduced from Wright (1978a, p. 207) with permission from the University of Chicago Press.

high). Thus, Wright used different values of size N_u of a random breeding unit and the migration rate m to calculate the theoretical distributions of gene frequencies for W_C , W_P and W_T (western total) (Fig. 7). The theoretical distribution now exhibited a hump like the observed distribution. From the values of F , Wright estimated the effective population size for W_P to be 7 or 8 and that for W_C to be about 100 (Wright, 1978a, pp. 209–211).

In the light of this analysis, Wright noted that the shifting balance theory offers a plausible explanation of the observed patterns of flower color distribution in *Linanthus*. He said that it is

plausible that among the continually varying genetic compositions of local populations, arrived at by random drifting of the

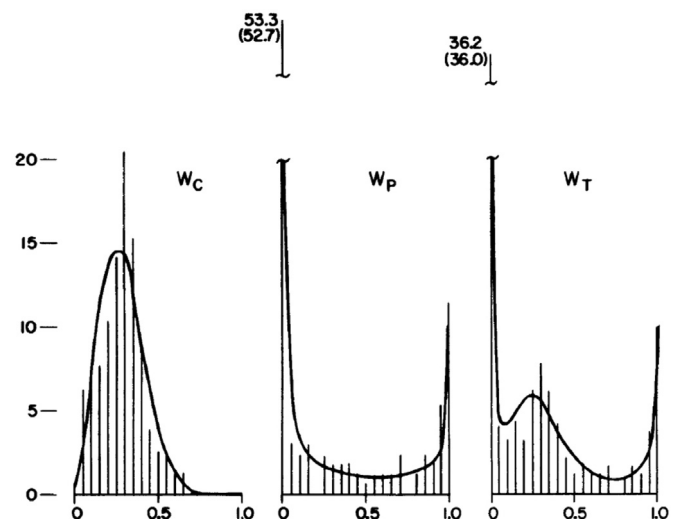


Fig. 7. The theoretical and observed distributions of gene frequencies in *Linanthus* under the assumption of non-uniform population structure. The x-axis is the frequencies of genes for blue (assumed to be dominant), and the y-axis shows the percentages of samples in Western central, peripheral, and total populations. Reproduced from Wright (1978a, p. 212) with permission from the University of Chicago Press.

¹⁹ Wright's analysis of Epling's long-term study is essentially the same as that found in Wright's 1962 manuscript.

frequencies at all other heterallelic loci, favorable interaction systems may be arrived at which spread over large areas by interdeme selection and incidentally have some effect on the selective advantage of white over blue (Wright, 1978a, p. 223, p. 223).

In other words, according to Wright, the interaction of random drift in local populations, migration between local populations, and selection for favorable genotypes across local populations (i.e., interdemic selection) can explain the observed patterns of flower color distribution at all levels from local patterns in the variable areas to global patterns in the entire geographical range of *Linanthus* in the Mojave Desert.²⁰

6. Conclusion

Gould and Provine have cited the development of Wright's shifting balance theory of evolution as one of the main cases of the hardening of the modern synthesis. But the hardening story does not adequately capture the development of Wright's theory. Thus, I have presented a more adequate account of the development of Wright's theory, highlighting two main points: First, while the community of evolutionary biologists hardened, Wright criticized hard-line selectionism and emphasized the balance of factors. Second, between the 1940s and 1970s, Wright used his theory of isolation by distance to give an increasingly sophisticated characterization of the balance of drift and selection in a subdivided population. I have argued for both of these points by analyzing Wright's long-term work on the distribution of flower color dimorphism in *Linanthus parryae*.

Let me conclude by noting two broader issues in evolutionary biology and philosophy of biology to which the account of Wright's work presented above is relevant. One is the theory of population structure. Since organisms tend to interact locally, a biological population exhibits a variety of spatial structures. Spatial population structure can change individual fitness by creating correlated interactions among individuals. Philosophers have thus far focused mostly on this consequence of population structure (e.g., Godfrey-Smith, 2008; Okasha, 2005; Skyrms, 1996).²¹ But, as Wright has shown, population structure can also affect the amount of genetic drift by reducing effective population size. Thus, population structure has implications for the interaction of drift and selection. This suggests that models of population structure used by philosophers to analyze the nature of selection have built-in assumptions about drift and its interaction with selection (e.g., Epperson, 2003; Holsinger & Weir, 2009; Rousset, 2004). One such assumption in Wright's theory of isolation by distance was the uniform structure assumption, and the examination of this assumption led to an improvement in his theory. There may be similar assumptions in the literature on selection in structured populations.

²⁰ One might say that Wright merely accommodated the data by introducing spatial variation in effective population size. This is a fair point, but Wright's final analysis does not seem ad-hoc because the uniform structure assumption, which he rejected in the final analysis, was almost certainly false. In this sense, his final analysis was more realistic, although he applied Equation (1) to different regions of the *Linanthus* population using different parameter values. For Wright, a successful explanation of the distribution of flower color in *Linanthus* appeals to a specific, local interaction of evolutionary factors. A similar lesson emerged from the evolutionary studies of shell patterns in the land snail *Cepaea* (Jones, Leith, & Rawlings, 1977). I thank John Turner for suggesting the potential adhocness of Wright's analysis and drawing my attention to the Jones et al. paper.

²¹ Abrams (2012) is an exception to my claim about philosophers' nearly exclusive focus on the effect of population structure on fitness.

The second issue is the application of mathematical models to the real-world phenomena. There is an extensive literature on the representational relationship between models and the world and the role of idealizing assumptions in model building (e.g., Bailer-Jones, 2009; Cartwright, 1983; Giere, 1988; Lloyd, 1988; Weisberg, 2013). Now, Wright was trying to make Equation (1) adequately represent the distribution of gene frequencies in *Linanthus* and use the resulting representation to support a balance-of-factors explanation of the distribution. A familiar account of mathematical modeling would make us expect that Wright made various assumptions to derive Equation (1) and then interpreted parts of the equation as representing parts of the real-world system (e.g., N is the effective size of the *Linanthus* population). Of course, this account is incomplete, and Wright's work on *Linanthus* sheds light on the neglected role of assumptions about the uniformity of population structure in the application of mathematical models in population genetics. In order to assign specific values to the parameters in Equation (1), it is not enough to say, for example, that N is effective population size. It is also necessary to say whether N takes a single value or multiple values in a given population. And to do this, Wright had to make an assumption about the uniformity of population structure. His work on *Linanthus* is valuable in revealing how this assumption allowed him to apply his mathematical model to a specific population in nature.

Acknowledgments

I thank James Lennox, Sandra Mitchell, Robert Olby, Elizabeth O'Neill, Paolo Palmieri, Alirio Rosales, Kenneth Schaffner, Jeffery Schwartz, and Kyle Stanford for comments on earlier versions of this paper and Charles Greifenstein of the American Philosophical Society Library for facilitating my access to the Sewall Wright Papers. I also thank Gregory Radick, John Turner, and an anonymous reviewer for comments and suggestions. Parts of this paper were presented at the 2009 meeting of the International Society for the Historical, Philosophical, and Social Studies of Biology. I wish to thank the audience for discussion. The archival research was supported by the Wesley C. Salmon Fund, University of Pittsburgh.

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