retrieved items grows sharply.

The text linking and retrieval system described in this report is applicable to text collection in arbitrary subject areas covering texts that vary widely in scope and length. Its operations depend on either the use of discursive English language queries that provide good descriptions of the wanted subjects or the availability of relevant text excerpts that can serve as initial queries. When a sufficient global text similarity exists between the available query vectors and the vectors representing the stored text items and local similarities are detected between certain paragraphs and sentences included in the sample texts, the conclusion follows that the texts are closely related. No other text search and retrieval approach currently contemplated appears to offer equal promise for unrestricted text environments and arbitrary subject matter.

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4. The 29-volume Funk and Wagnalls encyclopedia being searched consists of approximately 24,900 articles numbered in alphabetical order from 1 to 24,900. The article length varies from a few words (for cross-references) to many pages of printed text. The authors are grateful to the Microsoft Corporation for making available a machine-readable version of the encyclopedia.
5. Formally, evaluation parameters such as recall and precision are often used, representing the proportion of relevant items retrieved and the proportion of retrieval items that are relevant, respectively. Recall is the number of retrieved and relevant items divided by the total number of relevant items in the collection; precision is the number of retrieved and relevant items divided by the total number retrieved.
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Wright's Shifting Balance Theory: An Experimental Study

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Experimental confirmation of Wright's shifting balance theory of evolution, one of the most comprehensive theories of adaptive evolution, is presented. The theory is regarded by many as a cornerstone of modern evolutionary thought, but there has been little direct empirical evidence supporting it. Some of its underlying assumptions are viewed as contradictory, and the existence and efficacy of the theory's fundamental adaptive process, interdemic selection, is the focus of controversy. Interdemic selection was imposed on large arrays of laboratory populations of the flour beetle *Tribolium castaneum* in the manner described by Wright: the differential dispersion of individuals from demes of high fitness into demes of low fitness. A significant increase in average fitness was observed in the experimental arrays when compared to control populations with equivalent but random migration rates. The response was not proportional to the selection differential: The largest response occurred with interdemic selection every two generations rather than every generation or every three generations. The results indicate that the interdemic phase of Wright's shifting balance theory can increase average fitness and suggest that gene interactions are involved in the observed response.

WE REPORT THE RESULTS OF A 4-year experimental investigation of Wright's shifting balance theory of adaptive evolution (*1–4*). Wright's theory, proposed 60 years ago (*1, 3*), is one of the most widely known and comprehensive theories of adaptative evolution (*5*), regarded by many as "a cornerstone of modern evolutionary thought" (*6*, p. 265) and as "the dominant theory of evolution in the 20th century" (*7*, p. 625). However, there are several aspects of the theory that to date "have never been analyzed in detail" (*8*) and are unsupported by empirical data (*9*), either at the populational or molecular level. Recent mathematical investigations of Wright's theory (*10*) illustrate that, under certain conditions, interdemic selection through differential dispersion, the central adaptive mechanism of Wright's theory, can cause genetic change. However, it is not known whether the conditions necessary in the model are met by populations in nature. Our experiments with the flour beetle *Tribolium castaneum* demonstrate the efficacy of interdemic selection by differential dispersion for causing genetic change.

Wright (*3*) identified three phases important to his theory, all of which are acting simultaneously: (i) random genetic drift when "the set of gene frequencies drifts at random in a multidimensional stochastic distribution about the equilibrium set characteristic of a particular fitness peak" (*3*, p. 455); (ii) mass selection when the set of gene frequencies drifts far enough within one deme to cross over into the domain of attraction of a different adaptive peak—that is, "There ensues a period of relatively rapid change in this deme, dominated by selection among individuals (or families) . . ." (*3*, p. 455); and (iii) interdemic selection when a deme ". . . by excess dispersion, systematically shifts the position of equilibrium [of other demes] toward its own position" (*3*, p. 455).

Some phases of the shifting balance process appear to be in conflict with one another. In order for phase (i) to operate efficiently, small numbers of breeding adults and little migration are required, but these conditions make phase (ii), mass selection, inefficient unless selection is much stronger than random genetic drift. We do not know how much heritable variation among demes in local mean fitness can result from the combined action of random genetic drift and mass selection: "The relative importance of natural selection and random genetic drift . . . remains the most important unsolved problem in our understanding of the mechanisms that bring about biological evolution" (*11*, p. 164). We know little of the existence or the density of "local adaptive peaks" or the evolutionary role of epistasis for fitness (*8, 12–13*), but recent theory (*14*) indicates its potential importance. Little is known about the rate of origination of the genetic and phenotypic variation in average fitness among demes which are necessary for operation of the third phase: Just as individual (mass) selection requires genetic variation among individuals, interdemic selection requires genetic variation among demes (*15*). Last, the export of gene combinations in phase (iii) may require the dispersion of large numbers of adults from one deme to another and interfere with the first phase. In summary, quantitative information from the laboratory or field is lacking for each of the three phases.

Local breeding numbers, N_e, and migration among demes, m, affect the rate of genetic differentiation of demes for fitness, and small amounts of differential migration

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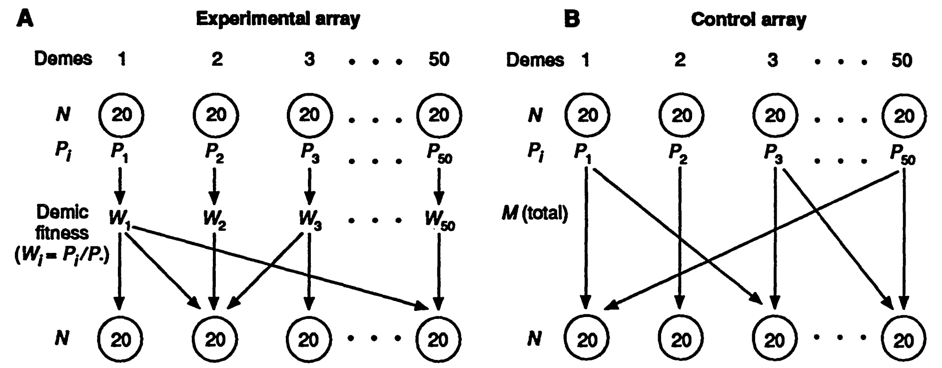

Fig. 1. (**A**) Schematic diagram of the laboratory model of Wright's shifting balance process: N is the number of breeding adults used to establish each deme at the start of each generation and P_i, productivity, is the number of adult progeny produced by N parents in 60 days; demic fitness, W_i, is equal to P_i divided by the average productivity, $P.$. (**B**) Schematic diagram of a control treatment: the number of migrants, *M (total)*, in this array is determined by the number of migrants in the corresponding experimental array.

(m) among demes, in the range $0.005 < m < 0.050$, can be sufficient for phase (iii) of Wright's process (*10*). If local breeding groups consist of 100 adults, this means that one to five migrants per deme per generation may be sufficient to export an adaptive peak or gene combination from one deme to another. In *Tribolium*, for values of N_e between 6 and 96 breeding adults per deme and for m of between 0.00 and 0.16 (that is, between 1 and 12 migrants per deme per generation), we found that genetic differences among demes for fitness developed rapidly, within 10 to 15 generations, especially for small numbers of migrants (*16–17*). The response to artificial interdemic selection was proportional to the observed amount of among-deme genetic variation. The interdemic selection (*16–17*), however, consisted of differential extinction and colonization rather than the differential dispersion of Wright's third phase. A basic relation between fitness variation among demes and the response to interdemic selection was shown but with a mechanism of interdemic selection different from Wright's. In addition, selection was strong, with selection differentials often greater than 0.50 phenotypic standard deviations.

Interdemic and individual selection for increased leaf area in the cress *Arabidopsis thaliana* resulted in a rapid response to interdemic extinction with high selection differentials [0.99 phenotypic standard deviations (*18*)]. Interdemic selection by differential extinction with large selection differentials increased emigration in flour beetles (*19*). As before, the mechanism of interdemic selection (*18–19*) was different from Wright's.

Two studies have coupled differential extinction with migration (*17, 20*), but the migration was either between demes of high fitness (*20*) or at random from among all demes (*17*), and both involved high selection differentials. No empirical studies of phase (iii), interdemic selection by differential dispersion, without extinction and recolonization have been reported.

A schematic outline of our experimental procedure is presented in Fig. 1, A and B. The experiment consisted of three pairs of experimental and control treatments. Each treatment was an array of 50 demes [300 demes total (*21*)] and each deme (*22*) was founded with 20 breeding adults (6000 adults total) taken at random from the cSM laboratory stock (*20*). Our measure of demic fitness is the census number of adult offspring (P) produced by 20 breeding adults in a 60-day period.

In the three experimental treatments, the census data were used to assign relative interdemic fitnesses. The relative fitness of the ith deme ($i = 1, 2, \ldots, 50$), w_i, was calculated as the ratio of that deme's productivity (P_i) to the average productivity within the array of 50 experimental demes ($\Sigma_i P_i/50 = P.$)—that is, $w_i = (P_i/P.)$. The relative fitness was then multiplied by 20 to determine the number of individuals chosen from this deme to found the next generation (*23*) (Fig. 2A). With this protocol, demes contribute migrants to the migrant pool in direct proportion to their productivity and demes receive migrants from the pool in inverse proportion to their productivity (Fig. 2A). In this way, we converted the variance in fitness among demes into differential dispersion among demes in the manner described by phase (iii) of Wright's theory and by Crow *et al.* (*10*). Our protocol ensured that the variance in among-deme relative fitness was equal to the among-deme variance in offspring numbers divided by the square of the mean offspring number ($P.$). The

Table 1. The selection differentials (S), numbers of migrants per deme per generation (N_m), for each generation (time) for the E1, E2, and E3 experimental treatments.

Time	E1		E2		E3	
	S	N_m	S	N_m	S	N_m
1	0.160	1.34	0	0	0	0
2	0.215	1.78	0.187	1.58	0	0
3	0.168	1.40	0	0	0.224	1.74
4	0.241	1.98	0.234	1.94	0	0
5	0.177	1.54	0	0	0	0
6	0.406	3.34	0.318	2.62	0.409	3.22
7	0.262	2.06	0	0	0	0
8	0.201	1.79	0.300	2.30	0	0
9	0.146	1.20	0	0	0.249	2.12
10	0.188	1.46	0.177	1.88	0	0
11	0.444	3.40	0	0	0	0
12	0.240	1.86	0.350	2.70	0.477	3.80
13	0.246	1.86	0	0	0	0
14	0.237	1.98	0.265	2.10	0	0
15	0.445	3.60	0	0	0.643	5.34
16	0.178	1.32	0.299	2.24	0	0
17	0.287	2.32	0	0	0	0
18	0.086	1.20	0.255	2.32	0.137	1.08
19	0.245	1.80	0.219*	1.48	0	0
20	0.231	1.64	0	0	0	0
21	0.184	1.56	0.087	1.60	0.259	2.00
22	0.210	1.60	0	0	0	0
23	0.262	2.24	0.135	1.04	0	0
24	0.145	1.28	0	0	0.167	1.32
Sum	5.604	45.55	2.826	23.80	2.565	20.62
Mean	0.234	1.90	0.118	0.99	0.107	0.86

*Interdemic selection was imposed two generations in a row by accident.

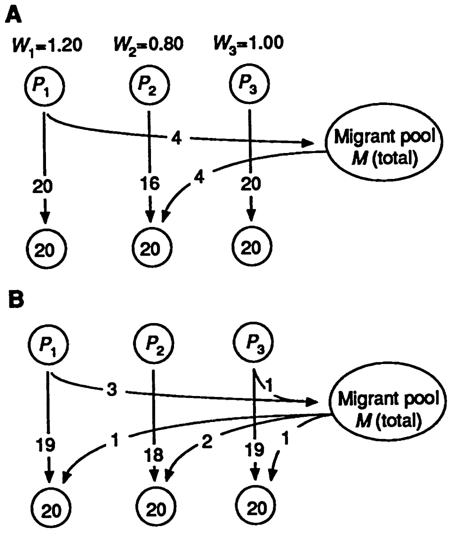

Fig. 2. (**A**) An example of the method used to impose phase (iii) of Wright's process on the experimental array of demes. Because deme 1 has a demic fitness in excess of 1.00, it contributes migrants to the pool. Because deme 2 has a fitness of less than 1.00, it receives migrants from the pool. Deme 3 has a demic fitness exactly equal to 1.00, so it neither contributes nor receives migrants. (**B**) An example of the method used to move migrants at random among demes in the control array. Deme 1 contributes three migrants to the migrant pool but receives only one migrant. Deme 2 receives two migrants although it contributes none to the pool. Deme 3 contributes and receives the same number of migrants. Total migrants in the control migrant pool is four because it is determined by the total number of migrants in (A), the experimental array.

among-deme variance in the production of offspring determined the amount and pattern of dispersion among demes.

Each of the three experimental treatments had its own control treatment of 50 demes. Migration among demes in the control array occurred at the same rate per deme as in the corresponding experimental treatment, but it was random with respect to deme productivity (Fig. 2B). The total number of individuals in the migrant pool of the experimental treatment determined the total number of migrants in the corresponding control. Thus, the same number of migrants moved among demes in the experiment and its control, and the amount of dispersion was the same in both (*24*). The important distinction is that the pattern of interdemic dispersion is differential with respect to demic fitness (*P*) in the experiment, whereas it is random with respect to *P* in the control.

The pairs of experimental (E) and control (C) treatments differed in the frequency with which the above manipulations were imposed. In the E1-C1 treatment pair, the experimental and control protocols were imposed every generation. In the E2-C2 treatment pair, the protocols were imposed every two generations. In alternating (nonselection) generations, 20 adults were chosen at random from each deme in the experimental array (E2) of 50 demes and each group of 20 was used to reestablish a deme; the same was done in the C2 control. There was no migration, either differential or random, every other generation in the E2-C2 treatment pair. In E3-C3 interdemic selection or random dispersion, respectively, was imposed every third generation.

We varied the frequency of interdemic selection among the treatment pairs in order to investigate the interaction between random genetic drift and directional interdemic selection. We expected random genetic drift and directional interdemic selection to affect the among-deme genetic variation in opposing ways: Random genetic drift operates to increase the genetic variation among demes, whereas directional interdemic selection should decrease the genetic variance for productivity among demes. In a strictly additive model, we would expect the response to interdemic selection to be proportional to the imposed selection differential, which, by design, is a function of the variance in productivity among demes. However, with nonadditive gene effects on fitness, random genetic drift might operate more rapidly to produce significant heritable variation among demes in gene combinations (*14*). We do not know what the distribution of adaptive peaks owing to co-dependent gene complexes might be. Furthermore, we do not know the efficiency with which interdemic selection by differential dispersion could "export" these gene combinations to other demes of lower fitness, although recent theoretical results (*10*) suggest that this could be small.

Using an additive model, we can predict the expected values of F_{ST}, the among-deme fraction of genetic variance (*2, 8*), for our control treatments (*24*). Given a ratio of effective (N_e) to observed (N) deme size of 0.90 (*25*), the expected F_{ST} increases almost linearly with generation: 0.0278 after one generation, 0.0548 after two generations, and 0.0811 after three generations with no migration. With only additive genetic effects and in the absence of environmental variation among demes, the interdemic selection differential is proportional to F_{ST}. Thus, the interdemic selection differential in the E2 treatment should be twice that in the E1, and that in the E3, three times that in the E1. Because the frequency of interdemic selection is the inverse of this, we expect the smaller selection differential applied every generation in E1 to produce the same response as a selection differential two (E2) or three (E3) times as large as that imposed every two or three generations, respectively. Our results (Table 1) differ from this expectation.

The interdemic selection differential in the three experimental treatments is the difference between the mean productivity of the selected parent demes ($\Sigma_i w_i P_i/50$) and the mean productivity of the unselected demes ($P.$), divided by the standard deviation of the unselected array (*12*). The standardized response to interdemic selection is the difference between the means of the experimental and control treatment pairs divided by the standard deviation of the control (*12*). The regression of the standardized response on the cumulative selection differ-

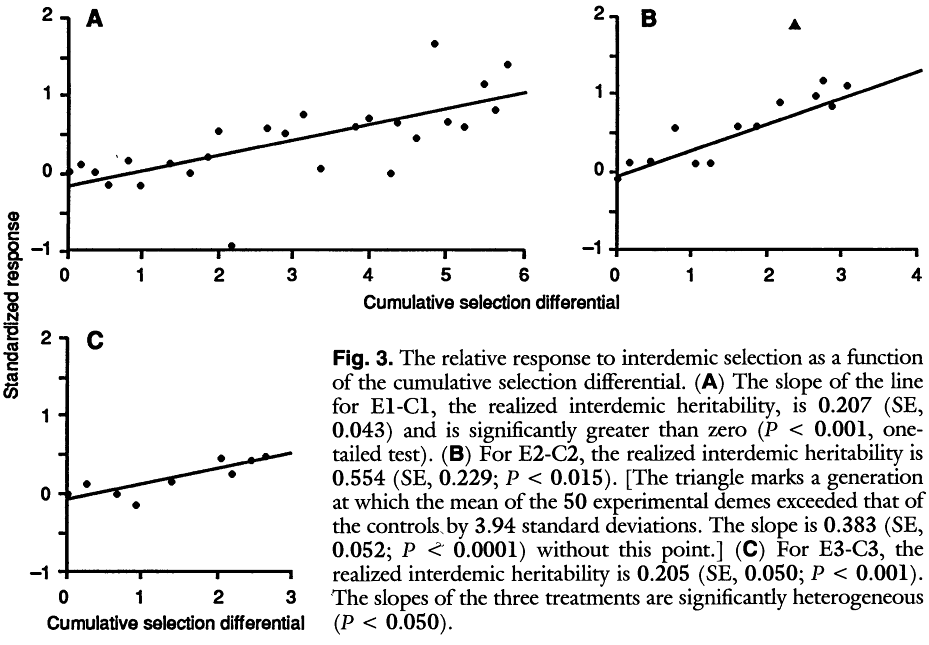

Fig. 3. The relative response to interdemic selection as a function of the cumulative selection differential. (**A**) The slope of the line for E1-C1, the realized interdemic heritability, is 0.207 (SE, 0.043) and is significantly greater than zero ($P < 0.001$, one-tailed test). (**B**) For E2-C2, the realized interdemic heritability is 0.554 (SE, 0.229; $P < 0.015$). [The triangle marks a generation at which the mean of the 50 experimental demes exceeded that of the controls by 3.94 standard deviations. The slope is 0.383 (SE, 0.052; $P < 0.0001$) without this point.] (**C**) For E3-C3, the realized interdemic heritability is 0.205 (SE, 0.050; $P < 0.001$). The slopes of the three treatments are significantly heterogeneous ($P < 0.050$).

ential is the realized interdemic heritability (*12, 26*). For an additive model, we expect the realized interdemic heritability to be homogeneous across the three treatments as discussed above.

During the experiment, we measured effective deme size and random genetic drift using a single locus, semi-dominant black body color mutation (*b*) segregating within the cSM stock and our experimental demes (*25*). In generations 13 and 14, we scored all C2 individuals for genotype at this locus. From the between-generation changes in the variance in gene frequency among demes, we estimated the effective numbers of breeding adults per deme during the course of the experiment. The average gene frequency of *b* per deme in C2 at generation 13 was 0.0625 (SE, 0.010) and the observed F_{ST} was 0.0288. In the following generation, $(t + 1)$, the average frequency was 0.0754 (SE, 0.014) and the F_{ST} was 0.0470. Using the relationship $F_{ST}(t + 1) = \{(1/2N_e) + [1 - (1/2N_e)]\,[F_{ST}(t)]\}$ and solving for N_e, we find that the ratio of $(N_e/N) = 0.90$ in agreement with earlier estimates (*25*) and single locus theory discussed above (*24*).

The selection differentials (S) (Table 1) are an order of magnitude lower than in previous experimental work. The total selection differential imposed in E1 was twice as large as that of E2 and two times as large as that of E3—that is, total interdemic selection was stronger in E1 than in E2 or E3. The amount of differential dispersion per deme per generation was low, averaging less than two migrants per deme per generation for all treatments (Table 1).

Figure 3 shows the realized interdemic heritability, the regression of response to selection on the cumulative selection differential, for all treatments. All slopes are significantly greater than zero, indicating a statistically significant response to interdemic selection in all three treatments (*26*). However, the significant heterogeneity of the slopes shows that the response differed among the treatments contrary to the additive expectation. The realized interdemic heritability was two times greater in the E2 treatment (0.383) than in the E1 treatment (0.207) despite the 50% lower selection differential. Furthermore, the realized interdemic heritability in E1 (0.207) was equivalent to that of E3 (0.205), again despite the much larger total selection differential in E1. Although E2 and E3 were nearly equal in total S (2.826 and 2.565, respectively) and average N_m (0.99 and 0.86, respectively), the response to selection was two times larger in E2 (*27*).

Our experimental design (Fig. 1A) is a laboratory model of Wright's shifting balance process. We observed a response to interdemic selection in all three experimental treatments, E1, E2, and E3 (Fig. 3). This shows that phase (iii) of Wright's process can cause an evolutionary change in mean fitness compared to controls with identical amounts of island model migration.

The relative response to interdemic selection was twice as large in the E2 treatment as in the E1 or E3 treatments contrary to additive expectation. The realized interdemic heritability for the E2 treatment was twice that of the E1 and E3 treatments (Fig. 3). Because the interdemic selection differential in E2 was only half that in E1 and because E2 and E3 had nearly identical selection differentials and migration rates, the greater relative response in E2 suggests a nonadditive genetic basis for fitness (*27*). Mathematical models of interdemic selection and sex ratio evolution have also found that selection in alternate generations can produce a response not possible with selection at every generation (*28*). Similarly, small changes in the mating structure have been shown to produce differences in direction of the trajectory of single genes (*29*).

In the C2 treatment, we used the *b* allele to measure among-deme genetic variation and found F_{ST} values between 0.03 and 0.05. This degree of genetic differentiation is characteristic of many natural populations of animals and plants (*4, 30*). Wright (*1, 3, 4*) argued that his shifting balance theory should affect evolution in species with this degree of genetic subdivision, and our experimental results provide empirical support for his arguments.

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21. In the first generation before any experimental procedures were imposed, only three arrays of 50 demes each were established. After the first census, each array of 50 demes was then split into an experimental and a control array (100 total demes) by imposing the protocols described. The number of demes in each treatment was reduced after generation 17 from 50 to 25, for reasons of tractability. This did not affect any of the treatment means but it lowered the selection differential in subsequent generations.
22. A deme consisted of 20 adults in 8 g of standard medium (by weight, 95% whole wheat flour, 5% by dried brewers' yeast, 0.03% fumigillin). All demes were positioned at random in a dark incubator (and rerandomized each generation) maintained at the standard conditions of 29°C and 70% relative humidity for 60 days at which time each deme was censused.
23. For example, if $w_i = 1.20$, then this deme would contribute 24 adults to found the next generation ($20 \times w_i = 24$). Of these adults, 20 would be used to reestablish the *i*th deme and 4 adults from this deme would be placed in a pool of migrants. If a second deme, say *j*, had a relative fitness, $w_j = 0.80$, then it would contribute 16 adults to found the next generation ($20 \times w_j = 16$). Specifically, the *j*th deme would be reestablished by drawing 16 adult offspring from it at random and adding to it 4 adults chosen at random from the total pool of migrants. A deme with a relative fitness of 1.00 would be reestablished by drawing 20 adults at random from that deme; it neither sent out nor received migrants.
24. For a neutral gene, uncorrelated with deme fitness, the F_{ST} in the experimental populations would be greater because the variance in the migration rate is greater. However, for a gene selected or correlated with demic fitness, F_{ST} would be smaller owing to the nonrandom dispersion from the high fitness demes into the low fitness demes.
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27. We do not have replication for the different selection treatments. However, under additive theory, there is sufficient migration among the 50 demes to make the array essentially a single panmictic population ($2N = 2000$). In a population this large, variation in the response to selection owing to random genetic drift is not expected to be great.
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