

# THE GENETICS OF STASIS AND PUNCTUATION

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## 1. THE THEORY

The theory of punctuated equilibria (16, 24, 25, 60) claims that most evolutionary change occurs in rapid bursts, at the time of lineage splitting (speciation), and that such punctuational events are separated by long periods of stasis during which little or no morphological change takes place. The theory arose from a study of the fossil record, and its acceptance or rejection ultimately will depend on our interpretation of that record. This review does not discuss how far the theory is correct, but rather asks what explanations can be offered for it. The question would be a waste of time if the theory were wholly false, of course. However, it seems clear that stasis is a real phenomenon, at least in some lineages at some times. It is harder to be sure about the nature of the changes, when they do occur. Thus the sudden replacement of one form by another in a

particular place may mean no more than that the new form evolved elsewhere; it does not by itself prove that the new form evolved suddenly, at the time of speciation.

The theory of punctuated equilibria was first presented (16) as the paleontological consequence of Mayr's (42, 43) theory of allopatric speciation, according to which new species arise when peripheral populations are isolated from the main body of the species. Later formulations of the theory have taken a more radical position, arguing that macroevolution can be "decoupled" from microevolution (60), that the "hopeful monsters" imagined by Goldschmidt (23) have played a critical role (24, 49), and that species selection rather than selection at the individual level is the major driving force of macroevolution (25, 60).

The simplest resolution of this controversy is to note that a change occurring over several thousand generations would be very slow to a geneticist but almost instantaneous to a paleontologist. Perhaps the best documented case of stasis and punctuation is Williamson's (72) study of fresh-water mollusks in the Lake Turkana region of Africa. The data show that morphological change was concentrated into brief periods, but also that, when changes did occur, they occurred in large populations over many thousands of generations. Commenting on these data, Jones (28) remarked that "one man's punctuation is another man's gradualism," although this is not the view held by Williamson (73).

There is, however, real disagreement among the various interpreters of the punctuated equilibria theory. Population geneticists can explain the pattern of evolution insofar as it is punctuational by saying that most of the time selection is stabilizing, leading to stasis, and occasionally directional, leading to punctuational change. The alternative view is that the failure of a species to change over millions of years must be explained in some other way—usually either by "developmental constraints," or by the inability of large populations to evolve; escape from these limitations leads to a burst of rapid evolution.

In section 2 I discuss the nature of developmental constraints and conclude that in the present context the potentially important constraints are those causing discontinuous variation. The most direct way of deciding whether such constraints have in fact been important in evolution is by studying species hybrids; this topic is reviewed in section 3. In section 4 I ask whether the often discontinuous pattern of variation in nature is caused by developmental constraints, or whether it is a consequence of sexual reproduction. Section 5 considers the alternative explanation of stasis proposed by the punctuationalists, namely, that there is something peculiar about large population size that inhibits evolutionary change. Finally, section 6 returns to the explanation of stasis in terms of normalizing selection.

## 2. CAN STASIS BE EXPLAINED BY DEVELOPMENTAL CONSTRAINTS?

Basic to the theory that stasis can be explained by developmental constraints is the idea that there are limits to the ways a population can change, determined by the ways organisms develop. Gastropod shells grow by accretion at the margin, for example, and partly in consequence their shapes are restricted to a set defined by as few as three parameters (50). I argue below that for our present purpose the important question is whether or not the constraints are continuous.

### a. *Constraints Leading to Continuous Variation*

Physiological constraints may lead to a trade-off between one aspect of the phenotype and another. For example, there is likely to be a negative correlation between the speed of limb movement and the force that can be exerted, because any increase in the leverage of a muscle will, other things being equal, increase the force and decrease the speed. This places a constraint on the kinds of animals that are possible. Of course, a change in the properties of muscle might make it possible to increase speed and strength simultaneously, but such changes are likely to be rarer than mere changes of shape.

In a second example, Williams (71) suggests that some genetic changes that increase the efficiency of an animal when young have an adverse effect on the same animal when old. For example, Rose & Charlesworth (54) found pleiotropic effects of genes affecting life history characteristics in *Drosophila* with high fecundity when young associated with a shorter life span. This is not surprising, because treatments that prevent females from laying eggs (even sterilization by X rays) prolong life (31).

These examples illustrate the rather obvious point that the range of phenotypes possible to a species is constrained. The causes vary from unbreakable laws of nature, like the law of levers, to historical features of development. Often the causes are unknown. When such constraints exist, they will present themselves to a geneticist as cases of pleiotropism. Some geneticists have argued that pleiotropism is unimportant as a constraint on evolution (37) because genetic correlations can be changed (1). In all probability we can expect the full range between easily broken correlations and almost unbreakable ones. Either way, however, such continuous constraints cannot explain stasis. They explain why species cannot evolve in any conceivable direction, but not why they do not change at all. For example, directional selection in *Drosophila* could increase fecundity at the expense of longevity or vice versa. If a species remains at a particular point on the constraint surface for long periods, it must be because of normalizing selection and not because there is nowhere it can go.

### b. *Constraints Leading to Discontinuous Variation*

There are two reasons why variation at the phenotypic level may be discontinuous. First, it is to be expected on theoretical grounds that continuous variation in some parameter at one stage of development will give rise to discontinuous variation later; such bifurcations are characteristic of all complex dynamic systems. A simple illustration is afforded by Turing's (63) reaction-diffusion theory of morphogenesis, according to which continuous variation in reaction and diffusion rates causes no change in the final pattern produced until a threshold is reached beyond which a new pattern appears. Oster et al (47) make the same point in discussing a visco-elastic model of morphogenesis. Empirically, many cases are known in which continuous change at the genetic level causes discontinuous phenotypic change (2, 27, 38, 41, 52, 75).

There is a second way in which the nature of the developmental system may impose discontinuities on phenotypic variation. We know that different gene loci are activated in different tissues or in different morphogenetic fields (36). This makes it possible, for example, for serially homologous parts to develop differently. In both arthropods and vertebrates, differentiation of initially similar parts has been an important process in evolution. This must often have required the evolution (e.g. by gene duplication) of new elements in the system of genetic regulation. The change from the activation of the same gene in two morphogenetic fields to the activation of different genes is essentially discontinuous.

The relevance of discontinuous phenotypic variation to evolutionary stasis depends on its cause. In the case of a threshold response to continuous variation, it could be that the threshold is never crossed because the underlying variable is selectively maintained well away from the threshold, perhaps by pleiotropic effects. If, on the other hand, new phenotypic variation requires new regulating elements, the necessary mutational events may be very infrequent. Either way, new phenotypes on which selection could act arise very rarely.

It is convenient to use the term *macromutation* for any genetic change leading to a striking change in phenotype, even if the change is a point mutation. Such macromutations are likely to be ill-adapted until compensating changes have occurred at other loci. This led Fisher (18) to argue that such mutations are unimportant in evolution. I have never found this argument entirely convincing (37; see also 49). It is true that a large random change in a car engine would make it less efficient, but organisms are not motorcars. Development is regulated, so that one change will be compensated for by others, without waiting for further mutation; in a striking example, Sliyer (56) describes a complex series of adaptive changes in the backbone and associated musculature of a goat born without forelegs and therefore forced to adopt a bipedal gait. Hence, although there is little to recommend Goldschmidt's (23)

concept of systemic mutations according to which a new morphology requires a complex change in chromosomal structure, one cannot reject a priori his concept of "hopeful monsters," interpreted as the initiation of evolutionary novelty by macromutations.

There is nothing particularly revolutionary about this idea. It does not require that the new mutant be reproductively isolated from the ancestral population; like any other mutant, its establishment in the population depends on selective superiority since it could hardly be neutral. Nor is it plausible that a new complex adaptation could arise in a single mutational step. What is plausible is that, if a macromutation is established, new selective forces will act on other loci, leading to further rapid evolution.

I therefore see no intrinsic implausibility in the idea that macromutations are important in evolution and may make possible changes that would not occur gradually. It is harder to decide whether, and if so in which cases, such mutations have in fact been important. The most direct approach is to study the genetics of species hybrids: if two closely related species differ morphologically, is the difference caused by many genes, each of small effect, or primarily by one or a few genes?

### 3. THE GENETICS OF SPECIES HYBRIDS

The idea that there is something qualitatively peculiar about the differences between species is not new; it was held by the early Mendelians, in particular by de Vries and Bateson. This belief led to extensive work on the genetics of hybrids between species and subspecies, particularly in plants. The main result of these studies was the conclusion that species differences are similar in kind to, although greater in extent than, those between individuals of a species. This conclusion contributed to the establishment of the "modern synthesis" in the 1940s.

There is one respect in which species hybrids do differ: often the hybrids are of reduced inviability or fertility. I return to this subject in section 5. For the present it is sufficient to make two points. First, every degree of isolation can be observed, from inviability of the F1 to minor infertility in the F2 or backcross generations; the degree of isolation correlates poorly with morphological difference. Second, breakdown depends on genes at many loci; a classic example is Dobzhansky's (12) study of hybrids between *Drosophila pseudoobscura* and *D. persimilis*.

More immediately relevant is whether morphological differences are typically polygenic, as Lande (33) and Charlesworth et al (7) argue. Clearly nothing can be learned unless the F1 hybrids are sufficiently fertile to give F2 or backcross progeny. If a difference is highly polygenic, then the F2 will be hardly more variable than the F1, and there will be no clear character segrega-

tion in the F<sub>2</sub> or backcross. If few genes are involved, the F<sub>2</sub> will be more variable than the F<sub>1</sub>. Wright (quoted in 6) established a method of estimating the number of loci involved. Lande (35) has extended the method and has applied it to six data sets; the two cases (eye size in cave fish, head width in *Drosophila*) involving morphological differences between wild populations are discussed below. There is also a semantic issue: how many loci make a difference polygenic? As a rough guide, if five or more loci of approximately equal effects on some trait are segregating, the population will respond smoothly to selection and single gene effects will not be detectable. For this reason, I suggest that such cases be regarded as polygenic.

The early work on plants is summarized by Stebbins (61, p. 259) as follows:

Although the F<sub>1</sub> progeny of an interspecific cross are usually as much like each other as are the different individuals of the parental species, the offspring in the F<sub>2</sub> and later generations are extremely variable, due to Mendelian segregation of the genetic factors responsible for the interspecific differences. . . . The striking fact about many of these progenies is not only their variability but also the presence of variants which look as if they have entirely "new" characteristics. . . . In some of these progenies, such as *Quercus*, types close to the original parents can be recovered in the F<sub>2</sub> generation, but in most others this is not possible unless a very large number of individuals is raised.

This testimony is ambivalent as far as the polygenic nature of differences is concerned: the difficulty of recovering the parental types supports a polygenic interpretation, but the extreme variability of the F<sub>2</sub> points the other way.

Stebbins's conclusions are borne out by the original papers on which they are based. A few examples (not all quoted by Stebbins) follow. Kristofferson (30) studied species crosses in *Malva*, a herbaceous perennial. In the cross *M. crispa* × *M. neglecta*, which involved considerable sterility, some traits gave monofactorial segregations—e.g. "crisp" (wavy-edged) and dissected leaves—and others, such as flower size and carpel number, were polygenic. In the backcross to *M. neglecta*, many plants were outside the range of the original parents and "some of the plants resembled scarcely *Malva*." Muntzing (46) studied species hybrids in deadnettle, *Galeopsis Tetrahit* × *G. bifida*. The parental species differ strikingly in leaf shape. The F<sub>2</sub> is more variable than the F<sub>1</sub>, but less so than would be expected if the difference was caused by only one or two loci.

Clausen (9) studied hybrids between ecotypes of a spring annual, *Layia*, in California. The maritime ecotype differed from the inland form in the absence of a central stem, horizontal side branches, and later flowering. For each trait, the full difference could be caused by as few as two loci, but different pairs of ecotypes differed at different loci. A final example (20) tells us little about the genetic basis of the difference but is interesting in suggesting a developmental threshold. In *Geum montanum* the fruits are wind-dispersed, with a long feathery plume; in *G. rivale* the fruits are hooked and are dispersed by animals.

In the F1 hybrids, both fruit types are found on a single plant, suggesting a threshold. Genetically *G. montanum* is tetraploid and *G. rivale* hexaploid, and it is likely that the genes responsible for the hooked fruits were introduced by hybridization with another genus.

Turning to animals, the data on *Drosophila* are disappointing, mainly because species that can be crossed are morphologically similar. Coyne (10) has studied hybrids between *D. melanogaster* and *D. simulans* and between *D. simulans* and *D. mauritiana*. The only morphological difference between these species is in the shape of the posterior process of the male genital arch. The former pair differ by at least four gene substitutions affecting this character and the latter (more recently diverging) pair by at least five substitutions; in each case, this is the largest number of substitutions that could have been detected by the methods employed. In the latter pair, gene effects of different chromosomes were approximately additive; in the former pair, they were less than additive. Muller (45) concluded that species differences are polygenic but offered little evidence. He quoted Spencer's study of *D. virilis* × *D. americana* hybrids, but the published paper (58) shows that the morphological differences between the species are too small for any conclusion to be drawn. Patterson & Stone (48) review extensive data on the viability and fertility of species hybrids but say nothing relevant to our present question. The most relevant data are those of Val (65), analyzed by Templeton (62) and Lande (35), on *D. silvestris* × *D. heteroneura* hybrids. Lande estimates that the dramatic difference in head shape is caused by genes at 6–9 loci.

Recently, Garcia-Bellido (22) has reviewed the morphological differences among *Drosophila* species, drawing attention to a series of qualitative differences, such as the number or type of rows of chaetae (innervated bristles) on the wing margin, the presence of chaetae at particular sites on the head and thorax, and the presence of rows of special chaetae on the forelegs of males. He regards these traits as the stable states of a bifurcating developmental process because they are uniform within species, and because (whatever phylogeny one assumes) at least some traits have evolved several times independently. Mutants exist that produce chaeta patterns characteristic of other species (21).

In view of Garcia-Bellido's suggestion that differences in chaeta patterns among species may represent different stable developmental states, particular interest attaches to any genetic analysis of such cases. The only example known to me concerns additional rows of chaetae on the forelegs of the male of some species of Hawaiian *Drosophila* (5). In five closely related species, there are two additional rows of bristles (cilia) on the dorsal surface of the foreleg tibiae that are used to stimulate the female during courtship. In one species, *D. silvestris*, some populations have the typical two rows, but in others the males have a much larger number of cilia with a greatly increased variance. There are additional cilia in the marginal rows, and a new, irregular, intermediate row. A

genetic analysis of the between-population difference in *D. silvestris* is still to be published, but Bryant & Carson (4) have published a brief account of hybrids (F1, F2, and backcross) between *D. silvestris* with the additional cilia and *D. heteroneura*, one of the species with only two rows. The results indicate that the interspecific difference is caused by a small number of sex-linked and autosomal genes.

The large variance of the *D. silvestris* populations with additional cilia is interesting. It suggests that the new phenotype has not yet been stabilized by selection of further modifying genes. Thus there is no reason to think that a phenotype with three rows of bristles is intrinsically variable as a consequence of some deep feature of *Drosophila* development. Waddington (67) argues that phenotypic uniformity was caused by stabilizing selection, and there is evidence (41, 52, 53) that the chaeta pattern can be made less variable by artificial selection.

The pattern of chaetae in *Drosophila* has also been altered by artificial selection (41, 52, 53)—i.e. by introducing a major mutant that disrupts the typical pattern and then selecting on the variation so produced. Sondhi (57) was able in this way to produce flies with a bristle characteristic of another family.

Turning to other animals, Wilkens (70) analyzed the genetic basis of eye degeneration in two cave populations of fish related to the surface-living *Astyanax* (the cave forms are best regarded as subspecies, although placed in a different genus). The difference is polygenic; Lande (35) estimates six loci. In contrast, differences in color pattern seem often to be caused by a few major loci with modifiers (8, 59, 64). These differences involve pattern as well as pigments and in two cases involve accurate mimicry.

Perhaps the most striking differences to be studied in hybrids are those found by Danforth (11) between the common pheasant, *Phasianus*, and the golden pheasant, *Chrysolophus*. For example, males of the latter species have a cape of some 200 feathers, modified in size, shape, color pattern, and detailed morphology, that can be raised to form an arc around the eye. Only one F1 male was obtained; it almost completely lacked a cape. Backcrossing to *Chrysolophus* again produced only a single male, which possessed a well-developed cape. In the next backcross generation, consisting of several males, the cape was uniform and approached perfection. Danforth concludes that "the occurrence of the highly distinctive *Chrysolophus* cape could be attributed to . . . one main and only a few reinforcing genes." He draws a similar conclusion for other features, such as the crest and modified wings and tail.

Danforth's conclusion is consistent with his evidence, but I find it hard to believe that such a complex structure as the *Chrysolophus* cape, requiring integration of feather movement, shape, and banding pattern to form concentric rings round the eye, could have arisen in evolution by a single mutational step. The data can equally well be explained by supposing that the full cape requires a



number of almost dominant genes that are expressed only in the presence of a single recessive controlling gene. The presence of such a control is made more plausible by the fact that the cape develops only in males. Unfortunately, the absence of female hybrids makes a full genetic analysis impossible. We must remember one point, however; the fact that a trait segregates in a cross as if caused by a single gene does *not* prove that it arose in evolution in a single mutational step, since we may be observing the segregation of a gene controlling many others. In the same way, the mutant *tetraoptera* in *Drosophila*, which replaces halteres with wings, does not prove that halteres arose in a single step.

These and other data on species hybrids lead to the conclusion that some differences are polygenic (e.g. head width in *D. silvestris*, genitalia in *D. melanogaster*, eye reduction in cave fish) and others involve major genes (e.g. crisp leaves in *Malva*, horizontal branching and absence of central stem in *Layia* ecotypes, color patterns in newts and butterflies, and perhaps secondary sexual characteristics in pheasants). This may be a disappointing conclusion to those who like clear-cut answers, but I cannot see that it is a surprising one. I remain open-minded about the possibility that development may impose discontinuous constraints on the pattern of phenotypic variation. If so, mutations of large phenotypic effect may sometimes initiate new evolutionary departures. It is also possible that, without any need for developmental bifurcations, a population may adopt new habits, either through learning and cultural transmission or from environmentally imposed necessity. If so, new habits would impose new selective forces and hence initiate punctuational change (37, 68, 69).

#### 4. THE PATTERN OF VARIATION IN NATURE

Whatever conclusions we may draw from species hybrids, it remains true that there are discontinuities in the pattern of variation in nature, at least at any one time and place, that make it possible to classify organisms into species. Why should this be so? There are three possible answers: that the discontinuities in organisms reflect discontinuities in the environment (i.e. there are discrete ecological niches); that they are imposed by development; or that they are consequences of sexual reproduction. Bateson (3) argued that since environmental variation is usually continuous it could not account for specific distinctions; therefore, "the discontinuity of species results from the discontinuity of variation."

In drawing this conclusion, Bateson overlooked the fact that sexual reproduction itself places a limitation on the range of phenotypic variation possible to a single species, because hybrids between very different parents are likely to be of low fitness. Thus the possibility arises that discontinuities are a consequence of sexual reproduction. The decisive test of this hypothesis is the pattern

of variation in apomictic taxa; if the hypothesis is correct, then agamic complexes should fail to show discontinuities and should resist classification into species. This seems to be true for higher plants such as *Taraxacum*, *Hieracium*, and *Rubus* (26, 61).

The situation is less clear in animals. In some taxa (e.g. *Cnemidophorus* lizards) the uniformity and discreteness of parthenogenetic "species" probably reflect their recent origin. However, the rotifer order Bdelloidea represents a serious problem. It consists of some 200 species classified into four families, yet no male has ever been discovered. Clearly parthenogenesis has set no absolute barrier to evolutionary change, but there are indications in the taxonomic literature that classification into species is arbitrary. Ruttner-Kolisko (55), writing of rotifers in general, says "whereas generic categories are well-defined, variability *within* genera is very great, so that the establishment of clear species boundaries in many—one might almost say all—cases is extremely difficult. Very frequently this has led to an excessive splitting of genera. . . . We have here in the zoological field conditions similar to those in the plant genera *Hieracium* and *Rubus*." Reporting a workshop on rotifer taxonomy, Dumont (15) writes: "C. Ricci remarked that she found it impossible to apply species concepts to Bdelloids. J. Donner admitted that all species names in Bdelloids should be regarded as preliminary." Thus it seems that Bdelloids do not offer any serious challenge to the view that discontinuities between species exist only if there is sexual reproduction. However, it is not clear whether the difficulty of applying the species concept to Bdelloids is peculiar to that asexual taxon, or whether it applies also the cyclically parthenogenetic monogononts; rotifers are not the easiest animals to study morphologically.

Thus in plants the data on parthenogenetic taxa support the view that discontinuities between species exist only if there is sexual reproduction. The data on animals neither contradict nor strongly support this conclusion.

## 5. CAN STASIS BE EXPLAINED BY LARGE POPULATION SIZE?

Mayr (43) supports his argument for the importance of peripheral isolates in speciation by claiming that large, widespread populations are less able to evolve. This claim has been taken over by the punctuationalists (e.g. 25, 60). This claim might be justified in two ways. First, in terms of selective forces, it could be argued that a widespread population must have achieved a satisfactory fit with its environment and therefore will not be subject to directional selection. Alternatively, the direction of selection will differ in different parts of the range, and gene flow will prevent evolution. The first alternative explains stasis in terms of normalizing selection and is discussed in section 6. The second is

probably fallacious, since different selective pressures in different places will lead to speciation without the need for major geographical barriers (17).

However, selective justification is not the argument the punctuationalists have in mind. Instead, they believe that there is something peculiar about the genetic structure of large populations that makes evolution difficult or impossible. This is mistaken: insofar as the rate of evolution is limited by mutation, the exact opposite will be the case [40; but see Lande (34) for an estimate that the mutation rate is sufficient to maintain rapid evolution even in rather small populations]. However, one evolutionary process may occur faster in a small population than in a large one. This is evolution from one state, say  $ab$ , to another of higher fitness, say  $AB$ , when the intermediate states,  $Ab$  and  $aB$ , are of low fitness. Such "adaptive valleys" can arise either from epistatic fitness interactions or from heterozygote inferiority. Perhaps the strongest reason for thinking that such events sometimes occur is that the chromosomes of related species or subspecies often differ structurally in a way that would lower the fertility of heterozygotes. Lande (32) estimates typical deme sizes from the frequency of such transitions.

If population structure permits chromosome evolution, it will presumably also permit the crossing of valleys arising from epistatic interactions between genes. However, it does not follow that innovation will occur only in peripheral isolates. Wright (74, 76) imagines that a valley may first be crossed by any deme and that the new genotypes, once formed, will subsequently spread through the whole species. On the time scale studied by paleontologists, Wright's "shifting balance" theory is a model of phyletic gradualism rather than of punctuational events in peripheral isolates.

As in the case of macromutations, we cannot rule out a priori the evolutionary relevance of the crossing of adaptive valleys by small local populations, but it is hard to decide how important such events have been in practice. Except, perhaps, in the case of structural changes in chromosomes, there is no obvious necessity to assume such events. In particular, the widespread occurrence of inviability in species hybrids might suggest that an adaptive valley has been crossed, but this is not so. It is easy to construct models in which an infinite random-mating population would evolve from state 1 to state 2 and yet hybrids between the two states would be of low fitness. In a haploid this requires at least three independent loci, but two loci are sufficient in a diploid with dominance.

Also, it is possible for a population to move from one adaptive peak to another without the need for chance events in a small population. Kirkpatrick (29) shows that, if there are two fitness peaks with an intervening valley, a large population with polygenic variance can shift several standard deviations in a few tens or hundreds of generations. Such a shift could be initiated by an

environmental change (altering the fitness surface) or by a mutationally induced change in the variance of the population.

Hence the presence of strong epistatic fitness effects in population hybrids is not evidence for valley-crossing. Recently "molecular drive" has been proposed as an explanation for hybrid inviability and infertility (13, 14, 19). The suggestion is plausible, although large differences in repetitive DNA have in some cases been shown to have little effect either on the phenotype or on chromosome pairing in meiosis (44, 51).

## 6. CAN STASIS BE EXPLAINED BY NORMALIZING SELECTION?

A geneticist can say little about whether stasis can be explained by normalizing selection. Clearly if selection continues to favor the same phenotype for many millions of years, then stasis will be the result. It may seem implausible that selection could be as conservative as this. However, we must distinguish between the physical and the biotic features of the environment. The physical environment has been changing rather rapidly during the past few million years. However, when the climate changes, organisms tend not to stay still and adapt to the change; instead, populations move so that physical conditions remain constant and are replaced by other species at the original site.

It is harder to know what to expect of the biotic environment. If we assume that physical conditions are constant and that each species evolves only because its competitors, predators, and parasites are evolving, we can draw two possible conclusions about the resulting dynamics (39; N. Stenseth, J. Maynard Smith, in preparation). One is that evolution will continue at a steady rate, including extinction, speciation, and phyletic change, as imagined in Van Valen's (66) "Red Queen" hypothesis. The alternative is that evolution of all species slows down and stops, being kicked into motion occasionally by changes in the physical environment. The choice between these alternatives does not seem possible on theoretical grounds and so will depend on paleontological evidence. If the latter is correct, it will explain highly variable evolution rates in selective terms but will predict that rapid changes should occur simultaneously in interacting species.

## 7. CONCLUSIONS

Directional selection acting on genetic variability of a conventional kind is able to produce changes at a rate that would appear virtually instantaneous in the fossil record. There is, however, a question as to how the observed variability of evolution rates should be explained. Variation in rate may simply reflect variation in the intensity of directional selection; punctuational change occurs

when a population crosses a selective threshold. Alternatively, variation in rate may be caused by developmental constraints of a discontinuous kind, arising either from bifurcations in development or from changes in systems of gene regulation.

Data on species hybrids show that the genetic basis of species differences is similar in kind to that of variation within species. Some species differences show polygenic inheritance, and others are caused by one or a few major genes. The fact that a trait behaves in a cross as if caused by a single gene does not prove that it arose in evolution by a single mutational step, because we may be observing the segregation of a gene regulating the activity of many others. Existing organisms, at least in a single place, typically show sharp discontinuities between species. This is not evidence for any discontinuities in the range of possible organisms imposed by developmental constraints, because the discontinuities are probably associated with sexual reproduction. The inviability and infertility of species hybrids are not evidence for the crossing of adaptive valleys in evolution, because a large population can evolve deterministically from one state to another and yet the hybrids between the two states can be of low viability.

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