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What's Wrong with the Received View of Evolutionary Theory?¹

John Beatty

Harvard University

This idea meant that heredity evolved-- an evolution of the hereditary mechanism-- an evolution of mitosis and meiosis. I had opened up an immense field of inquiry. I had to find out how the genes could control the chromosomes, how the chromosomes could control themselves at the same time that they were controlling the organism. I first discussed this problem in 1932. Formally anybody can repeat the idea and learn and write it down, but few have grasped its implications, as I think, for biology. (C. D. Darlington 1980, p. 74).

1. Introduction

In the world of academic specialties and subspecialties, philosophy of biology certainly counts as a self-respecting, if not otherwise respected, field of study. It has its own exemplary works, its own lines of communication, etc. In this regard, philosophy of biology might be compared with philosophy of physics. But such comparisons often reflect poorly on philosophy of biology, as David Hull grudgingly acknowledges in a recent review of the field:

A fellow philosopher of biology, waving a copy of my book, declared to the chairman of his department, "This is the best book out in philosophy of biology." The chairman replied, "Yes, but is it any good?" That, in a nutshell, is the reputation of philosophy of biology. Philosophers of science who are not bright enough to learn physics become philosophers of biology. On their side, philosophers of biology (and of the social sciences for that matter) complain that philosophy of science is philosophy of physics. (1979, p. 421).

Michael Ruse's recent review is a little more optimistic: "Philosophy of biology has nothing like the maturity that the philosophy of physics has, but to continue the metaphor for the moment, it has turned into

a gangling adolescent." (1979, p. 785).

Of course, biological problems have intrigued philosophers and philosophical problems have intrigued biologists for a long time. Classification, teleology, mechanism, holism, and vitalism are very old issues. So it may seem odd that philosophy of biology measures up so miserably to philosophy of physics.²

In accounting for this recent appraisal, though, we must keep in mind recent standards of appraisal. Much if not most recent literature in philosophy of biology concerns the extent to which biological theories conform to what is known as the "received" philosophical view of scientific theories, a descendant of the logical-empiricist view of theories. Quite often, this involves a comparison of biological theories and physical theories, since the latter are generally thought to square with--indeed, were the models for--the logical-empiricist and received views.³

In comparing biology and physics in light of the received view of theories, the issue certainly has not been the adequacy of the received view. The issue has been the adequacy of biology. The received view has, as its name suggests, been taken for granted. But the received view currently faces a competitor--a very different view of theories known as the "semantic" view. So now, instead of judging biology from the point of view of prevailing philosophy of science, we can judge rival philosophies of science from the point of view of biology. A discrepancy between the received view and modern evolutionary theory need not be considered an indication of the inadequacy of evolutionary theory; rather, that discrepancy might be counted as support for the rival semantic view, should the semantic view better accomodate evolutionary theory. That evolutionary theory was ever judged according to the received view seems ludicrous enough--any decent view of theories should account for evolutionary theory. But sometimes counter-examples to a view are not recognized as such until there are rival views that accomodate those examples.

I will argue that the semantic view is more sensitive to the nature and limitations of evolutionary theory than is the received view. In particular, the semantic view better accomodates the fact that evolutionary theory is bound to change as a result of the evolutionary process itself. This unusual feature of evolutionary theory provides a good reason for reconsidering the received view and paying close attention to the semantic view.⁴

2. Theories of Theories

Before I present the central statements and structure of evolutionary theory, I should outline the relevant differences between the received and semantic views. By way of very brief introduction, the "semantic" view is so called in order to distinguish it from the received view's dual, syntactic and semantic characterization of

theories. Lingering difficulties with the dual approach eventually provided the stimulus for the development of a purely semantic view. So a thorough characterization of the semantic view would focus on this distinction. It seemed best, though, to discuss this distinction in an appendix, since this is not the distinction I want to emphasize with regard to evolutionary theory (see Appendix 1).

The distinction I want to emphasize most concerns an aspect of the received view which perhaps is even more fundamental to the usual conception of a scientific theory. This distinction can be illustrated in terms of Newtonian mechanics (Giere 1979, pp. 63-81). On the received view, the axioms of Newtonian mechanics are the three laws of motion and the law of universal gravitation:

- L1: If there is no force on a body, its momentum will remain constant.
- L2: If there is a force on a body, then it will accelerate by an amount directly proportional to the strength of the force and inversely proportional to its mass.
- L3: If one body exerts a force on a second, then the second exerts on the first a force that is equal in strength but in the opposite direction.
- LG: Any two bodies exert forces on each other which are proportional to the product of their masses divided by the square of the distance between them.

In referring to these axioms as "laws of nature", the proponent of the received view intends that they have three essential characteristics. First, they are generalizations: either universal generalizations (of the form "All instances of kind A are instances of kind B") or statistical generalizations (of the form "X% of the instances of kind A are instances of kind B"). Second, they are empirical: their truth or falsity does not depend upon the meanings of their constituent terms and/or their logical form alone--experientially discernable features of the world are also relevant to their truth or falsity. Third, to the extent that they are true, they are true not only in the weak sense that they have no exceptions, but also in the strong sense that exceptions are not considered physically possible. As Hempel suggests, a statement "will not qualify as a law if it rules out certain hypothetical occurrences which an accepted theory qualifies as possible." (1966, p. 58). To use Hempel's own example, we hesitate to call the empirical generalization "All bodies consisting of pure gold have a mass of less than 100,000 kilograms" a law of nature, even though we suspect that there are no exceptions to the generalization. The reason we don't consider the generalization a law is that basic laws of physics and chemistry allow the possibility of producing a solid gold object with a mass greater than 100,000 kilograms (1966, p. 55). On the received view, at any rate, at the time a theory is

accepted or used for purposes of explanation, its axioms include what are thought to be laws of nature, satisfying the three requirements just described.⁵

On the semantic view of theories, Newtonian mechanics looks rather different. The usual laws are mentioned, but the form of the theory is more like a definition than a set of laws:

A Newtonian mechanical system = [df] a system of objects which behave according to Newton's three laws of motion and the law of universal gravitation.

This alternative reconstruction of theories was originally outlined in the late fifties and sixties by Patrick Suppes (1957, 1967a, 1967b), and was further developed in various ways during the seventies by Joseph Sneed (1971), Wolfgang Stegmüller (1976), Frederick Suppe (1972), and Bas van Fraassen (1970, 1972). A new introductory philosophy of science textbook by Ronald Giere (1979) outlines the simplest version of the semantic view. Needless to say, there are differences between the views which these authors have proposed; but there is a central, significant thesis. As van Fraassen suggests: "Like Suppes, I shall take it that (the "pure" part of) a theory defines the kind of system to which it applies; empirical assertions would take the form that a given empirical system belongs to such a kind" (1972, p. 311).

This view is clearly an alternative to the received view of theories, because, according to this view, theories do not even consist of empirical claims, much less laws of nature. Rather, theories stipulatively specify kinds of systems. This is an empiricist philosophy of science, however. It's just that the empirical claims of science are not considered to be components of theories. Rather, the empirical claims of science are made on behalf of theories. They assert that particular empirical systems are instances of the kinds of systems stipulatively specified by theories. For instance, we may claim, on behalf of the theoretical specification of 'Newtonian mechanical system', that molecules of gas in a closed container constitute a Newtonian mechanical system. Such empirical claims provide the explanatory link between the nonempirical theory specifications and the behavior of empirical systems. For having identified an empirical system as an instance of a specified kind, an investigator can then account for aspects of the behavior of the empirical system in terms of the consequences of its being an instance of the specified kind. For instance, having identified a closed container of gas as a Newtonian mechanical system, one can then explain relations between the pressure, temperature, and volume of the gas in terms of the consequences of its being a Newtonian mechanical system.⁶

Well, so much for now for the two rival views of theories. Newtonian mechanics can be reconstructed according to either view. So their differences may not seem very important at this point. As I'll argue shortly, though, the synthetic theory of evolution only fits the semantic view. After I describe the fundamental premises of the

synthetic theory, I will use that theory to further differentiate the received and semantic views of theories.

3. Evolutionary Theory

The synthetic theory of evolution gained prominence during the twenties and thirties after two decades of bitter quarrels over the role of natural selection in evolutionary change. Darwin's theory faced more difficulties than I could possibly survey here. As an indication of its troubles, though, a major sourcebook in evolutionary biology at the time (Kellogg 1907) offered twenty major objections to Darwinism and twenty-four alternative evolutionary theories as evidence that Darwinism was on its "deathbed" (see especially pp. 1-9).

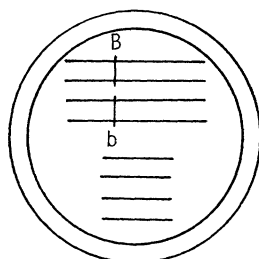
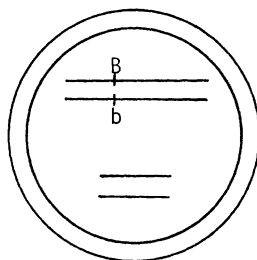
A major difficulty of Darwinism at this time was the lack of a suitable theory of inheritance. According to Darwin's theory, if small variations arise which even slightly increase the fitness of their possessors, and if those variations are inherited, the same variations will increase in frequency in a species over the course of generations. The applicability of the theory rests on the assumption that such small variations actually arise and are passed down without too much modification from parents to offspring. But at the turn of the century, there was no well-accepted theory of inheritance which accounted for the origin of these small variations, and which ensured their preservation from generation to generation. Mendel's laws, rediscovered in 1900, were thought at first to pertain only to the inheritance of large variations, and hence were not considered complementary to Darwinian evolutionary theory (see, e.g., Provine 1971).

The synthesis, to which the name 'synthetic theory of evolution' refers, was in large part a matter of reconciling Mendel's and Darwin's theories--invoking Mendel's laws in order to explain how the natural selection of small variations produces gradual, systematic, evolutionary change (see, e.g., Provine 1971, and Mayr and Provine 1980). At present, there is less emphasis on the gradualness of evolutionary change (e.g., Eldredge and Gould 1972). Mendel's laws are now used to link various rates of evolutionary change to natural selection.⁷

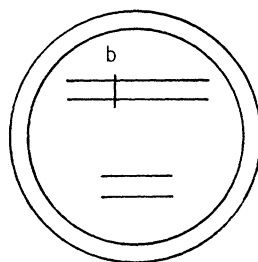
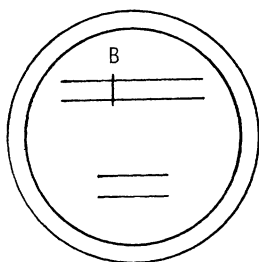
The fundamentals of this synthesis can be sketched briefly, beginning with Mendel's first law of inheritance. In the simplest terms, Mendel's law describes the statistical outcome of the process by which gametes (sperm and eggs) are formed from gamete-producing cells in the reproductive organs. This process is known as "meiosis", and consequently Mendel's law is said to describe "normal" meiosis (see Diagram 1 of the stages of meiosis).

During normal meiosis, the total hereditary material of gamete-producing cells is fractioned through a series of cell divisions in such a way that each gamete receives a complementary half of the original hereditary material. To describe the process in a bit more detail, the hereditary material of gamete-producing cells comes in pairs of morphologically similar, or "homologous" chromosomes. The genes

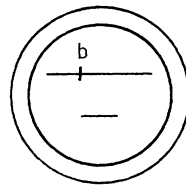
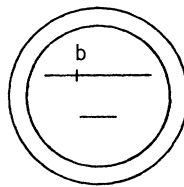
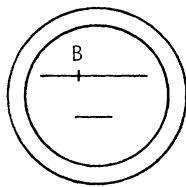
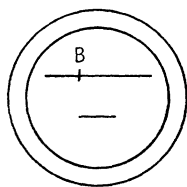
DIAGRAM 1
STAGES OF NORMAL MEIOSIS



First Division



Second Division



Gametes

reside linearly along each chromosome, and the two genes which lie opposite one another when the homologous chromosomes pair during meiosis are said to occupy the same chromosomal "locus" (in Diagram 1, B and b occupy the same locus). During meiosis, the chromosome pairs double and then divide twice so that each of the gametes formed receives one chromosome from each pair. Hence, each gamete receives one gene from each locus. Moreover, the probability that a gamete will receive one particular gene at a locus is one half. Thus, a common, brief formulation of Mendel's law is:

Each of the two genes at a locus has a probability of one half of being the single gene at that locus carried by a particular gamete. (Edwards 1977, p.3).

From this law alone, it is simple to deduce the central premise of the synthetic theory, the so-called "Hardy-Weinberg law", which describes the conditions for evolutionary equilibrium in the following terms:

Within a breeding group, as long as gametes combine randomly, and no forces affect gene frequencies from the time of fertilization to the time of gamete formation, gene frequencies will remain constant.

This law is as important to the synthetic theory of evolution as Newton's first law is to Newtonian mechanics (Ruse 1973, pp. 37-38). Each law allows investigators to recognize the presence in nature of unbalanced forces against an otherwise stable background: change in the momentum of an object indicates unbalanced physical forces acting on that object, while changes in the gene frequencies of a breeding group indicate unbalanced evolutionary forces acting on that group. One such evolutionary force is, of course, natural selection. To say that natural selection changes gene frequencies is to say that such changes can be attributed to fitness differences between organisms with different gene combinations. And to say that organisms with different gene combinations differ in fitness is to say that, on account of their physical differences, the organisms are likely to contribute different numbers of descendants to future generations.⁸ In addition to natural selection, migration, mutation, and chance fluctuations in gene frequency are other evolutionary forces. Taking into account the effect of these forces on the gene frequencies at one locus, the Hardy-Weinberg law is often formulated in a second manner:

If in a breeding group, B and b are the only genes at a particular locus, if their initial frequencies are p and q respectively, if organisms mate randomly with respect to their gene combinations, and if there is no selection, mutation, migration, or chance fluctuation in gene frequency, then after one generation the distribution of gene combinations will be,

$$p^2 BB : 2pq Bb : q^2 bb,$$

and this distribution will be maintained as long as the mating,

selection, mutation, migration, and chance-fluctuation conditions hold. (See Appendix 2 for the derivation of this law from Mendel's law.)

On the basis of this law, we can calculate the effects of fitness differences, mutation pressures, etc. on the rate of change of gene frequency.⁹ And so it is that the synthetic theory invokes Mendel's law to explain how natural selection and other evolutionary agents produce systematic, evolutionary change.

There you have an important part of modern evolutionary theory. However, you may be wondering what's become of that infamous, purportedly central premise of evolutionary theory known as the "principle of natural selection", and often formulated as "On the average, the fitter organisms leave more descendants." I have no doubt that evolutionary theory can be reconstructed in such a way that this principle becomes central. But one would expect to find the central premise of a theory in a prominent place in textbooks dealing with the theory. Yet a careful search through a classic, modern evolutionary text like Theodosius Dobzhansky's Genetics of the Evolutionary Process (1970) reveals no such principle. The same is true of Ernst Mayr's Animal Species and Evolution (1963). There Mayr dismisses the slogan "survival of the fittest" as unrepresentative of Darwin's interests in descendant contribution vs. mere survival (pp. 182 ff.). But Mayr proposes no alternative, general empirical principle in terms of descendant contribution vs. survival. In fact, in his earlier "Cause and Effect in Biology" (1961, p. 1504), Mayr refers to the descendant-contribution version -- "the fitter individuals will on the average leave more offspring" -- as a "trivial and meaningless circular statement."

In place of the principle of natural selection, one finds centrally located in Dobzhansky's and Mayr's texts the Hardy-Weinberg law--a sort of genetic principle of natural selection. And as a substitute, the Hardy-Weinberg law serves roughly the same purpose as the old principle of natural selection. It allows us to calculate the effect of fitness differences among different types--genetic types, in this case--on the differential perpetuation of those types. Thus, when we consider the extent to which the synthetic theory of evolution satisfies the canons of the received view, we need not dwell on the well-known objection that the principle of natural selection is tautologically rather than empirically true. As interesting an issue as that is, it is not crucial given the structure of the synthetic theory.

How well does the synthetic theory as we know it conform to the received view? First, there is no question that the Hardy-Weinberg law is empirical. If gametes were not formed according to Mendel's law--that is, if the probability was greater than one half that a gamete would carry one of the two genes at a locus, and that is certainly logically possible--then even in the absence of selection, mutation, migration, and chance fluctuation, there would be no genetic equilibrium until only one kind of gene occupied every locus through-

out the breeding group. Clearly, then, the truth of the Hardy-Weinberg law is not guaranteed by the meanings of its terms and/or its logical form.

The Hardy-Weinberg law is not only empirical, it is a universal generalization as well: it purports to describe patterns of gene-frequency change in all breeding groups. Moreover, the regularity upon which it is contingent, Mendel's law, has been accepted with such unshakable faith -- at least by some philosophers of biology -- that it would seem both laws are true in the strongest sense. Michael Ruse, for one, supports the physical necessity of Mendel's law and the Hardy-Weinberg law, on the grounds that,

. . . because the [Mendel's] Laws have such a wide range of applications, and because the Laws seem to complement so strongly the physical activities of the cell, it seems reasonable to suppose, as biologists do in fact suppose, that even in unexamined instances, Mendel's Laws are obeyed. However, to suppose this, is to do no more than to assume that in some sense the Laws must hold--in other words, since the Laws are not logically necessary, it would seem that on the wide basis of discovered evidence it is justifiable to hold Mendel's Laws to be nomically necessary. (1971, p. 779).

Furthermore,

Because of the way in which it follows from Mendel's First Law, the Hardy-Weinberg Law seems to be something which holds because it must, rather than something which holds just by chance. (1971, p. 779).

Ronald Munson similarly assesses the strength of population genetics: "The principles of population genetics are applicable without exception to all organisms Furthermore, [population genetics] at least purports to hold for all life forms whose reproduction involves passing on genetic material - that is, all life forms. Neither implicitly nor explicitly does it contain spatio-temporal restrictions." (1975, p. 436).

Thus, the synthetic theory of evolution appears to have all the marks of a good scientific theory, according to the received view of theories. Is evolutionary theory different from Newtonian mechanics with respect to the received view of theories? Apparently not.

4. The Evolution of Evolution

But I believe that appearances aside, and despite their noble titles, neither Mendel's "law" nor the Hardy-Weinberg "law" is a law of nature. The line of argument I will follow has been used before in debunking supposed biological laws, though its relevance in the case of the central premises of the synthetic theory has gone largely unnoticed.

An example of this line of argument can be found in Max Delbrück's

autobiographical remarks about the surprises awaiting a physicist-just-turned-biologist. As Delbrück describes the transition:

A mature physicist, acquainting himself for the first time with the problems of biology, is puzzled by the circumstance that there are no "absolute phenomena" in biology. Everything is time bound and space bound. The animal or plant or micro-organism he is working with is but a link in an evolutionary chain of changing forms, none of which has any permanent validity. Even the molecular species and the chemical reactions which he encounters are the fashions of today to be replaced by others as evolution goes on. (1952, p. 9).

As an example of the sort of impermanent regularities a physicist might find in biology, Delbrück cites "Weber's law", which states that the change in stimulation necessary to excite a nerve cell is proportional to the initial value of the stimulation parameter. For instance, if at an illumination of 100 footcandles, an increase of 5 footcandles is necessary to excite an optic nerve cell, then at an illumination of 1000 footcandles, a 10 times greater increase of 50 footcandles will be necessary to excite the cell. "Do we here deal with a truly general feature of the organization of matter in living cells?" Delbrück asked. No. This regularity, he argued, only looks like a law. The proportionality in question probably owes its universality to natural selection, which favors this stimulation mechanism over alternative mechanisms--organisms with this mechanism being fitter for some reason than organisms without. In Delbrück's words,

. . . natural selection [is] responsible for simulating something that looks like a physical law, natural selection acting like the overly faithful assistant of a credulous professor, the assistant being so anxious to please that he discards all those data which conflict with his master's theory. (1952, p. 12).

But a characteristic which owes its presence to natural selection or some other evolutionary agent may, in the future, also owe its replacement to natural selection or some other evolutionary agent. Recall Delbrück's warning that, "Even the molecular species and chemical reactions which [the biologist] encounters are the fashions of today to be replaced by others as evolution goes on." Thus, Weber's "law" cannot really be a law, since it is evolutionarily possible that different nerve-stimulation mechanisms prevailed in the past, and will prevail in the course of the evolution of species.

The same sort of argument was used by the logician William Kneale (1959) to debunk that favorite of all philosophers' laws, "All ravens are black." If ravens were ever tempted to live in a snowy region where a white coloration might be advantageous to their survival, Kneale argued, then natural selection would favor the white variants, so that in time all ravens would be white. Thus, "All ravens are black" cannot really be a law, since it is evolutionarily possible that

a different coloration will prevail in the course of the evolution of that species.¹⁰

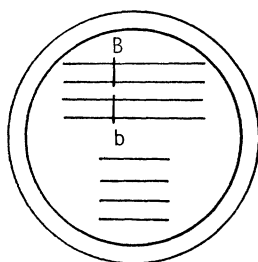
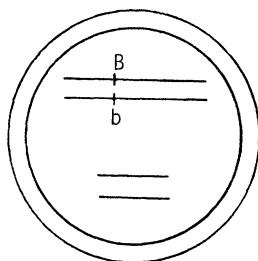
In short, there can be no law of nature to the effect that a genetically based trait is universal within a species or among all species. All genetically based traits are subject to evolutionary forces. As far as we know, all gene loci are subject to mutational change, which is itself an evolutionary agent. Thus, as long as a trait has a genetic basis, variations can arise.¹¹ And these variations can supercede established traits in a number of ways, including natural selection in favor of the new variation, and chance fluctuations in gene frequency if the population is small enough.

Of course, philosophers still use "All ravens are black" when hard-pressed for another law during lectures. And philosophers of biology still think of Mendel's law and the Hardy-Weinberg law as real laws of nature. But the fact is, as I will explain shortly, that the normal meiotic mechanism described by Mendel's law, and upon which the Hardy-Weinberg law rests, is itself a genetically based trait subject to evolutionary change. Normal meiosis is a feature of sexual organisms whose near universality might be accounted for in terms of the evolution of inheritable traits from common ancestors, but whose universality is not physically necessary. This fact has an interesting --if not bizarre--consequence. Since descriptions of evolutionary-equilibrium conditions, like the Hardy-Weinberg law, depend on genetically controlled meiotic mechanisms, those equilibrium descriptions may change as the evolution of the meiotic mechanism proceeds. That is, evolutionary theory may change as a result of evolutionary change. In this case, 'the history of evolutionary theory' has two senses: the history of theories about a particular evolutionary mechanism, and the history of the evolutionary mechanisms themselves.¹²

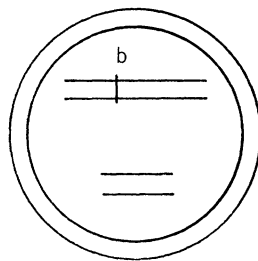
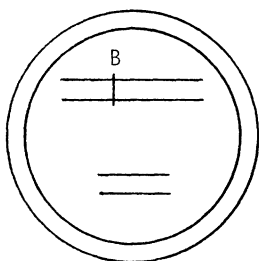
In support of the happenstance of "normal" meiosis, let us consider the evidence that meiosis is genetically controlled, and therefore subject to evolutionary change. Two kinds of genetic variation in the meiotic mechanism have received considerable attention: a variation known as "nondisjunction" and a variation known as "meiotic drive". Nondisjunction occurs when homologous chromosomes do not disjoin or separate during meiosis. As a result, some of the gametes formed contain both or neither of the homologous chromosomes--meaning that these gametes contain both or neither of the genes at each locus of the nondisjoining chromosomes (see Diagram 2).

This exceptional phenomenon was recognized microscopically as early as 1913, but its genetic basis was not established until 1933 when the geneticist J. W. Gowen reported his experimental findings that "... the processes through which the chromosomes pass during the meiotic divisions are in part, at least, subject to the same specific gene regulation that guides other bodily development and inheritance." (1933, p. 83). Through breeding experiments, Gowen determined that cases of the nondisjunction of one or all four pairs of chromosomes of Drosophila melanogaster were influenced by a single

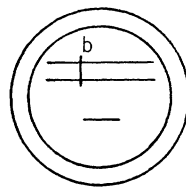
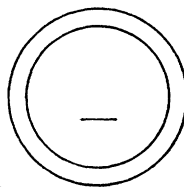
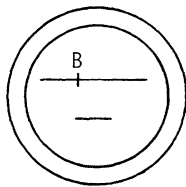
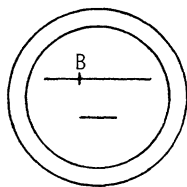
DIAGRAM 2
STAGES OF NONDISJUNCTIVE MEIOSIS



First Division



Second Division



Gametes

gene locus which he located on the third chromosome pair. Gowen's breeding studies are still accepted (Sandler et al. 1968, and White 1973, p. 469). In fact, there are now many other recognized instances of nondisjunctive mutants (Sandler et al. 1968, and White 1973).

Meiotic drive, another acknowledged exception to normal meiosis, occurs when an organism with two different genes at a locus (say, B and b) produces more than fifty percent of one genetic kind of gamete (say, B), on account of the genetic differences between the homologous chromosomes (Sandler and Novitski 1957, p. 105, and White 1973, p. 470).

Perhaps the most well-known case of meiotic drive involves the behavior of the so-called "t" gene in house mice, which is expressed in the form of taillessness. In 1953, the geneticist L. C. Dunn reported that ninety-five percent of the sperm from males with normal genes and t genes at the appropriate locus were of the t type.¹³ Evidence at present indicates that genes favoring the perpetuation of their own chromosomes through meiotic drive do so by affecting the homologous chromosome in such a way that the affected chromosome commits a positive act of sabotage on its maturing gamete (Crow 1979).

5. Evolutionary Theory Reconsidered (Part 1)

Thus, there are clear-cut exceptions to Mendel's law and the Hardy-Weinberg law--exceptions which raise the question as to whether these are proper laws of nature. One might argue, however, that such exceptional modifications do not serve to exclude these so-called "laws" from the category of laws of nature, since all supposed laws are to some degree inaccurate. As Michael Scriven argues, "laws are usually inaccurate; but they represent great truths so we forgive them their errors." (1961, p. 101). Michael Ruse uses a similar line to defend Mendel's laws in the face of exceptions: that is, if we do not count principles of inheritance as laws, on account of a few exceptions, we must also exclude previously supposed laws of physics, such as Snell's law and Boyle's law, both of which have some exceptions. It is more reasonable, Ruse suggests (citing Scriven), "to think of laws as being true within a certain range and to a certain approximation." (1973, p. 28). As Ruse continues, "... there can be few statements of science which have been found to satisfy the limited condition of unrestricted universality more fully. Since Mendel first proposed his laws, they have been found to hold for a range of organisms from elephants to cod-fish, from sea-weed to oak trees." (p. 29).

This somewhat looser, received-view analysis of Mendel's law is still unsatisfactory, however. Mendel's law may in fact be a good approximation of present inheritance patterns. But that principle is not an approximation of any physically necessary regularity. The evolution of non-Mendelian inheritance is theoretically possible. It is theoretically possible, then, that at some time in the future, or somewhere in the universe, Mendel's law will not even approximate inheritance patterns. Or looking back in time, if normal meiosis is a product of evolutionary modification, then there must have been some

point in the past when it was exceptional. Actually, the whole point of my stressing the discovery of meiotic mutants was not so much to prove that there are exceptions to Mendel's law, as to demonstrate that Mendelian meiosis rests on a mutable genetic base. Even if there were presently no exceptions to Mendel's law, its truth would be contingent upon the evolutionary status quo. But the evolutionary status quo is hardly permanent.¹⁴

Philosophers' motives in defending Mendel's law and the Hardy-Weinberg law have been less questionable than their means of defense. They have wanted to show that Mendelian genetics and the synthetic theory of evolution are legitimate scientific theories. It's just that the only standards of appraisal available to them were those of the received view of theories, according to which the central statements of a theory should be laws of nature.

But now that the received view has a rival in the semantic view, the adequacy of the synthetic theory, as a theory, cannot be judged simply in terms of received-view standards. Of course, if the synthetic theory satisfied neither the received view nor the semantic view, we would have good reason to be suspicious--either of biology or of the whole enterprise of philosophy of science. But that worry need not arise, for there is a very simple and very straightforward semantic account of the synthetic theory.

On the semantic view, a theory is not comprised of laws of nature. Rather, a theory is just the specification of a kind of system--more a definition than an empirical claim. In the case of the synthetic theory, an appropriate system specification is:

A Mendelian breeding group =[df] a breeding group whose members form gametes in accordance with Mendel's first law of inheritance.

Since the Hardy-Weinberg law is a deductive consequence of Mendel's first law, we can also say of a Mendelian breeding group that:

A Mendelian breeding group =[by consequence of its df] a breeding group whose genetic frequencies obey the Hardy-Weinberg law.

Whether Mendel's law or the Hardy-Weinberg law is really a law of nature is irrelevant from the perspective of the semantic view of the synthetic theory. The theory itself simply specifies a kind of system--it makes no empirical claims.

But, as I explained earlier, the semantic view is an empiricist philosophy of science. It's just that the empirical claims of science are not supposed to be components of theories. Rather, the empirical claims of science are made on behalf of theories. They assert that particular empirical systems are instances of the kinds of systems specified by theories. Empirical claims of modern evolutionary biology, then, include claims to the effect that particular breeding groups are instances of Mendelian breeding groups, and/or that particular breeding

groups are instances of Mendelian breeding groups with respect to the particular loci under investigation.

In this manner, the semantic view also satisfactorily accomodates the explanatory use of the synthetic theory. For having identified a particular breeding group as a Mendelian breeding group (with respect to the particular locus under investigation), the investigator can then account for the genetic-evolutionary behavior of the group with respect to that locus, in terms of the consequences of its being a Mendelian breeding group.

Admittedly, this procedure of reasoning is not explicit in the literature. Then again, investigators usually just assume that the breeding groups they study are Mendelian breeding groups. But general assumptions like this may be very misleading. As population geneticist James Crow suggests in a recent review, exceptions to Mendelian meiosis may have been long overlooked by investigators who attributed their abnormal results to experimental error (1979, p. 136). Who knows how many cases of mild meiotic drive--resulting in, say, 55:45 gamete ratios--have been overlooked for this very reason (Crow 1979, p. 146)? In any event, explanations of gene-frequency changes at a particular locus require some assumption about the nature of inheritance with respect to that locus. Since general assumptions about inheritance are not legitimate, such assumptions will have to be more restricted.

6. Evolutionary Theory Reconsidered (Part 2)

A final point, before concluding, concerns the so-called "principle of natural selection". I've said little about the principle so far, because the principle has no place in the synthetic theory of evolution as we know it. But there is a case to be made for reconstructing evolutionary theory in such a way that something like the principle of natural selection is among the axioms of the theory, and in such a way that Mendel's law and the Mendelian principle of natural selection, i.e., the Hardy-Weinberg law, figure in as special-case theorems (e.g., see Williams 1980). The reason for structuring evolutionary theory in this manner is that the theory is rather incomplete as it stands. Normal meiosis, as described by Mendel's law, is presumably a product of evolution. But the evolution of the meiotic mechanism cannot be accounted for in terms of a Mendelian principle of natural selection that itself presupposes normal meiosis. In order that evolutionary theory be more complete, then, the theory ought to be based on a more general principle of natural selection that in turn sheds light on the conditions under which Mendel's law and the Mendelian principle of selection hold. A candidate for this role is that old principle we think we know and think we love: the principle of natural selection.

Now if there were a law of natural selection upon which evolutionary theory could be reconstructed, my arguments for the semantic view of evolutionary theory might lose some force, though they would still

apply to the synthetic theory as we know it. However, in the first place, there is little agreement as to whether the principle of natural selection is a law. Given a reasonable definition of 'fitness', such as expected descendant contribution, and given a reasonable formulation of the principle of natural selection, such as "On the average, the fitter organisms leave more descendants", the principle comes awfully close to being true simply in virtue of the meanings of its terms and its logical form. Even among the defenders of the principle of natural selection, there is little agreement as to why it is a law. For instance, Robert Brandon (1978) argues that a propensity interpretation of "fitness" leads to a nonanalytic version of the principle, while Mary Williams (1970, 1973) argues that the principle is nonanalytic in virtue of the fact that 'fitness' is an undefined, primitive term of evolutionary theory. In short, there is little agreement as to how or whether the received view of theories accomodates even a reconstructed version of evolutionary theory.

I would not say that this is an uninteresting issue. But I still wonder whether it is a crucial issue. More to the point, I wonder whether evolutionary biologists need any sort of law of natural selection in order to account for the presence of a trait in a population in terms of natural selection. What is needed is a claim to the effect that natural selection is occurring or has occurred in the particular population in question, with respect to the particular trait in question. Some sort of assumption about the genetic basis of the trait --perhaps even a non-Mendelian assumption--would also be necessary in order to explain the effects of selection in one generation on the overall composition of the following generations. But the important thing to note is the difference between a general principle of natural selection, like, "On the average, the fitter organisms leave more descendants", and the restricted claim that natural selection is occurring in some particular population with regard to particular traits. Regardless of the empirical status of the general principle, claims of the restricted sort are clearly empirical. For instance, the truth of the claim that selection is favoring light-colored over dark-colored moths of a particular species depends on more than the logical structure of the claim and the meanings of its terms. The truth of the claim depends, in the first place, on whether the light-colored moths are actually contributing more descendants to future generations than the dark-colored moths, and that is certainly an empirical matter. The truth of such a claim depends, further, on whether the relative success of the light-colored over the dark-colored moths is due to chance or due to fitness differences. Only in the latter case, when differences in the descendant contributions of light and dark moths can be attributed to physical differences between them, is natural selection said to occur (see Note 8). When conjoined with a claim concerning the genetic basis of the coloration, the claim that selection is occurring can be used to explain or predict the ratio, or change in ratio, of light to dark-colored moths.

In general, proponents of the received view of theories have been so concerned about whether there is a law of natural selection that they

have not recognized the empirical and explanatory status of the more restricted claims about the occurrence of natural selection (Brandon 1978 is an exception). Interestingly enough, though, supporters of the empirical status of the principle of natural selection often end up defending instead only the empirical status of the more restricted claims. For instance, the evolutionist Francisco Ayala (in Dobzhansky et al. 1977) argues that the general principle of natural selection is not circular because, "Whether natural selection is involved in a particular genetic change, and whether natural selection favors a particular adaptation are questions to be resolved empirically." (p. 506, my emphasis).¹⁵

From the perspective of the received view of theories, Ayala's and others' arguments for the empirical status of nongeneral claims about natural selection are not terribly relevant to the legitimacy of an evolutionary theory based on the concept of natural selection. But their arguments are quite relevant from the perspective of the semantic view. On the semantic view, a theory based on natural selection would amount to a definition of 'natural selection'. And empirical claims within natural selection studies would be claims made on behalf of the definition--claims to the effect that natural selection is occurring in a particular population. In conjunction with claims made on behalf of definitions of different genetic systems, claims that selection is occurring or has occurred may be used to explain the presence or change in frequency of a range of traits, perhaps even including the "normal" meiotic mechanism. That there are no laws of genetics, and that there may or may not be a law of natural selection, does not deprive such accounts of their explanatory status.

7. Final Thoughts

In conclusion, I would like to suggest that, in light of the failure of the received view to accommodate evolutionary theory, the ability of the semantic view to accommodate that theory counts as a good reason to pay attention to the new semantic view, and to discount criticisms of evolutionary theory based on received-view standards. In case you are wondering, suspiciously, the semantic view of theories was not dreamed up for the special purpose of saving evolutionary theory. Even an incomplete survey reveals that the semantic view has been used to describe the structure of Newtonian mechanics (Giare 1979, Sneed 1971, Stegmüller 1976, Suppes 1957, 1967b, and Wessels 1976), equilibrium thermodynamics (Moulines 1975), and quantum mechanics (van Fraassen 1970, 1972). I think it is interesting and important that all those clumps of biological and physical knowledge that we call by the same name, 'theories', have enough in common that they can be cast in somewhat the same form--the form outlined in the semantic view. On the other hand, I do not think that interesting differences between physical and biological theories--like the possibility that physical theories may fit both the received and semantic views of theories, while biological theories may fit only the latter--should be explained away before biological theories can be considered adequate. Interesting differences should not be embarrassing differences. As the

proud evolutionist Ernst Mayr reassures biologists:

When physicists or philosophers "explain biology," they not only tend to use wrong terminologies but they usually throw away that which is typically biological... . Vitalism is now dead, as far as biologists are concerned, and a biologist can now talk about the differences between the philosophy of physics and the philosophy of biology without being suspected of being a concealed vitalist. (1969, p. 197).

And without being suspected, I might add, of holding inadequate theoretical standards.

Notes

¹Thanks to my friends who keep me philosophically well behaved, in this case especially Robert Brandon, Roger Buck, David Hull, Ron Giere, Ernst Mayr, Mark Pastin, Michael Ruse, and Mary Williams.

²In yet another review of the field, the philosopher of physics Mario Bunge refers to philosophy of biology as an "old yet under-developed discipline" and an "undisciplined discipline" (1979, p.155).

³This approach is stated quite explicitly in the introduction to Ruse's The Philosophy of Biology:

There are today no hard and fast "schools" of thought about the philosophical nature of biology. Nevertheless, like King Charles's head, one question keeps cropping up in discussions, namely whether or not biology is a science like the sciences of physics and chemistry. Since, in this book, we shall be examining the question from various angles, it will perhaps be useful to give here a very brief outline of what I think is still the dominant philosophical position on the theories of physics and chemistry. This is the position commonly known as "logical empiricism." (Ruse 1973, p. 10).

This can also be recognized in the titles of many publications, such as "Is Biology a Different Type of Science?" (Williams 1981), "Is Biology a Provincial Science?" (Munson 1975), "Is the Theory of Evolution Different?" (Ruse 1971), and "Is Biology Different from Physics?" (Ruse 1977).

⁴The semantic view also better accomodates other aspects of evolutionary biology, such as the role of optimal-design models in evolutionary theorizing (Beatty 1980).

⁵For instance, the widely accepted "covering-law" model of scientific explanation stipulates that descriptions of events to be explained must be deduced or strongly induced from laws in conjunction with descriptions of initial conditions (e.g., Hempel 1966, Popper 1935). To the extent that a theory is proposed to explain some range of phenomena,

then, that theory must consist of some statements which we reason to be laws.

⁶Of course, it is not likely that the specification of a system would ever be introduced without an empirical application of the specification. We certainly want to avoid the proliferation of inapplicable system specifications. So although we may, on the semantic view, abstract system specifications from their applications, we should not expect to find specifications without applications in practice. Sneed's (1971) and Stegmüller's (1976) versions of the semantic view take into account this close association of system specifications and empirical applications. On their "Kuhnian" version, theories are characterized not only in terms of the systems they specify, but also in terms of exemplary or paradigmatic applications of the system specifications. The paradigmatic applications may suggest further possible applications not originally associated with a system specification. Sneed's and Stegmüller's versions represent an important step in the direction of applying the semantic view to the dynamics (and not simply the structure) of science. For our present purposes, however, what is important about the semantic view is that it allows us to talk about science in terms of 1) system specifications and 2) empirical applications which may possess any degree of generality.

⁷Another major feature of the evolutionary synthesis was the recognition that the proper units of evolutionary change are reproductively isolated breeding groups (see, e.g., Mayr 1980). This development is taken for granted, rather than highlighted, in the discussion of the synthetic theory that follows.

⁸This discussion is based on definitions of 'fitness' and 'natural selection' such as are found in Brandon (1978) and Mills and Beatty (1979). For instance, as Mills and Beatty define 'fitness':

The fitness of an organism x in environment E is $n = [df]$
 n is the expected number of descendants which x will leave in E .
 (p. 275).

The expected number of descendants is calculated as follows. We can think of descendant contribution as an event with different outcomes O_1, O_2, \dots, O_n . Each outcome O_i represents a total contribution of i descendants. Now given a particular organism x , there is a certain probability p_i that O_i will occur. And there are probabilities p_1, p_2, \dots, p_n that outcomes O_1, O_2, \dots, O_n will occur. The expected number of descendants of x , then, is the weighted sum,

$$p_1 O_1 + p_2 O_2 + \dots + p_n O_n.$$

Each of the probabilities p_1, p_2, \dots, p_n is based on the physical design of x , just as the probability that a die will land with a certain side up is based on the physical design of the die.

As Mills and Beatty define 'natural selection', that process occurs when different kinds of organisms differ in their average descendant contributions on account of differences in their average fitness (pp. 282-284).

⁹For instance, if the frequencies of B and b are p and q respectively, and if the relative average fitnesses (i.e., the relative average expected descendant contributions) of organisms with the gene combinations BB, Bb, and bb are 1, 1, and 1-s respectively, then the change in frequency of B (Δp) in one generation is,

$$p = \frac{spq}{1-sq}^2$$

This equation follows from the Hardy-Weinberg law, given the fitness assignments I mentioned.

¹⁰It should be noted that Kneale's discussion of "All ravens are black" was actually in the context of an early, counterfactual analysis of scientific laws. For the informal purposes of this paper, the requirement that laws of nature support appropriate counterfactual conditionals has been replaced by the somewhat similar qualification that a generalization not count as a law if accepted theories allow exceptions to it.

¹¹Besides gene mutation, additional sources of variation, and hence additional evolutionary agents, include the recombination of alternative genes which have already arisen through mutation, and larger mutations causing structural changes in the chromosomes (e.g., see Mayr 1963, pp. 136-181).

¹²The evolution of the meiotic mechanism is the subject of several long-standing research programs. See, for example, C. D. Darlington (1932, 1939, 1958, 1980) and M. J. D. White (1945, 1954, 1973) on mechanical aspects. And see, for example, G. C. Williams (1975) and John Maynard Smith (1978) on adaptive aspects. Only mechanical aspects will be discussed in this paper.

¹³Dunn's introductory remarks concerning the consequences of his discovery for Mendel's law and the Hardy-Weinberg law are well worth quoting in full:

Among the causes responsible for changes in the relative frequency in a population of the members A and a of a pair of alleles, the most frequently cited are 1) the mutation of A→a and a→A at unequal rates; 2) selection, or inequality between the different genotypes in the production of surviving progeny; 3) differences between the genotypes in the rate at which the different genotypes enter or leave the population by migration; 4) chance fluctuations in the frequency of A and a due to sampling in small populations, leading to or toward fixation of AA or aa.

It can hardly be doubted that these factors, singly or in concert, are those most likely to be responsible for those disturbances in the genetic equilibrium of cross-breeding populations which lead to evolutionary changes. Nevertheless, a few cases are known in which variation of another kind must be taken in account. These are cases in which the disturbing factor is an inequality in the frequency of gametes A and a produced by the heterozygote Aa. Mendelian heredity and its corollary, Hardy-Weinberg equilibrium in panmictic populations, assume the equality of such A and a gametes as a matter of course, and the assumption is generally justified by direct evidence and by success in application. But the rule is not universal (pp. 139-140).

¹⁴Such an evolutionary viewpoint leads to a conception of meiosis quite different from the usual conception. For instance, contrast the claims considered earlier for the invariability of normal meiosis with R. A. Fisher's early evolutionary perspective on the subject:

The title chosen for our discussion [the General Addresses given at the sixth International Congress of Genetics] is "contributions of genetics to the theory of evolution," and that these contributions are of two kinds, somewhat sharply contrasted, is well illustrated by comparing Haldane's subject, "Can evolution be explained in terms of present known genetical causes?" with the heading under which I chose to speak, "The evolutionary modification of genetic phenomena." My own address might equally well have been entitled, "Can genetical phenomena be explained in terms of known evolutionary causes?" The one approach, as you perceive, is analytic and deductive. Genetic studies are regarded as revealing the mechanism connecting cause and effect, from a knowledge of which the workings of the machine can be deduced and the course of evolutionary change inferred. The other approach is inductive and statistical; genetics supplies the facts as to living things as they now are, facts which, like the living things in which they occur, have an evolutionary history and may be capable of an evolutionary explanation, facts which are not immutable laws of the workings of things but which might have been different had evolutionary history taken a different course. (1932, p. 165).

More recently, the evolutionary cytologist M. J. D. White warned, concerning the apparent invariability of meiosis, that:

The existence of fundamental similarity between the meiotic mechanisms of most multicellular organisms should not blind us, however, to the complex evolution which meiosis has undergone and the numerous detailed modifications which occur. (1973, p. 467).

¹⁵ Similarly, Michael Ruse (1973) purports to prove that the general principle "the survival of the fittest" is empirical. Yet the real conclusion of his argument is that the claim "natural selection is occurring" is empirical. As he argues:

Clearly, to claim (as biologists do) that a phenomenon like this [natural selection] occurs is not to talk in tautologies. Of course, one's claim might be false--one might never get a phenomenon like this in the world, or such a phenomenon, even if existent, might have no biological significance. But this, of course, is a risk that every scientific theory runs. In other words, it would seem that in supposing that there is natural selection, contrary to the claims of the philosophers just mentioned, biologists no less than physical scientists are making factual claims about the world. (p. 39, my emphasis).

Appendix 1. The Received View of Theories and the Semantic View of Theories

The "semantic view" of theories is so-called in order to distinguish it from the so-called "received view" of theories, which characterizes theories both syntactically and semantically. On the received view, the initial syntactic characterization of a theory consists in specifying what is known as an axiomatic calculus, which has four main components: 1) a vocabulary, or list of signs to be used in the formulation of the theory, 2) formation rules which govern the arrangement of signs into well-formed formulas, 3) a given set of well-formed formulas to be taken as axioms, and 4) rules of inference which license the inference of particularly structured, well-formed formulas from others (formulas derived from the axioms by the specified rules of inference are known as theorems).

This syntactic characterization is then followed by a semantic interpretation wherein the signs of the axiomatic calculus are interpreted as referring to various empirical entities and attributes. Only as a result of this interpretation do any of the axioms and theorems become empirical statements--statements whose truth or falsity is contingent upon empirical states of the world. Of course, proponents of the received view are most interested in interpreting the signs of the calculus in such a way that the axioms and theorems correctly describe the empirical entities and attributes designated by their terms. Such interpretations are said to delineate the "models" of a theory, where a model of a theory can be construed as a kind of system correctly described by the theory.

But this syntactic-semantic picture of theories raises an interesting problem. For standard formulations of most theories (in textbooks, etc.) do not assume the form of axiomatic calculi with appended interpretations. Indeed, it is questionable whether some theories (things we call "theories") like much of evolutionary theory, Freudian psychology, theories of the origin of the universe, and many others, can be characterized in this manner at all. At least, we are in a position to ask whether, and/or how, we might construct axiomatic calculi for different theories. And this suggests that there must be some means of characterizing and differentiating theories other than via their interpreted calculi. As Suppes expressed the problem in an article entitled "What is a Scientific Theory?":

The formulation of a theory as a logical calculus or, to put it in terms that I prefer, as a theory with standard formulation, gives an intrinsic characterization, but this is not the only approach. For instance, a natural question to ask is whether a theory can be axiomatized within standard formalization, that is, within first order logic. In order to formulate such a question in a precise manner, it is necessary to have some extrinsic way of characterizing the theory. (1967a, p. 60).

As an alternate means of characterizing a theory, Suppes proposed

that we simply specify the intended models of a theory (i.e., a semantic characterization), without reference to any particular axiomatic calculus (i.e., without a syntactic characterization). In other words, we are to characterize theories simply as specifications of the kinds of systems to which they can be applied. As van Fraassen relates the task of theories according to this characterization:

From this point of view, the essential job of a scientific theory is to provide us with a family of models, to be used for the representation of empirical phenomena. On the one hand, the theory defines its own subject matter--the kinds of systems that realize the theory; on the other hand, empirical assertions have a single form: the phenomena can be represented by the models provided. (1972, p. 310).

Since, on this view, theories are simply specifications of models, and since the specification of models is a matter of semantics, the "semantic view" of theories is an appropriate means of reference.

Appendix 2. The Derivation of the Hardy-Weinberg Law from Mendel's Law

Consider a locus which is represented in a population by only two genes, B and b. Among diploid organisms, there will be only three possible genetic types with respect to this locus, BB, Bb, and bb. Let us also assume that among parents in generation 0 (g_0), the distribution of genes is $pB:qb$ (where $p+q=1$), and the distribution of genetic types is $XBB:YBb:Zbb$ (where $X+Y+Z=1$).

Now if parents mate at random with respect to their genetic type, then the nine possible mating combinations will occur with frequencies described in the following matrix.

	male types		
	BB (X)	Bb (Y)	bb (Z)
female types			
BB(X)	x^2	XY	XZ
Bb(Y)	XY	y^2	YZ
bb(Z)	XZ	YZ	z^2

(For instance, $BB(\sigma) \times BB(\phi)$ matings will account for x^2 of all matings.)

If we also assume that Mendel's law (i.e., if we assume that each parent contributes one gene in regard to the locus in question, and that each of the genes at this locus of the parent has an equal chance of being contributed), we can calculate the proportions of genetic types of offspring which the nine possible matings will yield:

type	frequency	frequency of offspring		
		$\frac{BB}{X^2}$	$\frac{Bb}{X^2}$	$\frac{bb}{X^2}$
BB ♀ x BB ♂	X^2			
BB x Bb	XY	$\frac{1}{2}XY$	$\frac{1}{2}XY$	
BB x bb	XZ		XZ	
Bb x BB	XY	$\frac{1}{2}XY$	$\frac{1}{2}XY$	
Bb x Bb	Y^2	$\frac{1}{4}Y^2$	$\frac{1}{2}Y^2$	$\frac{1}{4}Y^2$
Bb x bb	YZ		$\frac{1}{2}YZ$	$\frac{1}{2}YZ$
bb x BB	XZ		YZ	
bb x Bb	YZ		$\frac{1}{2}YZ$	$\frac{1}{2}YZ$
bb x bb	Z^2			Z^2
proportions in g_1		$(X+\frac{1}{2}Y)^2$	$\frac{2(X+\frac{1}{2}Y)}{(Z+\frac{1}{2}Y)}$	$(Z+\frac{1}{2}Y)^2$

(For instance, given Mendel's law of segregation, Bb ♀ will contribute B half the time and b half the time, and BB ♂ will always contribute B. Therefore, half of the Bb ♀ x BB ♂ matings will yield Bb offspring, and half will yield BB offspring.)

Of course, the proportion of B genes in $g_0(p)$ equals the proportion of BB types plus one-half the proportion of Bb types. That is, in g_0 , $p = X + \frac{1}{2}Y$. Similarly, $q = Z + \frac{1}{2}Y$. Thus, the proportions in g_1 are

$p^2_{BB} : 2pq_{Bb} : q^2_{bb}$ (where p and q are the proportions of B and b in g_0). Moreover, the frequencies of B and b among the offspring of g_1 are again p and q. To see that this is the case, let us suppose that the frequencies of B and b in g_1 are p_1 and q_1 . As was reasoned above, p_1 equals the proportion of BB in g_1 plus one-half the proportion of Bb. Thus, $p_1 = p^2 + pq$. And $q_1 = q^2 + pq$. Substituting $q = 1 - p$ and $p = 1 - q$, we conclude that $p_1 = p^2 + p - p^2$ and $q_1 = q^2 + q - q^2$.

If, in addition to the assumption of Mendel's law and random mating we further assume that no factors disturb gene frequencies from the time of zygote formation to the time of gamete formation (in particular, if no selection, mutation, or migration occurs), we can conclude that gene and genetic-type frequencies in future generations will also be $pB : qb$ and $p^2_{BB} : 2pq_{Bb} : q^2_{bb}$. (We have already demonstrated that if the frequencies of B and b among parents are p and q, and if parents mate at random with respect to genetic type, and if Mendel's law holds, then the frequencies of genes and genetic-types among offspring will be $pB : qb$ and $p^2_{BB} : 2pq_{Bb} : q^2_{bb}$. If gene frequencies are not otherwise

disturbed-- i.e., if gene distributions among successive parent "pools" are also $pB:qb$, then gene and genetic-type distributions of successive generations will be $pB:qb$ and $p^2BB:2paBb:q^2bb$.)

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