dates of these books were 1972–1983; I set a criterion of at least five years after publication of "Phylogeny" for a text to be included. While two-thirds (14) cited at least one of his writings, only five cited "Phylogeny," not all of them favorably. (The five were Denny 1980; Eibl-Eibesfeldt 1975; Mortenson 1975; Nevin & Reynolds 1973; and Wilson 1975). The most frequent point made is that there is a parallel between individual behavior change and the evolution of behavior. This comparison is not at all new, having been made, perhaps most presciently, by E. L. Thorndike (1900a; 1900b), the founder of American animal learning psychology, in his astute 1899 lectures on instinct and learning at Woods Hole that followed a previous series of lectures by C. O. Whitman (1899), whom Lorenz and other ethologists hold to be the founder of comparative ethology (Burghardt 1973).

Ethologists have frequently argued that the field of animal learning has left out comparative, ecological, and evolutionary considerations in its rush to formulate general principles. A push for this impatience certainly arose from a primary interest in human learning and the desire to use controlled "scientific" studies with animals to legitimize applications to people. Certainly the power and successes of behavior modification principles in diverse areas of human behavior are a lasting tribute to Skinner. Yet even these successes have been most marked when a relatively eclectic approach is taken with respect to the behaviors recorded and the contexts employed. This is in marked contrast to the animal operant conditioning work which, with few exceptions, has continued to focus not only on rat lever pressing and pigeon pecking but has become insular, extremely esoteric, and removed from most of the concerns and issues of other students of animal behavior.

Indeed today, as behavioral ecology formulates models that cry out for the operant methodology, people other than traditional Skinnerians have had to examine the parallels and applications (e.g. Crawford 1983). I personally find extremely stimulating work such as Timberlake's (1983) which tries to apply a knowledge of the principles of animal learning and the evolved behavioral repertoires of their subjects in a way that makes me think a true integration of ontogeny and phylogeny, ethology and experimental psychology, just might be possible. Skinner's contribution to the study of animal behavior will endure; context and style have slowed, but not prevented, their incorporation into ethology.

Operant conditioning and natural selection

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Who says Skinner has no sense of humor? In "Phylogeny" he tells us that fishermen do not set nets because of any internal intention, purpose, or desire to catch fish. They do so merely because their net-setting behavior has been reinforced in the past and has therefore become more frequent, just as spiders do not spin webs because of any intention, purpose, or desire to catch flies, but merely because their web-spinning behavior has been naturally selected in the past and has therefore become more frequent. "Even if we could discover a spider's felt intention or sense of purpose," says Skinner, "we could not offer it as a cause of the behavior"; presumably the fisherman's felt intention, which we *can* easily discover, is equally irrelevant to the explanation of his behavior, or can supply only a "fictional explanation" (Skinner 1953, p. 278).

Variations on this familiar theme can be found throughout Skinner's writings over the past half-century. Is he willing to confirm, after all these years, with the tide of cognitive psychology running high, that he never intended these statements to be taken literally? If not, then will he certify the following behavioral analyses, which suggest (as Blanshard 1967 and others have pointed out) that novelists, dramatists, historians, philosophers, and ordinary people the world over have been governed by a unanimous illusion? (a) Romeo's feeling of love for Juliet, and his mistaken belief that she was dead, were in no sense causes of his suicide; his suicide can be explained only as the result of external influences which somehow increased the frequency of his suicidal response from zero to one. (b) Hitler's feeling of hatred toward the Jews is irrelevant in explaining his genocidal policies; the Final Solution must be attributed to contingencies of reinforcement which increased the frequency of his genocidal behavior. (c) Skinner does not propound this doctrine because he believes it to be true; he propounds it (frequently) merely because he has been reinforced in the past for doing so. This last example suggests, by the way, that Skinner's behaviorism is a self-defeating doctrine, since whenever he propounds it he implicitly denies that he believes it, or at least that it has any valid claim to truth (see Branden 1963; Locke 1966).

In "Phylogeny" Skinner draws an analogy between operant conditioning and natural selection in the provenance of behavior. A certain response is more likely to recur if it is associated with ontogenic contingencies that are reinforcing, just as a different response may be more likely to recur if it is associated with phylogenic contingencies that favor it through natural selection. I have always felt suspicious of this analogy, and I now think I have put my finger on one cardinal deficiency of operant conditioning theory in comparison with the theory of natural selection. *Operant conditioning theory offers no mechanism to explain changes in response frequency.* In the (modern) theory of natural selection, responses become more frequent because, when exposed to certain phylogenic contingencies, organisms that possess genes for these responses produce more offspring, on average, than do other organisms that lack such genes, and these offspring tend to resemble their parents because they inherit their parents' genes. In the theory of operant conditioning, on the other hand, responses become more frequent when organisms are exposed to certain ontogenic contingencies of reinforcement, but no mechanism is offered to account for this. In fact, the events that function as reinforcers are defined simply as those that increase the frequency of the responses they follow: "the only defining characteristic of a reinforcing stimulus is that it reinforces" (Skinner 1953, p. 72); the theory does not presume to explain how or why response frequency increases. Operant theory, in sharp contrast to natural selection theory, purports to be merely descriptive rather than explanatory (see, e.g., Skinner 1938, p. 44; 1950), and therein lies one of its crucial weaknesses.

But in spite of its purportedly atheoretical character, operant theory does entail claims that can, at least in principle, be empirically falsified. For example, in "Phylogeny" Skinner asserts that "what we may call the ontogeny of behavior [can be] traced to contingencies of reinforcement." Mills (1978a; 1978b) has raised several objections to this assertion, but I shall confine my remarks to just one, which arises from experiments on autoshaping. Brown and Jenkins (1968) demonstrated that the key-peck response in pigeons develops when the key in a Skinner box is illuminated, even when the pecking does not speed up the delivery of food reinforcements. Williams and Williams (1969) showed that the ontogeny of this kind of behavior cannot be traced to any accidental or adventitious reinforcement. More recently, Stiers and Silberberg (1974) found that, although rats will not learn to press a bar if there is a random relationship between the presentation of the (retractable) bar and food reinforcement, they will do so if there is a predictable relationship, even when bar pressing *delays* the delivery of food reinforcement.

Skinner has recently gone on record as saying: "I do not often

read my critics" (Skinner 1983b, p. 28). Since he will undoubtedly read this commentary, and the others in this issue, I only hope that I shall be able to understand his response.

Consequence contingencies and provenance partitions

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When, about 15 years ago, I had to prepare a lecture intended to inform a conference of neuroscientists about the views of ethologists on the development of behavior, I thought it would be a good idea to contrast these views with those of behaviorists. One of the themes I thought of featuring was the behaviorists' Olympian disregard of biological evolution. The title of the lecture was going to be "The Phylogeny of Behavior Ontogeny." My dismay was great when idly leafing through a pile of *Science* issues left by my office predecessor I stumbled upon B. F. Skinner's "Phylogeny," There was the preeminent theoretician of behaviorism holding forth on the very topic I supposed he and his brethren chose to ignore. I quickly modified both the tack and the title of my presentation (Delius 1970).

However, as laudable as I found Skinner's late interest in evolution, I was disappointed by "Phylogeny." It was neither a source of theoretical inspiration nor a reflection of the state of the art. On the contrary, it seemed intent on reversing hard-won progress. It reified in the guise of "ontogenic behavior" and "phylogenic behavior" the strict dichotomy between innate and learned behavior, a division that even ethological diehards had by then been forced to give up. All the arguments and the evidence against such a black-or-white distinction that had been marshaled by then (see Hinde 1966; Marler & Hamilton 1966) seemed to have bypassed Skinner. A rigid commitment leads him to equate behavioral ontogeny exclusively with the changes of response probabilities due to reinforcement contingencies, that is, with operant conditioning. Not even classical conditioning is expressly acknowledged to play a role in the development of behavior. Imprinting is, summarily and wrongly, dismissed as just another instance of operant conditioning. Nonlearning influences of environmental variables on the ontogeny of behavior are ignored. The provenance of "ontogenic behavior" is simply and purely operant conditioning and nothing else.

In contrast, Skinner ascribes the provenance of "phylogenic behavior" to the contingencies of natural selection acting upon a collection of fixed action patterns and does not allow it any ontogeny. This is logically consistent within his conceptual framework but ignores the fact that it conflicts with the evidence then already extant. That phylogeny exerts control over behavior via ontogeny and through genes is conveniently ignored. Behavior genetics is all but dismissed on the technical ground that its results do not square with Skinner's expectation that genes should express themselves in "units" of behavior.

Conversely, "ontogenic behavior" apparently does not have a phylogeny except that Skinner admits obliquely that baseline responding and certain reinforcers may have an evolutionary provenance. Considering that Skinner equates ontogeny with operant conditioning, that might be a fair reflection of contemporary behaviorist opinion. But there were already signs that it would not endure (Garcia & Koelling 1966). Following earlier ethological suggestions (Lorenz 1965; Tinbergen 1951) it soon became apparent that the phylogeny of learning is a more complex and incisive issue (Seligman 1970).

Instead, attention is drawn to the analogy that exists between the processes underlying phylogeny and ontogeny (sensu Skinner). Contingencies of selection in one case and contingencies of reinforcement in the other are identified as the moving agents. This parallel still has some reality, but it would have been fair to point out that other authors, more recent than Descartes, had dealt with it in some detail (e.g. Pringle 1951). The comparison of the outcomes of schedules of reinforcement with the effect of schedules of selection that might have been illuminating remains superficial; Skinner, perhaps sensing that it would have shown up the limitations of the analogy, chose not to find out what evolutionary biologists had to say about the matter. The exciting possibility of an "experimental analysis of phylogenic behavior" is surprisingly negated by alluding to natural selection's action in the unrecoverable past. Artificial selection is unnatural and thus deemed not really relevant. Ad hoc pleading is then necessary to immunize from a similar criticism artificial reinforcement, the basis of what should now correctly be the "experimental analysis of ontogenic behavior." Arguably, the failure to provide objective, as opposed to hypothetical, accounts of the natural ontogeny of behaviors as a product of natural reinforcement contingencies was already in 1966 corroding the attractiveness of radical behaviorism.

Why has the paper had so little impact, even among Skinner's own following? It is simply that the attempt to contain the explosion of knowledge that had in the meantime occurred within the very lean ontological framework conceived some 30 years earlier (Skinner 1938) yielded an inadequately narrow account. It could not compete against the up and coming eclectic, much richer, multidisciplinary account of behavior (Delius 1985), which, to be sure, incorporates a great deal of what Skinner and his disciples have discovered and described with truly admirable acumen. The sad fact is that simplicity, contrary to widespread opinion, is not a principle that organisms often care to respect.

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Difficulties with phylogenetic and ontogenetic concepts

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Skinner complains that explanatory entities such as "instincts," "drives," and "traits" still survive. But evidently he fails to realize that these concepts have been redefined and in most cases replaced. "Phylogenetically adapted," for example, is preferred to "instinctive" nowadays. The term refers to the source of information controlling the process of differentiation during embryogenesis and ontogeny. If, for example, motor patterns develop without corresponding patterned input from the environment then it is reasonable to assume that the wiring of the neuronal networks underlying these skills developed in a process of self-differentiation according to the developmental recipes encoded in the genome of the individual in question. To argue that some unidentified environmental factors might have contributed to the patterning comes close to referring to some mystical force. Those poor mice whose forelimbs were amputated by Fentress (1973) at birth and which nonetheless developed the complete coordinated pattern of preening the head with the (nonexisting) forelimbs – as could be deduced from the movement of the stumps, the contraction of the remaining muscles, and the head and eye movements coordinated to the movement patterns of the "arms" – could not possibly have learned by any of the traditional ways of learning. All the details