Discussion of Comments on “The Representative Animal”

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I thank S. S. Glenn, I. H. Iversen, and E. A. Wasserman for their discussions of the target paper, and for the opportunity to clarify my own thoughts on points raised by these reviewers.

Wasserman's Contribution

Do those who study rats, pigeons, and monkeys believe them to be good substitutes for human beings? Or is it believed that their behavior might be sufficiently similar to humans and many other species to help in elucidating fundamental laws of behavior? My interest differs from either alternative; it is in the study of the fit between the behavior of an animal and its everyday environment. The traditional approaches have generated lawful behavioral relations, but these have an unknown relation to the behavior of the animal in its everyday environment. For example, studies of the control of responding by events not present at the time of the response (delayed matching to sample; e.g., Wasserman, 1993a) have discovered laws that hold for pigeons and other common laboratory species. But these laws do not allow guesses as to whether pigeons cache food that they are able to find several months later, or whether chimpanzees will be able to find food buried many hours previously (Maier & Schneirla, 1935, pp. 448–449; Sherry, 1988).

In a slightly different vein, field studies have shown that cliff swallow (*Hirundo pyrrhonota*) parents individually recognize their young acoustically when they leave the nest, whereas in the barn swallow (*Hirundo rustica*), the young are not

individually recognized. Traditional auditory discrimination studies of these two species would not have suggested the radically different discrimination of the young in the two species (Beecher, Loesch, Stoddard, & Medvin, 1989). However, traditional discrimination studies were then carried out on these two species after the findings of the field work, the results of which added to the understanding of the field behavior by showing different information content in vocalization of the two species.

The goals of experiments aimed at, say, behavioral fit to the environment clearly differ from the goals of experiments aimed at the comparative study of cognition, but a summary of the preceding two paragraphs suggests that a major value of traditional approaches lies in the application of these to questions arising from ecological considerations (Watson, 1914, pp. 30–31). These latter questions are outside the questions generated by the traditional experiments themselves.

One fundamental difficulty of comparative behavioral research that has been stressed by Kennedy (1992, pp. 1–18) is its anthropocentric concentration. Experiments attempt to examine, in non-human animals, theoretical processes derived from language that deals with human behavior. The terms *intelligence*, *memory*, *learning*, and *concept* for example, are nouns used to talk about human behavior. These nouns are names of classifications of human behavior (frequently deliberately undefined, Wasserman, 1993a, p. 212) that are based upon continuing interactions with humans at an intimate level, and that may be useful in talking about the way individuals adjust to their environments. It is these classifications that are typically used in planning experiments on pigeons (Hulse, 1993; Wasserman, 1993b). If everyday pigeon behavior was studied as closely as we are forced to study everyday human

I thank Henry Marcucella and Fabio Idrobo for their observations on previous drafts of the reviewers' comments.

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behavior, a number of classifications of pigeon behavior would emerge. Although some of the classes would overlap with human classes, others probably would not. This is one factor that makes it difficult to test different species in "essentially equivalent conditions" (Wasserman, 1981, p. 252; 1993b), because it is not known whether the same human type classifications are being tapped in experiments using different species. Notwithstanding this difficulty, parallels have been reported by Wasserman (1993a, 1993b) between human and animal performance in experimental tasks. Pigeons gave about 80% correct responses to novel photographs of cats, cars, flowers, and chairs after training on an original set of photographs of these four groups of objects. However, when subjects were trained using different groups of photographs, each group containing cats, cars, flowers, and chairs, performance was poor to novel exemplars (Wasserman, Kiedinger, & Bhatt, 1988). This performance parallels human performance to these two arrangements of the stimulus objects. The pigeon might, perhaps, be considered a "distinctive species" with respect to humans in this research. But these coincidences may not indicate similarities beyond the immediate experiments. For example, pigeons responded more to truncated triangles than obstructed triangles, the opposite of the human response to such figures (Cerella, 1980).

In the penultimate paragraph of his contribution, Wasserman touches on evolutionary considerations and ways to conduct comparative behavioral research. The history of comparative psychology illustrates the difficulties of working in this area. For example, one thrust to find a phylogeny of behavior in the earlier part of this century focused on animal learning, particularly on Harlow's learning-set phenomenon (Gottlieb, 1985, pp. 60–61; Harlow, 1959). This failed for a number of reasons discussed by Warren (1973, pp. 483–491). One factor was the increasing skepticism that different species could be trained using equivalent learning-set tasks because of the largely unknown behavioral differ-

ences possibly relevant to performance in these tasks (Richelle & Lejeune, 1980, p. 100). Second, the intraspecies variation in performance in these tasks often exceeded the differences among species. Third, there appeared to be no relation between learning-set performance and the phylogenetic status of the species estimated from taxonomic arrangements of different species of extant animals.

A final reason, not mentioned by Warren, was the essentially nonempirical basis of the comparative behavioral research. Taxonomic systems are based on differences and similarities in the morphologies of different animals, as well as on interbreedability, genetic, and other differences. Such systems, for the most part, attempt to capture the natural relations among different species, and their success in doing this was attested to by the fact that preevolutionary systems could readily be seen as phylogenies following Darwin's theory of evolution (Mayr, 1966, pp. 5–16). The comparative method was used differently when it was taken over by psychology. First, it was not applied to empirical variables, such as morphology, but to hypothetical variables, such as learning (Gottlieb, 1985, pp. 61–62) or memory (Wasserman, 1993b). Second, work was not directed towards erecting a scheme that represented the natural behavioral relations among the different species (Brookshire, 1976; Gottlieb, 1985, p. 63). One way to approach this is to consider behavioral plasticity as especially adapted to meet environmental contingencies that are highly critical for survival (Tinbergen, 1951, p. 221, special dispositions to learn; Johnston, 1985, p. 4), but the study of the phylogeny of such behavior is likely to be a difficult task (Klopfer & Hailman, 1967, pp. 186 on). To quote Sherry (1988, p. 79), "if we are to be honest, nothing is known about the evolution of learning." The study of learning within an ecological context does not necessarily limit investigations to cataloging properties of behavior (although this may be an essential starting point) because many different abilities, such as spatial orientation, are common to many species and may

be studied across species (Shettleworth, 1993).

The study of the evolution of some character of an extant animal is the study of the history of that character. The history of behavior cannot be directly studied, but some contact with behavior is possible through the study of the evolution of the nervous system using endocranial casts of fossil material (Edinger, 1948, pp. 21, 44–47, 86–87; 1961). For example, paleoneurological studies of cetaceans indicate that early forms showed strong development of the cerebellum and the vestibular branch of the VIII nerve, but no indication of excessive development of the auditory division of the nerve or parts of the brain stem, mid-brain, and cerebrum seen in extant cetaceans (Edinger, 1955). Unlike extant forms, early cetaceans also possessed an olfactory system. These data suggest that the enlarged vestibular system and cerebellum were necessary for orientation in the three-dimensional medium, and that sensory systems, other than audition, guided behavior.

Glenn's Contribution

The second paragraph of Glenn's contribution suggests that readers of the original paper could come away with the impression that it is not useful to study the behavior of one species to find out information about a second species. It was not my intention to give this impression, especially because my own work has been shown to generalize across a number of species.

My interest lies in investigating the fit between behavior and its control by acoustic events in the everyday environment. The physical properties of sounds, sound fields, and the properties of sound sources, for example, in the everyday environment impose restrictions on the kinds of sound-source behavioral interactions of small land-dwelling mammals that can take place in the everyday environment. These restrictions have existed over the lifetime, and the evolutionary history, of each animal, and it seemed likely that performance in audi-

tory discrimination tasks that incorporated these restrictions may be superior to the performance of tasks in which these restrictions are removed or altered. This was found to be the case for rats (Harrison, 1992; Harrison & Beecher, 1969).

Because many of the restrictions on behavioral interactions with the acoustic environment hold for many species of land-dwelling mammals, other species should show the same kinds of fit to the acoustic environment as rats. This was found to be the case in cats, dogs, bats, squirrel monkeys, and rhesus monkeys (e.g., Downey & Harrison, 1972; Harrison, Iversen, & Pratt, 1977; Heffner & Heffner, 1990; Lawicka, 1979). This rationale for across-species comparison differs from the traditional one represented by the opening quotation of my original paper, in that in the present scheme generalizability across species depends upon similarities of behavioral fit to some aspect of the environment of the two species. Although the results of experiments in behavioral fit to the acoustic environment, for example, may generalize across land-dwelling mammals because of acoustic similarities, generalization is likely to be much less to the results of work on hearing in flying birds in which hearing may have a radically different fit to the environment.

The work on behavioral fit is not concerned with the investigation of the relative contributions of the life history and the evolutionary history in determining the degree of fit between the behavior and the everyday acoustic environment. Thus, the work does not contribute to notions of behavioral homology (e.g., homology of reinforcement in different species, Glenn, p. 227) and analogy, nor to the understanding of the evolution of the behavior, and hence to the kinds of questions discussed by Glenn. The work is simply concerned with the fit of the behavioral phenotype to the environment.

Glenn refers to the "unlearned reaction 'approach sound source'" (pp. 226–227) and discusses the overriding of this response by reinforcing other responses. This usage of "unlearned reaction" suggests that behavior can be divided into

two categories, innate (instinctive, genetic) and learned (acquired). However, this dichotomy is not used here, behavior being considered to be the joint product of genetic make-up and life history (i.e., to be phenotypic; Huntingford, 1984, pp. 104 on; Johnston, 1985, p. 3; Lehrman, 1970; Whitney, 1976, p. 83). In line with this, "approaching a novel sound source" is a behavioral phenotype. Animals have a long life history of being reinforced for approaching low-level novel sound sources, and this history is one of the components of the sound-approach phenotype. The "different processes" quoted by Glenn (p. 226) refers to the fact that when arrangements found in the everyday environment are incorporated into the experiment, the behavior fits the task, whereas in the unnatural arrangement facets of the behavior do not, and so these have to be eliminated. The attachment behavior of human infants, to use Glenn's example, is a product of the genetic make-up and life history of the child, and is thus phenotypical, and is an example of species-specific behavior of *Homo sapiens*. The interactions between genetic make-up and life history may be complex, as found, for example, in song development in song sparrows (Marler & Peters, 1989).

Glenn raises a number of examples of the unclear use of language in my contribution that have led to assumptions that I did not mean to convey. Glenn points out that words are used in different ways by different people, and this may be a source of misunderstandings.

The first example has to do with the use of the term *species phenotype* (p. 228). Glenn points out that each member of a species has a unique behavioral phenotype because of its different life history. A species is defined as a population of interbreeding animals (Mayr, 1966, p. 19 on; Mayr, Linsley, & Usinger, 1953, p. 15 on). Glenn, Ellis, and Greenspoon (1992, p. 1333) use a similar definition. Some populations of rats, for example, are of the species *norvegicus*. The species of a particular rat picked from that population is also of the species *norvegicus*. Individual rats have a particular life his-

tory and genetic make-up, and their behavior is the product of both these aspects; that is, it is phenotypical. A sample of phenotypical characters, such as morphology or behavior, could be measured in the interbreeding population to find the population variation of these characters. Behavioral measurements of any additional rats would, with a high probability, lie within the measured variation of the sample of the population.

In the light of the preceding definitions, my statement "each species brings a different . . . phenotype to the experiment" (p. 210) may be clarified as follows. If a single *norvegicus* rat was purchased from the population of an animal breeder and studied in an operant task, its performance (a phenotype) will be that of a rat. If 5 *norvegicus* rats were purchased from the population of the animal breeder and studied in the operant task, the phenotypical performances of 5 rats would be available. The five phenotypical performances may be grouped and used as an estimate of the variation of performance in the task in the breeder's population. Knowledge of this variation indicates the probable performance of additional rats in the task purchased from that supplier. Whether a single rat or group of rats is being referred to will be clear from the context of the "species phenotype." The phenotypical performance (with its variation) referred to here is that found in rats, and is thus a species-specific phenotype. If cats were studied in the apparatus, a different population of species-specific phenotypes (of cats) would be obtained. My statement was also sufficiently unclear to give the impression to Glenn that it referred only to behavior that members of the group have in common (Glenn's "innate" behavior, p. 226). This is not what was meant. The variation of behavioral characters in a population may include an absence of some behavior. For example, some members of *sapiens* are unable to perform behavioral tasks that involve differential control of responding by red and green stimuli, but they bring the species-specific behavioral phenotype of *sapiens* to the experiments because the difficulties in

red-green discriminations are included in the behavioral variation of the interbreeding population.

A second example Glenn gives of the confusing use of language is my statement "species-specific behavior is all the animal . . . has" (p. 210). A single animal is being referred to here, and the particular behavior it brings to a task will be within the variation of that behavior found in the interbreeding population of which this rat is a member. If it behaved in any other way, it would not be a member of that population; that is, it would not be a *norvegicus* rat but some other species. All an animal will ever do in any particular task is to behave as any other animal of the same species, within the population variation. A rat always gives rat-like behavior. For example, Iversen (1993) studied three Long-Evans hooded rats in a matching-to-sample task and found that their response patterns indicated that the rats had acquired a discrimination of specific stimuli and their positions. The performance of these 3 rats would, presumably, fall somewhere within the performances given by a number of Long-Evans hooded rats large enough to allow an estimate of the variation in this task found in the breeder's population.

The effect of very different life histories can be analyzed as follows. Two rats purchased from a supplier could be given completely different life histories by being studied in very different behavioral tasks. If these 2 rats were then studied in the same new task, their performances would probably be grossly different. Each would be giving the species-specific phenotypical performance in the new task of *norvegicus* with its particular conditioning history. What the experiment would show is the way the performance of animals of the same species differs when the animals are given different life histories, but the differences found will always be characteristic of *norvegicus* rats. The same conclusion would be reached if groups of rats had been studied in the different tasks. The within-group performances of each group in the new task would be the same, within population

variations, but the between-group performances would differ, within the population variation, in the same way as the single animals.

A third example was found in the sentence "Thus, one species is likely to abstract certain stimulus features from the environment, be subject to certain stimulus filtering, and have a strong tendency to emit a number of characteristic responses" (p. 210). Glenn suggests two possible meanings of this statement. The first suggests that the environment functions as it does as the result of natural selection only. The second is that the notion of behavioral environment is a function of genetic make-up and life history (p. 228). This latter alternative was the intended meaning. Glenn and I are in agreement that the "behavioral environment" (in the sense of von Uexkull, 1957) is determined by the behavioral phenotype of the organism.

Iversen's Contribution

Iversen discusses the results of a study (Neill & Harrison, 1987) on the relation between sound quality discrimination and sound location discrimination and go/no-go and go-right/go-left discrimination procedures. Konorski and his colleagues (1967, p. 438; Dobrzecka, Szwedkowska, & Konorski, 1966; Lawicka, 1964, 1969) investigated auditory discriminations using these procedures with the results described by Iversen. These data were interpreted by Seligman (1972, p. 3 on) as an example of a constraint on learning. The experiments of Neill and Harrison were designed to show how the fit of an animal's behavior to acoustic events might account for Konorski's results. In emphasizing the notion of fit, the relation of their results to problems raised by Seligman's idea of constraints and preparedness was not adequately realized. This gap has been filled by Iversen's discussion of their data.

Two points need clarification. Iversen refers to "the subject's natural (untrained) reaction" (p. 232). In view of the stress on the phenotypical nature of behavior in the discussion of Glenn's con-

tribution, the word *untrained* should be taken to mean not deliberately trained by an experimenter. The animal, however, has had extensive training in approaching low-level novel sound sources simply as the result of its everyday activity (see Iversen's example on p. 232). A similar comment applies to Iversen's use of "trained behavior and natural behavior." Here "natural" behavior is that which fits the everyday environment.

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