ANIMAL BEHAVIOR: A Continuing Synthesis

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INTRODUCTION

As a synthetic discipline, animal behavior lives by the wits, good will, and agreement of the scientists creating it. Current interest in animals is high, and powerful new techniques are available to establish the mechanisms, development, evolution, and function of behavior. Yet the coherence of the discipline is low, its conceptual center increasingly little more than a weighted average of new interests and old allegiances. Some of this lack of coherence can be traced to incomplete integration of parts of the original synthesis of the field. The present review considers four areas of conflict and truncated development for which further integration should contribute to a more stable base: (a) research differences, (b) methods of comparing behavior, (c) the dynamics and structure of behavior, and (d) cognitive abilities.

The Historical Synthesis of Animal Behavior

The discipline of animal behavior emerged in the late 1950s and early 1960s from the synthesis of comparative psychology and ethology. The initial interaction of these fields was dominated by sharp disagreement over the relative importance of instinct and learning in determining behavior (Lehrman 1953). Ethologists emphasized functional stereotyped motor movements and stimulus sensitivities that occurred without specific experience, presumably based on genetic programming. Psychologists emphasized the malleability of development, often focusing on nonfunctional outcomes as evidence of the importance of learning. A concise illustration of this conflict is Grohmann’s (1939) demonstration that pigeons reared in confined boxes flew at the first opportunity, pitted against Dennis’s (1941) discovery that vultures raised in similarly constricted circumstances failed to fly and fell to the ground when placed on a perch.

The unexpected outcome of this apparently intractable conflict was synthesis of the new and energetic discipline of animal behavior (Hinde 1966; Marler & Hamilton 1966). A major factor promoting this synthesis was the surprising number of interests shared by ethology and comparative psychology, including concern with development, motivation, evolution, adaptation, physiological mechanisms, small stimulus-response units, and stimulus control. Other shared concerns included a strong empirical orientation and a distaste for vitalism. A critical role in the synthesis also was played by personal ties between individual researchers, such as between the ethologist Lorenz and the psychologist Lehrman. The contributions of Frank Beach along these lines are described in a brief memorial (Dewsbury 1989b), while Tinbergen (posthumously) and Robert Hinde were recently honored with essay collections documenting their influence (Bateson 1991; Dawkins et al 1991).
Current Status of the Synthesis

The synthesis of comparative psychology and ethology has been quite successful. Authors of the last three chapters on this subject in the *Annual Review of Psychology* have documented the robustness of animal behavior research (Dewsbury 1989a; Mason & Lott 1976; Snowdon 1983). Opportunities for professional publication continue to increase with the expansion of old journals and the introduction of several new ones (*Journal of Biological Rhythms, Behavioral Ecology,* and *Journal of Cognitive Neuroscience* are recent examples). To stay current with just the titles of relevant books and chapters published each year requires a significant amount of time.

There are, however, some mixed indicators. The relative success of the field in securing government support for basic research is uncomfortably low. Though training funds in animal behavior recently received a slight increase, American government agencies typically fund only 10–15% of research proposals in this area (see Myers 1990, for an account of the process from the applicant’s view). University positions related to animal behavior appear to have decreased. Research with dogs, cats, and rabbits has declined steadily (Viney et al 1990). Paranoid feelings remained high for years in reaction to E. O. Wilson’s (1975) argument that comparative psychology had died and ethology and physiological psychology would follow by the year 2000, cannibalized by integrative neurophysiology, sociobiology, and behavioral ecology. Though concern has subsided, self-doubt continues. Bateson & Klopfer (1989) edited a volume entitled “Whither Ethology?” Demarest (1981) presided for several years over a self-examining newsletter on comparative psychology. Leger (1988: ix) noted, “I know of no discipline that has devoted so much time, effort, and printer’s ink to a lengthy debate concerning its territorial limits . . . .”

At an accelerating pace important discoveries relevant to animal behavior come from outside the discipline. These discoveries provide fascinating opportunities for assimilation but also may bring into question the adequacy and stability of the synthesis. Recent advances in allometry (Gittleman 1989b) and the hormonal control of natural behavior (Wingfield & Moore 1988) have been dominated by physiologists. Molecular neuroscience has assumed a major portion of the search for basic mechanisms of learning, kin recognition, hormonal control of behavior, and rhythmicity (see Becker et al 1992; Martinez & Kesner 1991). Research in motivation has been co-opted by animal welfare concerns (Dawkins 1990; Hughes & Duncan 1988). The task of modeling animal behavior has leaned heavily on approaches developed in other fields. These approaches include: optimality, from economics and applied mathematics (Alexander 1982); connectionism, from cognitive psychology and computer science (Grossberg 1988); and stochastic dynamic modeling (Mangel & Clark 1988) and nonlinear dynamical systems (Beltrami 1987), from mathematics and physical systems.
Relevant new fields, such as artificial life, spring up without warning, complete with conferences, a newsletter (Alife Digest), and journals (Adaptive Behavior and Artificial Life). Slightly older fields, such as sociobiology and behavioral ecology, continue to pursue different visions of causation (though see the suggestion of Krebs & Davies 1991 and Bell 1991 that behavioral ecology return to mechanism). Other fields, such as neuroethology (Ingle & Crews 1985) and developmental psychobiology (Blass 1986) waver between animal behavior and closer ties to neuroscience. Changes in fundamental ideas, like the nature of evolution (Eldridge 1989), reinterpretations of the modern evolutionary synthesis (Provine 1988), and the active role of genes in daily behavior (Rusak et al 1990) provide continuing challenges to the task of constructing a coherent account. Because animal behavior remains a synthetic discipline, the critical issue for the field is maintaining an historically grounded coherence while assimilating the flood of new developments.

A Reconsideration of the Synthesis

In several respects the original synthesis was incomplete. For some the gap between comparative psychology and ethology has closed (Dewsbury 1990). But others still see marked differences in training, research focus, comparisons, procedures, and models—differences sufficiently large to promote separate professional allegiances. For example, the International Ethology Conference and the journal Ethology maintain a separate identity, as do the International Society of Comparative Psychology, the Journal of Comparative Psychology, and the International Journal of Comparative Psychology. Some even feel the name “animal behavior” is an issue because it might be seen as excluding humans. We are all animals here and we have a worthy heritage. Much of the historical coherence of animal behavior has been provided by Tinbergen’s (1951) four questions concerning evolution, function, mechanism, and development of behavior. These questions explicitly encourage a balance of approaches and causal levels, establish boundaries to the field, and help highlight research concerns overshadowed by rapid developments in other topic areas (e.g. Barlow 1989; Bateson & Klopfer 1989; Dawkins 1989). However, Tinbergen’s questions by themselves do not provide a unifying picture of the fit between animal and environment. The clarity of the ethologist’s original picture has been lost in the ensuing forty years. The purpose of the present review is to reconsider some unresolved conflicts and undeveloped strengths of the original synthesis in the hope that their further development and integration might help provide a more coherent center for the study of animal behavior. Even with this regrettable restriction it was possible to sample a only small portion of the thousands of excellent publications since the last review.
PERSISTENT RESEARCH DIFFERENCES

Field vs. Laboratory Methods

In the extreme view, comparative psychologists have been associated with a laboratory approach to research—the use of arbitrary stimuli, “artificial” laboratory-bred animals, automatic recording of arbitrary response elements, and extensive statistical analysis. Ethologists have been associated with a field approach to research—including extensive observation of animals in uncontrolled field conditions, a focus on highly complex behaviors, and impressionistic reporting. These stereotypes, always of doubtful accuracy, are inappropriate now that laboratory and field approaches have become increasingly difficult to distinguish (Blanchard et al 1989; Dewsbury 1990; Gibbons et al 1992). However, differences remain in how frequently individual investigators use the full range of research options.

Some researchers argue that field work must precede laboratory analysis (external validity first, see Kamil 1988). Others feel that phenomena must be established in the laboratory before dealing with the complexity of the field (internal validity first). The best long-term strategy is to include a range of approaches, thereby providing both sorts of validity and avoiding obstacles that arise simply from pursuing one approach exclusively. For example, a high degree of environmental control of stimuli allowed remarkable insight into the development of structure in birdsong, but the recent demonstration that live tutors produce different effects than tapes highlights the importance of also checking environmental influences on behavior in less constrained circumstances (see Marler 1991; Petrinovich 1990).

There is no single correct environment or species for research or observation, just the need to avoid downplaying either the contribution of the animal or the contribution of the environment. Different environments and species provide different opportunities to analyze the fit between animal and environment. Heidiger (1950) drew on this perception in arguing that the behavior of animals in zoos often was determined by so-called fight and flight distances. In a similar vein, Tinbergen & Perdeck (1950) and Hailman (1967) explored the possibilities of using artificial stimuli to analyze the mechanisms underlying begging in young birds. Even quite restricted environments can reveal characteristic animal/environment relations. For example, Olson (1991) used artificial learning problems to explore memory differences in corvids related to food caching, and Timberlake & Washburne (1989) used artificial moving stimuli to explore how the feeding ecology of rodent species affects conditioned reactions to movement predicting food.

Timberlake (1990) argued that behavior in even the most restricted laboratory environments is related to evolutionary determinants: first, because animals do not have a separate evolved repertoire for dealing with restricted environments; second, because even the most rigorous laboratory scientists carefully modify their procedures, apparatus, and measures to deal with the
specific species under study (see Skinner’s 1938, 1959 account of developing the leverpress for rats). To recapitulate, there need be no fundamental conflict between laboratory and field, provided we view them as different opportunities for reconstructing and predicting the fit between animal and environment.

**Genes vs. Environment**

The basic question of whether behavior is determined by genes or environment appeared to be resolved in the original synthesis. The concept of epigenesis captured the notion that development is not directed toward a preformed end, but occurs as an interaction between genes and environment (Oppenheim 1982). However, the nature of this interaction has proved difficult to analyze. Notions such as open instincts (Mayr 1974) and learning-instinct intercalation (Lorenz 1965) are not particularly epigenetic in the scope of interaction they allow for. Development does not occur as the programmed or even as the statistical interaction of genes and environment. Instead it seems to consist of individual, largely self-organizing processes involving genes, cells, physiological systems, and the “outer” environment (Thelen 1990; Wikler & Finlay 1989). Like evolution, development is not goal-directed but based on “spit and bailing wire”; that is, on making do with what is available. It is a vector that has direction in terms of its constituent processes (Oyama 1985).

Perhaps the most difficult point to grasp is that genes are not causal entities (Bateson 1988). Information about the “finished” animal does not reside exclusively in the genes any more than it resides in the environment. Identifying genes as causal agents remains a useful fiction because it makes possible simple manipulations and predictions of behavior in a particular environment. The fiction is made more attractive because proposed alternatives to simple causation often invoke maximal dialectical complexity (everything affects everything), a stance that gives only vague guidance to research (Kuo 1976). At present, the most rapid progress toward an understanding of development appears to come from using experimental manipulations to open windows during ontogeny that reveal how developmental processes work (Blass 1988; Moore 1990; Sinervo & Huey 1990; Thelen & Ulrich 1991).

**Rules Guiding Research**

Many successful scientists, just like successful authors and parents, often reconstruct their lives to yield a set of rules to follow (see Dewsbury 1985). Some recommend starting with first principles and deducing predictions that pit one hypothesis against another (strong inference). Others advise their students to observe extensively and without preconception, drop everything to follow a new lead, and then persist in the face of adversity. In practice most adept scientists appear to be more like game theorists, using conditional rather than absolute rules—deduction and induction, observation and manipulation, strong inference and demonstration, one species and many (Maynard-Smith
Scientists also differ in individual abilities and predilections. Beer (1980) suggested that ethologists tend to be visually oriented, leading to their concern with behavioral form. Conversely, many psychologists began in physics and engineering, making them comfortable with the construction of apparatus and simple causal models.

Three additional suggestions may be useful in guiding integrative research: (a) assume “a modicum of ignorance” (a phrase of Nottebohm’s), (b) try to view things from the animal’s perspective, and (c) be aware of the functional systems that underlie behavior. On the issue of ignorance, it is often useful (after considerable training in an area) to return to being a little naive, to test the interpretation so obvious it’s almost not worth checking, to question traditional procedures, to ask why the form of a response varies over time. Researchers inevitably accrue methods, measures, and models that constrain their questions and interpretations. A well-placed, simple question can reveal an important issue, e.g., Petrinovich (1990).

As to taking the animal’s view, most scientists remain cautious because of the risk of falling into anthropomorphism—the projection of human thoughts and feelings into other animals. Though some have argued for its heuristic value and complexity (Fisher 1991), there is little evidence that research has been advanced in the long run by assuming that animals are fundamentally human in their thinking and behavior (Staddon 1989). The term theromorphism—meaning animal-centered as opposed to human-centered (von Uexkull 1934; see also Burghardt 1991; Simmons 1989)—better captures the present idea. Based on knowledge of an animal’s sensory and motor equipment, its integrating and processing capabilities, and its motivational structure, dynamics, and decision rules, one attempts to enter into the animal’s view of the circumstances. This is usually a difficult bootstrap endeavor involving asking repeated experimental and observational questions about an animal, and considering carefully the answers. It provides, though, an integration of intuition and experimental results that is essential both in setting up reasonable experimental manipulations and in interpreting and modeling more freely occurring behavior.

Finally, a recurrent theme in this discussion is that animals are sets of functional systems that operate within and influence the context of environment, physiology, behavior, social relations, and evolution. A simpler causal approach often dominates because researchers appreciate the power of analyzing and modeling the effects of one or two variables at a time. The problem with this simpler approach is the danger that our “picture” of the animal—our means of organizing knowledge—will become dependent primarily on our experimental procedures and simple causal models. Such a picture often is not transferable to new situations or even to different manipulations. For example, careful manipulation and measurement of copulation in single pairs of rats produced initial insight into the underlying physiological mechanisms (Rose 1990). However, broader comparisons of mammalian copulatory patterns
(Langtimm & Dewsbury 1991) introduced considerations of phylogeny and adaptation. Examining the social context of mating in rats clarified the roles of female and male choice as well as the selection pressures on the mechanisms (McClintock 1984). The hormonal analysis of reproduction provided further insight into evolutionary processes and mechanisms (Moore 1990).

Taking a systems approach has enabled researchers to organize information to develop a view of animal and environment that is conceptually and experimentally more tractable and heuristic.

METHODS OF COMPARING BEHAVIOR

Comparison has been touted as the heart of both comparative psychology and ethology (e.g. Dewsbury 1990; Lorenz 1950). Comparisons provide information about evolution and ecology, as well as suggesting and testing hypotheses about mechanism. Yet nowhere in animal behavior is the absence of a satisfying synthesis clearer than in the lack of agreement about the nature of appropriate comparisons. Thoughtful discussions have been offered by both psychologists and evolutionary biologists (Beer 1980; Bell 1989; Clutton-Brock & Harvey 1984; Dewsbury 1990; Gittleman 1989b; Hailman 1988; Harvey & Pagel 1991; Riley & Langley 1993). Given the diversity of answers, it is tempting to steal a page from philosophers of science and claim that the comparative method is whatever is used by scientists in making comparisons (see Adkins-Regan’s 1990 review of comparative work on sex hormones and behavior).

In the absence of a single compelling rationale, it may be useful to categorize comparisons of behavior based on levels of concern with dimensions of genetic and ecological relatedness. Figure 1 shows four resultant categories: protoevolutionary comparisons (those not focused on either genetic or ecological relatedness), phylogenetic comparisons (focused on genetic but not ecological relatedness), ecological comparisons (focused on ecological but not genetic relatedness), and microevolutionary comparisons (concerned with both genetic and ecological relatedness).

Historically, comparative psychology focused on comparisons of mental life and physiology (protoevolutionary comparisons) combined with behavior genetics and development (microevolutionary comparisons). Ethologists focused on phylogenetic comparisons of behavior patterns in limited groups (homology), and ecological comparisons based on the form and function of behavior (convergence or divergence). Given these differences, it is not surprising that ethologists and psychologists often talked past each other (see Lorenz’s, 1950, lament that comparative psychologists didn’t do comparative research). As we shall see though, separations have blurred and empirical methods have emerged that cut across all categories (Harvey & Pagel 1991).
Protoevolutionary Comparisons

Faced with a large number of diverse species, most scientists are driven to impose some form of comparative order. A few scientists strive to add even more species for perspective and uniqueness (Adkins-Regan 1990). In neither case is the predominant focus on phylogeny or ecology, but on abstract relations such as trends, scales, and universal laws. I refer to such comparisons as protoevolutionary because their focus is not on the course of evolution but evolution is their broad concern.

<table>
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<th>Classification, Trends, Grades, and Levels</th>
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| Comparisons across species in psychology readily can be traced to the interests of Darwin (1871) and Romanes (1884) in establishing a continuum of mental life from simpler animals to humans. Comparative psychologists developed more careful measures and reliable tests to document trends, grades, and levels in intelligence (e.g. Aronson 1984; Bitterman 1965; Krushinski 1965; Razran 1971) and in sensory-motor capabilities (Warden et al 1935). Recent examples of this analytic approach include development of a scale of categorization complexity (Herrnstein 1990) and the use of Piagetian stages of object permanence in human infants to grade species [e.g. primates (Parker 1990), dogs (Gagnon & Dore 1992), cats (Dumas & Dore 1991), and Psittacine birds (Pepperberg & Funk 1990)].

Biologists also have a history of classifying and grading species in a relatively nonevolutionary fashion, primarily with respect to morphology. For

![Figure 1 Types of comparison](image-url)
example, animals have been classified grossly on the basis of radial vs. bilateral symmetry and polarized vs. unpolarized synapses, and more precisely on the basis of single cone vs. three cone retinas, and eusocial vs. asocial behaviors. Trends across groups have been noted, such as the decrease in genetic relatedness and increase in aggression in Wilson’s pinnacles of sociality (1975), or changes from two-chambered to four-chambered hearts across classes of vertebrates (Hodos & Campbell 1990). Within smaller groups, behavior characteristics have been ordered in grades relating to differences in complexity of function or design features; for example, grades of cooperation in nest spinning ants (Holldobler & Wilson 1990), or sociality in primates (Martin 1974), or in bees (Michener 1974).

The major objection to such comparisons is the tendency to interpret trends, grades, and levels as progressive and as representing the actual course of evolution. Hodos & Campbell (1969, 1990) pointed out that many psychologists assumed they were documenting the progressive evolution of mental life from lower animals up to humans, an assumption often more clearly related to the scala naturae of Aristotle than to the course of evolution. Biologists, too, have inappropriately seen evolution and progress in some trends and grades (Gottlieb 1984; Nitecki 1988). For example, the three-chambered heart found in amphibians could be viewed as an intermediate evolutionary stage between the two-chambered heart found in fish and the four-chambered heart of mammals and birds. Instead, the three-chambered heart appears to be an adaptation of a four-chambered heart to the skin-aeration possibilities of an amphibian ecology (Hodos & Campbell 1990). The most conservative approach does not assume that classification schemes, trends, grades, and levels represent evolutionary history or progress. Instead, these comparisons must be reconciled individually with the course of evolution by working out the relations among mechanism, selection, and phylogeny.

SCALING FUNCTIONS AND ALLOMETRY  The process of scaling is based on fitting a function through a scatter plot relating variables such as body mass and basal metabolism rate (McNab 1989) or brain volume and body weight (Jerison & Jerison 1988). The result typically is a power function plotted as a straight line in log-log coordinates. The development of these relations is often referred to as allometry (Schmidt-Nielsen 1984; Thiessen 1990), because it typically involves the relation between body size and other variables, such as brain size, neural complexity, learning ability, metabolism, efficiency of locomotion, or reproductive success (e.g. Clutton-Brock & Harvey 1984; Gittleman 1989a). In most cases, each point is a species, but in recent comparative work many researchers (e.g. Gittleman 1989b) have made each point a genus in order to avoid influencing the function by correlated phylogenetic or ecological variables. Allometric functions are presumed to be determined by general physical relations and limitations, and thus should be present in all animals, though different taxa may have different exponents relating the variables.
Taken by themselves scaling functions deal with correlation rather than causation. They represent broad statements about the evolutionary landscape that make little contact with specific evolutionary history, development, or mechanisms. Recent research, though, has used deviations from allometric relations to indicate the effects of particular mechanisms and environments (e.g. McNab 1989). Also the use of convergent correlations and experimental manipulations can facilitate causal interpretations of allometric relations. For example, Sinervo & Huey (1990) tested the mechanisms underlying size-related locomotion differences in related lizard species. By directly manipulating adult body size through partial removal of yolk from the eggs of one species, they showed that burst speed but not stamina was affected by body size.

UNIVERSAL LAWS  A primary goal of science is to develop general principles or laws, preferably expressed as mathematical functions. In physics, the laws of mechanics hold true almost without regard to the entities involved. Laws of chemistry and biology more frequently require that the nature of the entity be taken into account. For example, to predict chemical reactions it is necessary to know the elements involved.

It is probably unfortunate that many behavior researchers have tried so hard to emulate physics (Bolles 1988) when chemistry would have made a better model. The fit of billiard ball and environment is not the same as the fit of an animal and its environment. Something like a dynamic “periodic table” relating animals, environments, and behavior is necessary before more accurate general laws are possible. Still, the development of general laws is a natural goal of science. Below are two examples of the search for laws of animal behavior.

Beginning in the 1930s many comparative psychologists focused attention on the development of universal laws of Pavlovian and operant conditioning. As more species were examined it became clear that similarities in learning were greater than differences (e.g. Macphail 1985; Skinner 1959). To be sure, similarities were highlighted by tuning apparatus and procedures to minimize differences attributable to the sensory, motor, and motivational aspects of a species (Timberlake 1990). Still, the similarities were remarkable, even across markedly divergent phyla (e.g. Maier & Schneirla 1935). More recently, Bitterman and his colleagues have shown that honey bees demonstrate a majority of the specific learning effects found in laboratory rats (e.g. Bitterman & Couvillon 1991). Neuroscientists have related universal learning laws to general cellular mechanisms (Hawkins & Kandel 1984). Some psychologists have attributed universal learning laws to the convergent evolution of associative processes (Dickinson 1980).

In biology, the past 20 years has seen a universal law approach emerge in behavioral ecology based on the principle of optimality. The basic assumption is that evolved behavior maximizes net benefit to the animal, both immediately (in terms of, for example, energy) and ultimately (in terms of individual
reproduction and inclusive fitness). The principle of optimality is presumed to drive behavior regardless of ecology and without consideration of underlying mechanisms (Grafen 1991). Cleverly applied, it can predict a wide range of phenomena including foraging behavior (Stephens & Krebs 1986), group size (Pulliam & Caraco 1984) territoriality (Davies & Houston 1984), mating systems (Davies 1991), and parental care (Clutton-Brock & Godfray 1991). Kin selection (a form of optimality based on maximizing reproductive success at the level of the gene rather than the individual) has been used to explain altruistic behavior (Grafen 1991).

Most general principles of behavior, such as those concerned with learning and optimality, arise initially from a relatively narrow base of experimentation. Integration of concerns about mechanism, phylogeny and ecology comes later. To their credit, researchers in optimal foraging have shown increasing interest in the mechanisms (so-called “rules of thumb”) that produce near-optimal behavior for a species in particular circumstances (Stephens & Krebs 1986).

For example, a bird may leave a patch based on the rule “search elsewhere after 20 seconds without food,” or it may choose between alternative patches based only on the immediate probability of payoff (a hill-climbing rule). In some environments these rules produce optimal behavior, but in other environments they may fail miserably as optimal strategies.

Comparative learning researchers also have been concerned with the mechanisms that underlie learning. But, with a few exceptions they tend to regard deviations from expected results as constraints on general learning principles rather than as new information about specific adaptive mechanisms. In contrast, the research of Garcia and his coworkers (e.g. Garcia et al 1989) has consistently analyzed taste aversion learning as a specific functional adaptation.

MODEL SYSTEMS A fourth class of protoevolutionary comparison is the model systems approach, an approach used frequently by physiologists to choose animals suitably qualified to test particular phenomena. The assumption underlying a model system is that a general substrate of action exists for many taxonomic groups and that its ruling principles can be investigated readily in particular preparations. Thus physiologists studied nerve conduction in squid because a giant axon was readily accessible in this species. More recently scientists have taken advantage of the relatively small number of pathways and neurons in simple marine molluscs to study the nature of learning (e.g. Alkon et al 1987). The many uses of chickens as a model system have been documented by Andrew (1991).

Ethology, sociobiology, and behavioral ecology have also begun to use data and general principles derived from work with other animals to analyze human behavior (e.g. Groebel & Hinde 1989; Hinde 1991 on Tinbergen). Wilson (1975) and those immediately following him bore the brunt of public dismay that the same analysis could be applied to human and nonhuman animals. But
work has continued in this vein, appearing frequently in journals such as *Ethology and Sociobiology* (see Mulder 1991). For example, Daly & Wilson (1988a,b) melded an anthropological approach with that of genetic relatedness to predict patterns of parental solicitude and homicide in humans. Thornhill & Thornhill (1991) have examined the relation of characteristics of human rape to variables that have been shown to influence reproductive fitness in other animals. The evidence is compelling that some of the variance in human behavior is controlled by the same variables that determine the behavior of other species.

In sum, the precise procedures, generality, lawfulness, and heuristic value of protoevolutionary comparisons are the source of their attractiveness. Drawbacks often include lack of attention to phylogeny, specific selection pressures, mechanism, and development. Considerable care is required to avoid viewing all trends as progressive, attending to other species only as they relate to humans, or ignoring important species differences in the search for universal laws. Still, there seems little reason to shun protoevolutionary comparisons provided they are seen not as an endpoint, but as a starting place.

**Phylogenetic Comparisons**

Ethology began in this century with biologists comparing the form and development of motor acts in related species (Wheeler in ants; Heinroth in European songbirds and ducks; Whitman in pigeons and doves—see Thorpe 1979). Including the study of behavior was a natural extension of the taxonomic tradition in biology. Though enthusiasm for tracing phylogenetic relations waned for a bit, recent technical advances such as DNA fingerprinting and multivariate statistics have provided some insight and a glut of information about phylogenetic relations among species (Brooks & McLennan 1991).

**BEHAVIORAL HOMOLOGIES** Behavioral homologies refer to similarities in the topography (form) and sequencing of behavior based on phylogenetic linkage. The lack of a completely satisfying definition of behavioral homology has caused some investigators to dismiss the concept (Atz 1970). But the data acquired in the study of behavioral homologues appear potentially useful in filling in the phylogeny of behavioral and brain mechanisms, plus serving as another source of evidence about the overall course of evolution. For example, Lorenz (1950) used patterns of shared similarities and differences in courtship behavior to infer the course of evolution in a family of ducks (anatidae). The extent to which all species of ducks showed the same displays marked their closeness phylogenetically. Subgroups of ducks sharing unique displays were viewed as having split off from the root stock over evolutionary time. Later work combined evidence from behavior patterns with that based on morphological or physiological analysis to produce convergent evidence about phylogeny [e.g. Van Tets’ (1965) work on Pelicaniformes; and Archibald’s thesis work on unison calls in cranes, reported extensively in Grier & Burk (1992)].
A more recent form of specifying homologous relations is based on the uses of multivariate classification statistics. Typically, combinations of morphology and/or behavior are used to differentiate related groups of animals. For example, Eberhard (1982) combined data from web-building with information on predatory and courtship behavior to produce a taxonomy of related spiders. Losos’ (1990) analysis of 13 species of lizards indicated that limb proportions and locomotor behavior evolved together, while Langtimm & Dewsbury (1991) showed that similarities in copulatory behavior among the Sigmodontian rodents were traceable to a common ancestor.

BEHAVIORAL AND NEUROPHYSIOLOGICAL SERIES A second method of phylogenetic comparison is to arrange living species in a sequence based on small and apparently systematic differences in behavior or neurophysiology. Such a sequence can present a compelling hypothesis of evolutionary development, though determining the validity of the sequence requires independent data relating the species. In behavior, a classic example is Kessel’s (1955) arrangement of the courtship behavior of empid flies in a sequence beginning with courting males presenting the female with captured prey and culminating with a species in which the males present empty gossamer puffs. Similar series can be generated at the level of neurophysiology. A well-known example is the argument by MacLean (1990) for the triune evolution of control circuitry in the brain (first brain stem, then paleocortex, and finally neocortex). Masterton et al (1969) showed changes in brain development across branching phylogenetic groups of mammals, as did Kroodsma & Konishi (1991) in comparing songbirds with their suboscine relatives. Robinson (1991) warned that a large inductive database with many intermediate forms is necessary to infer a series that allows a distinction between evolutionary pressures and phylogeny. Brooks & McLennan (1991) argue strongly for a more computational approach in establishing such series.

ANIMAL MODELS The (nonhuman) animal model approach is predicated on the notion that basic physiological substrates and behavioral qualities of a model species are homologous to those of humans. This approach has become a cornerstone of modern medical research (Alter et al 1991). Common laboratory animals are used as stand-ins for humans in determining, for example, the potency of a particular tranquilizer, or the physiological processes of aging (e.g. Gold & Stone 1988). Considerable objections have been raised (e.g. Regan 1983) to the extent and type of commercial product testing using animal models, resulting in changes in procedures and decreases in the amount of testing. The most sweeping objection, though, that work with nonhuman animals has no relevance to humans, is wrong, and even speciesist. Though no scientist would question the worth of continued research on determinants of the generalizability of results from animal models, specific results and principles stemming from animal models have long been useful in work with humans (for a nondisease
example see Squire's 1992 review of converging human, primate, and rat data relating the hippocampus and memory).

A common interest in the use of animal models is in relating the behavior of other mammals to that of humans. For example, Young & Thiessen (1991) documented similarities between the cephalo-caudal organization of washing in humans and grooming in rodents. A less provocative finding is that all female mammals show a high degree of similarity in the hormonal regulation of their reproductive behavior (Rosenblatt 1989). The most explicit phylogenetic comparisons are between humans and the great apes, especially chimpanzees. For example, Tomonaga & Matsuzawa (1992) found that humans and chimpanzees showed the same dominance among perceptual categories in a matching to sample task. Outer contour elements were perceived the most readily and straight-line elements the least. The relation of language learning in apes and humans has been the source of fascinating data and continued debate (Gardner et al 1989; Savage-Rumbaugh 1988). In social behavior Manson & Wrangham (1991) have reported parallels in intergroup aggression in chimpanzees and humans. Some of the difficulties with behavioral homologies are considered at the end of the next section.

Ecological Comparisons

Ecological comparisons focus on the importance of selection pressures in producing divergence or convergence of behavior among species.

CONVERGENCE The classic ecological comparison is based on behavioral and morphological similarities among species with dissimilar genetic make-up but similar environmental pressures. Usually an attempt is made to relate the similarities in a face-valid way to assumed selection pressures. Early work done by Hailman (1965) and others showed that unrelated cliff nesting shorebirds, such as gannets and gulls, exhibit quite similar behavior and morphology, presumably on the basis of the common selection pressures of the cliff environment. More recently, Logue (1988) provided evidence for a convergence of strategies among vertebrates to avoid poisonous foods, and Vander Wall (1990) discussed ecological similarities among diverse food hoarders. Sherry et al (1989) found that families of food-storing passerines show a larger hippocampus relative to the telencephalon and body weight than non-food-storing families.

LIFE HISTORY THEORY In this view, selection for optimal strategies predicts general types of ecological convergence that approach the breadth of universal laws. Animals are grouped on the basis of their adaptations to common ecological pressures and a configuration of their behaviors is predicted. A now classic example is Ridley's (1983) demonstration that precopulatory guarding of the female by the male in invertebrates and anurans was predictable from whether females were receptive during predictable brief periods of time. More recent examples include the suggestion of Driver & Humphries (1988) that random
movement by prey is the result of common predation pressure, and Davies (1991) review of the data used to support the view that mating systems follow from the defendability of resources (food for the female, and females for the male).

DIVERGENCE Divergence comparisons involve looking for deviations from homologous behavior or morphology that can be related to changes in inferred selection pressures. For example, Glickman & Sroges (1966) investigated the exploratory behavior of zoo animals, looking for overall phylogenetic grades in reactivity. However, the data compelled a different interpretation relating exploratory behavior to the ecological variables of food variety, predator pressure, and the importance of social communication. More recently, Dewsbury (1988) used deviations and similarities in behavioral profiles to relate reproductive strategies to ecological circumstances, and Beecher (1990) predicted and showed that parent-offspring recognition was better in swallows that were colonial rather than solitary nesters. Also Brown (1989) developed evidence that the vocal repertoires and auditory sensitivities of old world monkeys are determined by their functions in conjunction with the acoustic characteristics of the habitats. Dukas & Real (1991) supported the prediction, based on the requirements of sociality, that a social bumblebee should show faster learning about reward than a solitary carpenter bee.

DEVIATIONS FROM ALLOMETRIC RELATIONS This is a form of divergence comparison based on using allometric scaling functions as a central tendency against which to scale the deviations of individual species. For example, Jerison’s (1973) encephalization quotient is based on the relation of the brain size to body weight ratio of a single species relative to the ratio typical of their taxonomic group. The resultant deviations can be related to ecological variables. McNab (1989) noted that the fundamental relation between basal rate of metabolism and body mass in carnivores is a power function with an exponent of .67 (Schmidt-Nielsen 1984), but it is influenced (in nonlinear ways) by the food type (vertebrates, invertebrates, leaves, fruit, and mixed diets), and the basic ecology (arboreal, burrowing, aquatic, arctic). Used in this way, allometric scaling becomes a type of ecological comparison (see also Harvey & Krebs 1990).

Finally, adaptive correlation is a form of divergence comparison based on demonstrating a suite of relations between morphology or behavior and presumed selection pressures. Cullen (1957) provided a classic example by documenting the differences in agonistic and reproductive behaviors between shore and cliff-nesting gulls and explaining them in terms of the different selection pressures produced by the cliff habitat. Another classic example is the correlation among feeding niche, morphological characteristics, and behavior in Darwin’s finches (Grant 1986). A variant of this approach is the work of Gaulin et al (1990) and Gaulin & Wartell (1990) showing that across species
and genders of rodents, average home range size is correlated with the spatial learning abilities shown by animals in laboratory tests.

There is a very long history of concern with the adequacy of the concepts of homology and convergence, a concern that has been compounded by applying these concepts to behavior (see Beer 1980). One fundamental difficulty is that each type of comparison considers only half of the evolutionary variables; one considers the evolutionary history, the other the selection pressure of the environment. Another difficulty is that most conclusions about phylogenetic and ecological relations are not checked by experimental manipulations. Studies such as Hailman's (1965) attempted to improve the accuracy of causal inferences by controlling rearing environments, but this approach appears to have gone out of favor. Recent statistical techniques provide alternative means of separating phylogenetic and ecological influences (e.g. Harvey & Pagel 1991).

**Microevolutionary Comparisons**

Microevolutionary comparisons are concerned with the contribution of both phylogeny and ecology to behavior. Historically, comparative psychologists focused on artificial selection (Plomin et al 1990) and ethologists focused on ritualization—the evolutionary process in which motor patterns become specialized for communication (Eibl-Eibesfeldt 1975). Both were concerned with general principles of development and the nature of critical periods (e.g. Immelman et al 1981).

**Genetics and Development** Much of the work on behavior genetics continues to focus on simple causal models, often statistical in nature. For example, Wheeler et al (1991) were able to change the rate of wing vibrations in *Drosophila* by the exchange of a single gene. An important window on the relation of genes and selection pressures has been provided by the use of DNA fingerprinting to link members of a population (Everitt et al 1991). DNA-based investigations of bees have shown that hormonal control of tasks differs within subpopulations in a hive (Robinson et al 1989). DNA-based investigations of birds have contradicted our assumption that many species are exclusively monogamous (Weatherhead & Montgomerie 1991).

Changes in behavior and development increasingly are treated as important contributors to evolution (Bateson 1988). Because development stands between genes and their expression, it can be selected for as a critical mediator of evolution. Arnold (1990) noted that development is a dimension of the phenotype and genotype instead of an alternative to direct inheritance. King & West (1990) proposed the concept of inherited niches to account for the effects of differences in ecological pressures on song development in cowbird subpopulations. A similar explanation may underlie the demonstration of Goldthwaite et al (1990) that ground squirrels do not show specialized defensive reactions to snakes in arctic populations that are now free from snakes.
Gottlieb (1992) argued that because of the large amount of "silent" DNA in all phyla, persistent changes in phenotype can occur in response to changes in the environment, with no change in genotype. For the more statistically oriented, allometric functions can be plotted with individuals (or individuals at different times) as the points, to look for similarities and differences in functional relations across development (Gittleman 1989a). Finally, as indicated previously, many processes of development have proved remarkably accessible to experimental investigation (Miller 1988).

BEHAVIORAL STRATEGIES WITHIN SPECIES Tinbergen and his students provided evidence that populations show ranges of behavioral strategies associated with different reproductive success [e.g. Patterson (1965) on group vs. isolate nesters in gulls]. Work has expanded exponentially on within-species differences in life history strategies—such as body size at maturation, courtship method, mate choice, and parental care. Lessells (1991) reviewed a considerable body of literature relating life-history strategies to reproductive success and evolution. These strategies are often modified by different environmental conditions, and are even affected by the relative distributions of the strategies of other animals in the population. The notion of evolutionarily stable strategies (Maynard-Smith 1982) and the ideal free distribution approach (Milinski & Parker 1991) are designed to capture the conditional, frequency-based nature of appropriate behavior.

MICRO-MODEL SYSTEMS The division between protoevolutionary and micro-evolutionary comparisons is not always clear, particularly in the areas of general principles and model systems. The assumption in both types of comparison is that careful analysis of the behavior of a small number of subjects will reveal information of general applicability. One distinction is that the microevolutionary approach focuses on comparisons within the same or closely related species. For example, Ketterson & Nolan (1992) and Marler & Moore (1991) used hormones to engineer new phenotypes in free-living male birds and lizards. These phenotypes were used to illustrate the effects of behavioral variation on fitness, and to infer general evolutionary trajectories within a population.

Integration

Explicit comparisons provide a powerful technique for disentangling the determinants of behavior, but it should be apparent that these four general categories of comparison are not fixed. They are intended to provide a framework acknowledging diversity while encouraging a more coherent approach. There may be considerable advantage in studying the same topic across all four categories. For instance, behaviors related to kin selection can be dealt with as a protoevolutionary trend, as a homologue, as examples of ecological convergence, and as the product of the genetic makeup of a particular population.
Similarly, the same empirical technique (e.g. allometric scaling, profiles, ideal free distribution) can be used in comparisons of any sort.

Should one of these types of comparison be preferred? In a recent paper Hailman (1988) argued that an adequate comparison requires including multiple species in all four categories of a table similar to the present one. Homology is inferred only if related animals in different niches show it and unrelated animals in the same niches do not. Convergence is indicated only if unrelated animals show similarities that their relatives in different circumstances do not. This is a worthy approach, but it focuses only on establishing homologues and convergence and the price is high in terms of subjects required.

Careful work in any single category provides useful data. Robinson (1991) cited several examples of how the painstaking accumulation of data from unrelated insects eventually led to insights concerning adaptation and phylogeny (Eberhard 1980; Robinson 1985). However, using several types of comparison probably will advance knowledge more rapidly than focusing on a single type. Phylogenetic or ecologically-based explanations often overlook simple proximal causes (Barlow 1989). On the other side, an exclusive focus on proximal determinants can produce general principles unconnected with function and evolution. For example, the general principles of learning established by laboratory psychologists are not very helpful in explaining or predicting naturally occurring phenomena such as song learning in birds (Timberlake & Lucas 1989). Finally, an exclusively ecological comparison may ignore the importance of general processes and exaptations (Riley & Langley 1993).

One effective approach to comparison would be to begin with protoevolutionary observation and analyses of the regularities and functional relations among the stimuli, responses, and states involved, move on to ecological and phylogenetic comparisons, and cross to microevolutionary analysis of mechanism and development. For an example of such a shift, consider that the study of learning began with the protoevolutionary approach of trends and grades, moved through general principles and model systems, into ecological comparisons (Balda & Kamil 1989) and the beginning of microevolutionary considerations (Arnold 1981; Bateson 1988).

It is assuredly not necessary that all research in animal behavior be explicitly comparative. For example, the sequence of research above is appropriate for any study of animal behavior whether comparative or not. In terms of Tinbergen’s questions, this research example begins with an interest in mechanism, incorporates function and evolution, and returns to mechanism at a more profound level. However, this particular sequence of research types is not critical in advancing the field. What is important is the development of a picture of the animal and environment that helps integrate the results of different types of research.
THE DYNAMICS AND STRUCTURE OF BEHAVIOR

Motivation

At the time of the initial synthesis, the study of motivation was a critical substrate of both comparative psychology and ethology. Motivation fell out of favor with psychologists because neither deficit motivation nor incentive effects could be tied firmly to physiology, and the relations between deprivation manipulations and behavior differed with both the type of manipulation and the measure of behavior used. Perhaps most importantly, motivation was considered superfluous because, given a sentient organism with a few reflexes, researchers felt able to construct the form and dynamics of new behavior by employing operant and Pavlovian conditioning techniques. Motivation persisted only as a broad causal principle related to general arousal and attraction.

Ethologists from Tinbergen (1951) through Baerends & Drent (1970) began with a more complex view of motivation that combined regulation with hierarchical structures of states, releasers, and action patterns spread across levels of organization. However, despite its central position in ethological thinking, motivation declined in popularity for reasons similar to those in comparative psychology. Drive was not unitary (Hinde 1966), and the concept of action-specific energy failed to account for many examples of the initiation and cessation of behavior (e.g. Dethier 1976). Motivation became an unnecessary ghost in the machine.

To the surprise of many, motivation seems to be making a comeback. First Toates (1986) and then Colgan (1989) wrote small primers. The former surveyed motivational systems, the latter considered three basic research topics. The first topic was the motivational systems developed by ethologists, which they inferred from the timing, sequencing, and organization of behavior. The second topic was regulatory physiological systems for which control circuitry is inferred from lesions, stimulation, and measurement of hormonal levels and metabolic indicators (e.g. Stricker 1990; see also Mrosovsky 1990). The third topic was the adaptation and regulation of behavior from the viewpoint of optimality and game theory (e.g. Krebs & Davies 1991).

Three more research topics might have been added: one focusing on social contexts of motivation, particularly the developmental, ecological, and strategic aspects, including kin selection (Cheney & Seyfarth 1990; Slobodchikoff 1988); another focusing on the generation of response components and stimulus processing rules for particular states (Gallistel 1990); a final chapter could have dealt with recent work on computer simulations of animals. Imaginary animals can be taught to categorize inputs, learn sequential dependencies, and filter noise for signal (Grossberg 1988). Mechanical “insects” wander through their environments (Beer 1990), and complete worlds of computerized reproducing animals can be turned loose to evolve in sometimes wildly disparate ways (Langton et al 1991).
The study of learning very early became a protoevolutionary endeavor, one tied intimately to apparatus, procedures, and general principles. Within the last 20 years, a part of this massive literature (e.g. Spear et al. 1990) has moved slowly in the direction of a functional ecological approach. Bolles & Beecher (1988), Gallistel (1990), Gould (1986), Kamil & Roitblat (1985), Kamil et al. (1987), and Zentall & Galef (1988) deal with the role of learning in solving ecological problems in both restricted and relatively unrestricted circumstances. Other researchers have focused on laboratory versions of ecological learning problems, ranging from examples of perceptual learning (Suboski 1989), to the learning of the time and location of food availability by garden warblers (Biebach et al. 1989), and how gouramis defend territories (Hollis 1990).

One of the most fascinating continuing research stories concerns memory for stored foods in the bird families of corvids and parids. An interesting recent outcome is that field differences in the memory of caching and noncaching corvids show up in tests of memory in an analogue of the radial arm maze (Balda & Kamil 1989), and also in even more constrained laboratory tests (Olson 1991; see Shettleworth 1990). Species that depend heavily on memory to retrieve caches in the field do better on even arbitrary laboratory tests of memory. Similar differences have been obtained for storing and nonstoring parids (Krebs et al. 1990). Such evidence raises the possibility of using related species in studies of ecology and phylogeny (Kamil 1988). Similar opportunities appear to be developing in the study of bird song (Kroodsma & Konishi 1991; Nottebohm 1991).

**Regulatory and Structural Behavior Systems**

As the study of both motivation and learning moves toward ecological and microevolutionary comparisons, it will be necessary to provide an animal-based rather than a procedure- or apparatus-based framework. Such a framework may serve as a basis for integrating other research as well. Behavioral ecologists working on the determinants of foraging have begun to confront effectively the ways in which animals distribute their energy resources across feeding alternatives and the demands of different systems (McNamara & Houston 1990). Caraco & Lima (1987) and Lucas & Walter (1991) have examined the influence of metabolic balance on sensitivity to risk. Laboratory investigations have become concerned with the regulation of feeding by non-metabolic influences such as local cost and time windows (Collier & Johnson 1990; Cuthill et al. 1990; Plowright & Shettleworth 1991). Other researchers have pressed for the consideration of the circadian and ultradian rhythmicity of behavior (Brady 1988; Silver 1990).

An approach compatible with much of this work is the concept of behavior systems deriving in part from traditional ethology (Davey 1989; Davis 1984;
Fanselow & Lester 1988; Heiligenberg 1991; Timberlake & Lucas 1989). This approach combines hierarchical motivational systems with a dimension of appetitive to consummatory motivational modes related to the physical and temporal proximity of incentives. Learning occurs in terms of integrating sensory-motor control circuitry, tying it to motivational states, and relating these elements to the environment. Such a systems approach encourages analysis of the levels of regulation (e.g., Cools 1985; Fentress 1991), consideration of interactions among different motivational states: for example, fear and thermoregulation in chicks (Rovee-Collier et al. 1991), and comparison of regulation and learning in sexual systems (e.g., Domjan & Hollis 1988, Everitt 1990), and social systems relating to feeding in rats (Galef 1990, Timberlake 1983).

A behavior systems approach also makes ready contact with development (e.g., Hall 1990; Hogan 1988; Hogan et al. 1991), and with the neurophysiological underpinnings of particular behaviors—for example, the reproductive behavior of reptiles and mammals (Bronson 1989; Crews 1988), and fear and aggression of rats in semi-natural environments (Blanchard & Blanchard 1990; see also Brain et al. 1990). Fanselow (1989) and Fanselow & Lester (1988) have shown that avoidance and escape behavior is controlled by a sensory dimension of predatory imminence, associated with varying response probabilities, stimulus control, and brain structures. Lammers et al. (1988a,b) have distinguished specific areas of the hypothalamus of rats related to social grooming, attack, teeth-chattering, flight, and escape jumps.

In short, amplifying the concept of behavior systems provides many opportunities for producing a more coherent and heuristic picture of the fit between animals and their environments. A system of behavior can provide a framework for integrating the answers to Tinbergen’s questions and the results of different methods of comparing behavior. Finally, a systems approach can provide an organization for dealing with issues of animal cognition and animal welfare.

**COGNITIVE ABILITIES**

Even for normally reserved scientists, it is fascinating and delightful that chimpanzees sign (Gardner et al. 1989), vervet monkeys warn of specific predators (Cheney & Seyfarth 1990), starlings mimic and rearrange human sounds and music (West & King 1990), rats and gray parrots count (Davis & Perusse 1988; Pepperberg 1990), and pigeons distinguish between slides of cats and chairs (Wasserman et al. 1988).

Compared with the enthusiastic rebirth of interest in animal cognition, the behaviorist period of strict avoidance of the attribution of mental life appears at best a long fallow period (Wasserman 1993), and at worst an anomalous dark age that has finally been set right by the cognitive revolution. Nevertheless, behaviorism made a critical contribution to the study of animal cognition
because it compelled scientists to try to ignore the projection of their own psychology onto animals long enough to begin to discern determinants of behavior in clearly defined external variables. The development of both comparative psychology and ethology required the rejection of poorly defined causal agents—mentalism and instincts in psychology, vitalism in biology—to allow science to emerge.

Comparative Cognition

Comparative cognition is the domain of scientists interested in how different species process and integrate stimuli (Boysen & Capaldi 1992; Honig & Fetterman 1992; Kesner & Olton 1990; Ristau 1991; Roithblat 1987). However, the field is split along much the same lines as traditional learning, into protoevolutionary approaches (anthropocentric) and ecological approaches (Shettleworth 1993). The anthropocentric stance is fueled partly by interest in the classic continuum of mental life (Wasserman 1993) and partly by the success of traditional research on universal laws of learning. Recent work on representation, counting, remembering, and categorization has been summarized in Gallistel (1989, 1990), Wasserman (1993), and Honig & Fetterman (1992). The processing of auditory stimuli by birds and mammals has also received attention (Dooling & Hulse 1989).

Much of the work relating nonhuman and human language and intelligence falls largely in the protoevolutionary camp (e.g. Gardner et al 1989 and Parker & Gibson 1990 on primates; Herman et al 1990 on dolphins). This work has profited from analytic efforts such as those pioneered by Premack (1983) to break down cognitive phenomena into components that can be tested separately, an approach followed by Washburn & Rumbaugh (1991) in studying counting in monkeys and by Gisiner & Schusterman (1992) in studying categorization in sea lions.

As for the ecological approach to cognition it is basically theromorphic, animal centered. The work of von Uexkull (1934) on the functional fit between the filtering of the sensory surround and behavior in the woodtick serves as a classic precursor. Gallistel (1990) recently reviewed studies of the ecological relevance of abilities such as memory, timing, and navigation. Yoerg (1993) also dealt generally with the relation of ecology and learning phenomena. The work on food storing in birds alluded to in the learning section provides examples of the ecological approach (see also Kallander & Smith 1990), as does the work of Cheney & Seyfarth (1990) on vervet monkeys, work on the critical evaluation of foraging “information centers” in social species (e.g. Richner & Marclay 1991; Zentall & Galef 1988), and Real’s (1991) article on choice behavior and the evolution of cognitive “architecture” in bumblebees.

I believe cognitive research will be better served in the long run by moving in the same direction as other research in animal behavior, namely toward ecological, phylogenetic, and microevolutionary concerns. In maintaining an
anthropocentric approach that is not clearly evolutionary, scientists tend to ignore the ecological and evolutionary basis of the phenomena they study, focusing instead on general principles and concerns of definition and experimental procedure. The result can be an unforeseen limit on research procedures and interpretation. For example, the eight-arm radial maze has been used extensively to study memory, based on the presumption that rats were rewarded for efficient search by finding the maximum number of pellets in eight choices. However, Timberlake & White (1990) showed that rats efficiently search maze arms in the absence of any food at all, presumably based on evolved mechanisms facilitating foraging efficiency and increasing environmental familiarity in the absence of food.

**Mental Life and Consciousness**

For many scientists, the return to a concern with animal consciousness (e.g. Bateson & Klopfer 1991; Griffin 1981) is a return to a problematic approach to animals that it took centuries to escape (Burghardt 1985). Given there is little convincing data that the introspectively revealed contents of human consciousness play a primary causal role in most human behavior, how do we explain the fascination with animal consciousness? Beer (1992) has suggested that our interest in mental life is based on our “folk psychology,” basically a “toolkit for coping with the cognitive and conative demands and tensions of human life.” In other words, our interest in and ideas about consciousness reflect a human strategy for interacting with the world. Because of the questionable status of folk psychology and its intimate ties to human language, it is difficult to defend pouring large resources into a frontal attack on animal consciousness. The direct approach has failed badly in the past, and has yet to pay large dividends even in analyzing human behavior, despite high current interest and firsthand access to data.

There is more support for exploring mental states such as intentions (e.g. Dennett 1987). However, care must be taken. The use of such intentional terms as “Machiavellian” or “deceptive” to describe the behavior of nonhuman animals often has been more successful in stirring controversy than in specifying the determinants of behavior. Most scientists agree that mental terms must be treated experimentally as intervening variables for which we need to provide convergent behavioral, physiological, and comparative analysis.

Given the number of people concerned with mental states, some progress would be expected from an experimental approach analyzing components of processing and motivation. For example, Martin et al (1991) showed a separation in rats between determinants of discriminative and affective effects of opiates. The work of Povinelli et al (1991) suggests that rhesus monkeys are not able to infer the knowledge states of humans, though in similar circumstances chimpanzees apparently can (see also Whiten 1991).

In a way, the notion of deception is not necessarily more amorphous than the concept of, say, timing. Both involve stimulus processing and behavioral
results. The difference is that the processes involved in timing are better analyzed and the concept has only a little explanatory value and interest by itself. In contrast, the concept of deception has compelling popular explanatory power for behavior, even though the concept is still clearly in transition. For example, Gyger & Marler (1988) inferred that deception in food calling is used by male domestic fowl to attract hens, but Moffatt & Hogan (1992) argued that hens so rapidly track the relation of calls to food that deception would not be effective. Research into both deception and timing would be served well by conceptualizing them within a functional system, and analyzing the component processes that comprise them (e.g. Adams & Caldwell 1990).

Animal Welfare and Rights

The historical inability of scientists to agree on how to study the mental life of nonhuman animals and its continuity with the mental life of humans, has come back to challenge the field of animal behavior. Freely ascribing mental states to other animals piques general interest, but it also allows activist philosophers to freely claim the existence of suffering in nonhuman animals without the convergent evidence and careful analysis that would be required for humans (e.g. Regan 1983; Singer 1990). Bekoff & Jamieson (1991) argue that because the criticisms of animal research raised by these philosophers are similar despite their differing “schools,” the criticisms must point to a central truth. But an obvious alternative is that these activist philosophers began with their conclusions in place and reasoned backwards to produce a fit with their first principles.

A large number of scientists have become engaged in the laudable attempt to bring together concepts of animal welfare and research (e.g. Dawkins 1990; see Carlstead et al 1991 for application of a systems approach to the reduction of stereotyped behaviors). There are now many journals focused on animal welfare and conservation issues (e.g. Anthropozoos, Applied Animal Behavior Science, Zoobiology) while others (e.g. American Journal of Primatology) devote considerable space to and publish special issues on these topics.

Less fortunately, oversight committees and bureaucracies are increasing at every level, all with rules that can take on a life of their own independent of the good intentions with which they were created. For example, the expense of stainless steel caging and hospital-like stainless steel covering on all surfaces in animal housing rooms has unaccountably become a requirement of good care. The increased concern with animal welfare has in some ways improved the state of animals in science, but in too many cases it is still difficult to determine whether the importance and size of improvements outweighs the cost to research. The issues are many and complex (Novak & Petto 1991).

Equally problematic for research is the inability of scientists to communicate with the public as effectively as do animal rights groups. The knowledge of scientists ought to be more influential with the environmental and biodiversity movements and pet lovers than the anti-science stance of many
animal rights groups. Yet too often important and well-intentioned remarks of visible scientists, such as Jane Goodall, fail to emphasize that our increased knowledge about animals and their cognitive processes comes from research not from intuition. Intuition alone usually produces contradictory and poorly founded beliefs.

In a recent radio interview, a leader of the largest animal rights organization in the United States stated with great feeling that her goal was to let every animal run free through meadows in the sunlight. Her sentiment was compelling but she utterly misunderstood a critical point. Given alternatives of cover or darkness most animals would prefer not to run through sunlit meadows, not even mammals, the small cladistic group she probably was thinking of [40% of mammals are rodents, and another 20% are bats (Vaughan 1978)]. We cannot allow such projections to represent nonhuman animals to the public or to governing officials. It is demeaning and even dangerous to us all.

TOWARD CONTINUING SYNTHESIS

A primary path of science is toward specialization, inevitably accompanied by fragmentation. Specialization is a sign of progress, but it is also both a problem and an opportunity for a synthetic field like animal behavior. The key to progress in such a field is continued synthesis. Wilson (1975) was basically right in his vision that sociobiology, behavioral ecology, and integrative neurobiology would combine with the classic study of behavior. What he failed to see was that behavior and its fit with the environment is the basis for this integration.

In any continuing synthesis Tinbergen's four questions are useful in encouraging balance in the ways phenomena are considered. The different methods of comparison reviewed above facilitate relating phenomena to trends, scales, general laws, and phylogenetic, ecological, and microevolutionary analyses. What ultimately defines a continuing synthesis, though, is not balance or methods, but the parsing and integration of the resultant knowledge by means of a flexible and heuristic picture of the fit between animal and environment. A picture I find attractive stems from modifying the basic behavior systems approach of the ethologists to emphasize greater roles for learning and development, stimulus processing and integration, response organization and coordination, and the co-regulation of hierarchical and interacting motivational states.

This view also treats behavior (including perception) as a bidirectional link between animal and environment in both local and ultimate senses. Locally, behavior creates environments as much as local environments create behavior. This point is particularly salient in highly social species. In an ultimate sense, behavior is the ambassador of environments to the genes as well as the representation of the genes in environments. Filling in this picture will require continuing research that combines elements of laboratory and field by provid-
ing sufficient stimulus support to engage processing mechanisms, response components, and motivational states relevant to the functional behavior system under study, but in a way that allows manipulation and measurement of the determinants of the fit between animal and environment.

Finally, continuing synthesis demands hard-nosed, innovative collaboration between disciplines, an ideal that faces important realities of finance and defended territories. J. P. Scott (1973:34) addressed both the promise and the problems of such research:

Anyone who works on the new frontiers of science finds that the conventional disciplinary boundaries disappear, and become important only when we consider university organization and finance ... scientific progress is brought about through cooperation between involved individuals ... and segregation based on separation of disciplines may be just as harmful as that based on race.

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