Ethology and Attachment: A Historical Perspective

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An outline is presented of the assumptions underlying earlier and contemporary ethology. An example of ethological analysis is presented, with a focus on the ontogeny, mediating mechanisms of causation, function and evolution of cricket songs. In a historical frame, conceptual and methodological origins of modern ethology were sketched out and the significance of important trends explored. The conclusion of the analysis of this chapter is that researchers of human development studying attachment under the aegis of ethological theory have moved in a direction that diverges from the conceptualizations and research emphases of contemporary ethology. This paper describes elements of the ethological approach to attachment in an attempt to facilitate an interdisciplinary exchange among ethologists, and developmental psychologists. Its purpose is to share a historical perspective and habits of thought, and to communicate theoretical and methodological developments and that have had an impact on the ethological study of behavior.

At the, outset, our goal is to tell what ethology is about, in a historical context. As an example, the treatment considers the development, mediating mechanisms of causation, as well as the function and evolution of the cricket's song. Then we extrapolate some conceptual and methodological lessons of interest and of use to a wider audience. Our treatment proceeds with an appraisal of the contributions of ethology to the study of human attachment. Finally, we focus on some of the issues of relevance both to ethology and developmental psychology, and evaluate whether or not human-development theory and research on attachment in the frame of ethology have diverged from the emphases of contemporary ethology.

What Ethology Is About: A Historical Perspective On Some Conceptual And Methodological Extrapolations

Ethology has been described as the biology of behavior (Eibl-Eibesfeldt, 1975; Hinde, 1982; Tinbergen, 1963). While ethology has a relatively long and interesting history (Burghardt, 1986; Jaynes, 1969), for its most recent recognition it owes much to the contributions of a small group of investigators, among whom Lorenz (1965, 1970, 1971, 1974), Von Frisch (1967), and Tinbergen (1951, 1972) have received widest recognition.

Currently, the ethological literature on various aspects of animal (including human) behavior is so voluminous and varied that it leaves one wondering what it is that ethologists do not study. Faced with similar concerns, Tinbergen (1963) suggested that, once behavior is adequately described and operationalized, ethologists study its ontogeny or development, its immediate causation or mechanisms, its adaptive significance or function, and its evolutionary origins. In the words of Hinde (1982):

> Suppose you were asked, 'Why does your thumb move in a different way from the other fingers?' You might give an answer in terms of the anatomy of the hand - the differences in skeletal structure and muscle attachments between the thumb and the other fingers: that would be an answer concerned with the immediate causation of thumb movement. You might give an answer in terms of the hand's embryology describing how, as the finger rudiments developed, one came to have a different structure from the others. Or you might give a functional answer-an opposable thumb makes it easier for us to pick things up, climb trees, and so on. Or finally you might say that we are descended from monkey-like creatures, and monkeys have opposable thumbs, so of course we do too. This would be an answer in terms of evolutionary origin. All of these answers would be correct: no one would be complete. In the same way, ethologists are interested in questions of all four types of behavior. Indeed they believe that, although logically distinct and independent, questions concerning immediate causation, development, function and evolution are sometimes inter-fertile (p. 21).

As an example, we will briefly review the literature of cricket songs. The research involved is representative of ethological methodology. Our review includes the types of questions asked, the experimental subjects employed, the nature of the behavioral response studied and its measurement, comparative analyses within and across species, as well as how ecological example also can illustrate the process characteristic of ontogeny, causation, function, and evolution of species-typic isolation and of identification in simpler invertebrate systems. Invertebrates, and insects in particular, tell an interesting story (e.g., Wilson, 1975) and their message (even though unheard of in this volume) is important for an understanding of species-typic behavioral development.

Cricket-Song Study as an Example of Behavioral Analyses in Ethology

There are approximately 3,000 species of crickets, of which field crickets make up a special group of about 400. The field crickets are the most familiar. Relatively large, they are yellowish-brown insects known for their loud, musical chirping. Male crickets produce sounds by rubbing together stridulating areas located on the forewings and utilize a rapid fluttering motion to produce a typical vibrato chirp. The receiving auditory organs are tympana located within slits on the forelegs. Most cricket species chirp at night, some during the day, and others both day and night. In general, understanding of neurophysiological mechanisms involved in cricket bioacoustics has few parallels, if any, in the animal literature (Alexander, 1966; Bentley & Hoy, 1974; Ewing & Hoyle, 1964; Huber, 1962; Rose, 1986).

In a southeastern region of the United States during summer there are as many as 20 different species of tree crickets producing discrete sounds, mostly the male's calling song, the function of which is to attract the female for mating. How does a female distinguish the sounds of a conspecific? Studies have demonstrated that males of each species have a particular pulse rate in their song, and it is this pulse rate that provides a female with discriminative cues. It is also interesting to note that the metabolic and physiological processes in a cricket are functionally affected by outside temperatures, so that a pulse rate in the song changes with temperature, earning some species the appropriate label of "thermometer crickets." The refinement of the evolved system is remarkable when one considers that physiological mechanisms which determine females' responsiveness to a signal change at the same time in a fashion that parallels the males' pulse rate. The sound-producing repertoire of the male cricket serves a number of functions.

1. facilitating and establishing sexual contact (the calling song);
2. mediating sexual attraction at a relatively short distance (the courtship song);
3. signaling departure of a courted female (the courtship-interruption song);
4. repelling or dominating other males (the aggressive sound);
5. maintaining contact between a mated pair (the postcopulatory song);
6. a wide range of what appear to be recognition sounds (e.g., Alexander, 1966, 1968).

How does this brief commentary on cricket bioacoustics illustrate the importance of acoustic communication in cricket speciation and evolution? What are some of the factors that maintain the species-specific integrity of a gene pool of some 20 different species of tree crickets that are not geographically isolated? The species-specific characteristics of the male calling song and the recognition of that song by a conspecific female were identified as an important isolating mechanism (Alexander, 1966; Dixon & Cade, 1996; Walker, 1957; Wiedermann & Loher, 1984).

Viewed in the context of our understanding of evolutionary processes, crickets tell an interesting overt and covert story in evolutionary terms. Among the 3000 cricket species, many are isolated by their geography and habitat. When a number of species occupy the same habitat, then temporal, ethological, or mechanical isolating mechanisms maintain species integrity. Thus, one species will chirp at night and another during the day (temporal isolation). If more than one species occupy the same habitat and "sing" at the same time, then the differences in the pulse rate (ethological isolation) maintain species identity. Acoustic signals and communication serve in the prezygotic isolation of closely-related species.

The literature on the ontogeny of acoustic communication in crickets also deserves more attention from behavioral scientists than it has received to date. It should be kept in mind that many insects mature without hearing the signals of their own species, and that they sense many sounds that have absolutely no resemblance to signals that they as mature adults must eventually produce. As Alexander (1968) has pointed out, there must have been intensive selection pressure for resistance to irrelevant acoustic influences and toward fixed relationship between acoustic genotype and acoustic phenotype.

Experiments investigating the genetic correlates of communication signals in several species of crickets offer further support to this thesis (e.g., Alexander, 1966, 1968; Bentley & Hoy, 1974; Fulton, 1933). For example, as early as 1933, Fulton hybridized Nemobius allardi and Nemobius finnulus. These two sibling species of ground crickets mature at the same time, overlap geographically and ecologically, but sing different songs. Fulton was able to develop F1 and F2 hybrids, carry out F1 backcrosses with parental species, and analyze the songs of various crosses. Fulton's results were generally clear cut and straightforward. Pulses in the song of F1 hybrids were delivered at a rate intermediate between those in the songs of the two parental generations. The songs of backcross progeny were more like the parent utilized in the backcross. Subsequent literature on other species has further elucidated the genetic determination of the song pattern of each cricket species. The songs are phenotypic expressions of different genotypes, thereby offering evidence that links together genetic information, developmental processes, structural and functional organization of the neuroendocrine system, and behavior (e.g., Bentley & Hoy, 1974; Schildberger, 1984).

In summary, crickets are sensitive to stimuli in other sensory channels: acoustic, chemical, visual, tactile, and thermal. This review has used one example to demonstrate how discrete acoustic signals function in species-typic isolation and identification, while it also offers overt and covert evidence for the proximate and the ultimate causation of such behaviors.

On the Relationship Between Ethological Theory and Research: Levels of Organization-Levels of Analysis

The development and the use of theory have been valued by researchers across disciplines and areas of inquiry. The characteristic thinking has been that theory generates research models and questions, thereby requiring that the empirical answers to those questions be referred back to evaluate merits of a particular model or, if need be, to modify or even discard an existing theory. Disciplined empiricism requires a theory, however informal or preliminary it may be or however difficult an investigator may find testing assumptions stemming from it.

The appreciation of what ethology is about is more meaningful if one is reminded of the early intellectual antecedents of present-day ethology. The clash involving an emphasis on laboratory-discovered facts as contrasted to naturalistic observation culminated in three famous debates at the French Academie des Sciences around the year 1830, in which the naturalistic evolutionary point of view suffered a profound defeat. Baron Cuvier had laboratory facts on his side, but as we have learned subsequently, by arguing for the immutability of the species, he was wrong in principle, whereas Geoffroy Saint-Hilaire was right in principle without the appropriate facts (Jaynes, 1969). The debates contributed to polarization between the two camps, with Cuvier's side insisting on the laboratory analysis and founding comparative psychology, while Geoffroy Saint-Hilaire's camp emphasized naturalistic observations and established ethology. Comparative neurophysiologist and protege of Cuvier, Pierre Flourens, the author of *Psychologie Comparee* (1864), is credited with developing a comparative psychology that synthesized the mechanistic neurophysiological approaches of Des-cartes' human psychology with Cuvier's animal psychology. It is worth noting, however, that during that same year and consistent with the intellectual bias of his school, Flourens (1876) published another book, leading French science's attack on Darwin's Origin of Species (1859). The comparative psychology that developed in North America around the turn of the century embraced the Darwinian view ofthe world, but it remained a laboratory science, and its failure to appreciate the importance of the ecological-naturalistic dimension of behavior contributed to its decline (e.g., Lockard, 1971).

By comparison, throughout the nineteenth century the naturalistic bias was advanced by other prominent biologists. Alfred Giard (1904) emphasized ethology and E. Haeckel (1898) pushed for "oecology" (presently ecology), then and now defined as the study of the relationships among organisms and environments. It is no accident that the more recent pioneers of ethology sought to avoid a dichotomy between field and laboratory research, and they succeeded in doing so under the conceptual framework of evolutionary theory (e.g., Eibl-Eibesfeldt, 1975; Hess, 1973; Jaynes, 1969; Lorenz, 1981; Schneirla, 1966; Thorpe, 1963; Tinbergen, 1951).

Levels of Organization-Levels of Analysis

Any behavioral problem can be conceived as varying along dimensions identified as levels of analysis. Each level can be defined in terms of its position on an information continuum. The major unifying and consensually valid theme in the ethological perspective is the synthetic theory of organic evolution.

When Darwin and Wallace in the 1850s proposed their theory of evolution by natural selection of the fittest and by specific examples demonstrated how these processes could account for the evolution of organisms, they planted the seeds of the powerful scientific and intellectual conceptualization that is still unfolding. From Malthus, Wallace and Darwin knew that organisms reproduced in far greater numbers than could be sustained by a particular environmental setting. Their observational evidence was that populations remain relatively constant. They therefore concluded that a large proportion of the offspring must fail to survive. Moreover, they knew that animals compete for the available resources of the environment and thereby participate in an active "struggle for existence"
(Darwin, 1859/1869). As Darwin (1859/1869) indicated:

> ... owing to this struggle for life, any variation, however slight and from what-ever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving for, of the many individuals of any species which are periodically born, but a small number can survive. (p. 61)

Even though it was most important for the evolutionary theory that heritable variations be present in each generation, Darwin nevertheless freely conceded his ignorance of the mechanisms of inheritance. It was not until about 1900 that Mendel was rediscovered and that Hugo de Vries proposed his mutation theory by pointing out the likely possibility that the obvious morphological changes he observed in the evening primrose might provide the variations on which natural forces could exert selection pressure.

The major breakthrough and the beginnings of the modem synthesis surfaced in the 1930s, when R. A. Fisher (1930) published *The Genetical Theory of Natural Selection*, Dobzhansky (1937) produced *Genetics and the Origin of Species*, followed by Oparin's (1938) *The Origin of Life*, Mayr's (1942) *Systematics and the Origin of Species*, and Huxley's (1942) *Evolution: The Modern Synthesis*. These works brought together diverse areas of human knowledge and inquiry. Organic evolution began to be viewed as a by-product of the chemical evolution of matter and biophysics, biochemistry and molecular biology surfaced as the new and exciting areas of inquiry. The new neo-Darwinian synthetic theory of organic evolution made sense out of taxonomy. It explained the fossil record as well as the fitness of adaptations between organisms and their habitats. The cell theory put forward convincingly in 1839 by German microscopists, Schleiden and Schwann, was given a new vision: The cell is a Mendelian unit carrying the genetic code of stored variability that is crucial to evolution and, at the same time, is a physiochemical entity obeying the laws of physics and chemistry. The bridge between particle physics and human evolution and ecology was formed. The door was left open for the new generation of Nobel laureates such as Watson and Crick (1953), who, by their elucidation of the double-helical, physiochemical structure of the DNA molecule and its role in heredity, provided one of the major empirical validations for the new synthesis.

Unfortunately, the behavioral sciences were largely left out of the modem synthesis (Dawkins, 1986; Hess, 1973; Lockard, 1971; Lorenz, 1965; Wilson, 1975). The reasons were many. The pursuit of the mysteries of life focused the concerns of the biological sciences on the molecular universe, thereby leaving the behavioral territory to psychology, sociology, anthropology, and psychiatry). In turn, many professionals in these disciplines found the nativist, materialist, determinist implications of the modem synthetic theory of organic evolution to be either irrelevant or difficult to accept and incorporate procedurally, professionally, politically, and personally. For example, until very recently the lack of emphasis on the role of hereditary factors in behavior has been one of the hallmarks of North American psychology and sociology. Thus, many behavioral scientists were surprised by the "unconventional" decision of the Nobel Foundation in 1973 to award the prize for physiology and medicine to three ethologists, Karl Von Frisch, Konrad Lorenz, and Nikko Tinbergen, thereby acknowledging the efforts of those individuals in bringing the study of behavior under the umbrella of the synthetic theory of organic evolution. With the subsequent ad-vent of sociobiology (e.g., Wilson, 1975) and cultural materialism (Harris, 1966, 1979), the initial surprise gave way to exchanges characteristic of a paradigm clash (e.g., Cavalli-Sforza & Feldman, 198 1; Gould, 1980; Rose, Lewon-tin, & Kamin, 1984; Lumsden & Wilson, 1981; Trivers, 1985).

Current ethology is occupied with four hierarchical biological questions and concerns: What are the ontogeny, causation, function, and evolution of behavior? Explanation and understanding require that attention be given to each of these questions and concerns and to the various levels of interrelationship among them. The magnitude of the hierarchical concerns requires a breadth of synthesis that transcends levels of analysis from genotype to behavior and ecology--a synthesis that transcends the extremes of levels of biological organization.

In general, the consensus among ethologists has been that: (a) organic evolution has been a by-product of the chemical evolution of matter, (b) animal species, including Homo sapiens, are the products of natural selection, and (c) genes are chemically code for phenotypic expressions. In terms of reproductive success, natural selection favors those animals whose genes, through their phenotypic expressions, successfully interact with the environment of the ecosystem. The above-listed considerations stem from the world view shared by ethologists (Dawkins, 1986). Even so, some considerations are often neglected. We now attempt to relate these considerations to levels of analysis in the behavioral sciences.

The ethological model incorporates in a hierarchical fashion levels of organization from subatomic particles to ecosystems. No level of organization or analysis is conceived as more "important" or "adequate" than another, since a position on the information continuum is not in itself a criterion for importance or adequacy. The reduction of a behavioral problem to a neurophysiological one, or of a neurophysiological one to a biochemical one, does not in itself generate a more fundamental or a more important explanation of the original behavioral problem. Surely, we recognize that the water molecule has characteristics and properties independent of those of hydrogen and oxygen. At the same time, we must note that knowing the characteristics of hydrogen and oxygen does provide us with some important information about water. Thus, it follows that the usefulness and appropriateness of her particular level of analysis is circumscribed by theoretical orientation, parameters of the problem under investigation, and contextual circumstances, as well as by general purposes of the discipline or the investigator. Thus, as our introductory example indicates, a student in modem ethology investigating the behavioral biology of the cricket song would find it necessary to acquire at least some sophistication in language and the tools of genetics, neurophysiology and neuroanatomy, quantitative behavioral analysis, systematics, ecology, and evolution.

Ethology And Attachment

The attachment behavior of young precocial fowl toward biologically-appropriate adults or surrogates including humans, was noted two thousand years ago (Hess & Petrovich, 1977). Konrad Lorenz's (1935) paper on companions as factors in the socialization of birds represents the first post-Darwinian experimental attempt to deal extensively with the phenomenon of "imprinting" (see Petrovich & Gewirtz, Chapter 5; for a review of the literature from a historical perspective, see Hess, 1973; Hess & Petrovich, 1977). The more recent interest in human attachment has been sparked by the elegant contributions of Bowlby (1958, 1969/1982, 1973, 1980) and by the derivative approach and refinements of Ainsworth (1969, 1982) and her associates (Ainsworth, Blehar, Waters, & Wall, 1978). Among students of human development, these contributions have come to be known as the ethological approach to attachment.

The attachment theory proposed by Bowlby (1969/1982) was developed in an attempt to extend and improve traditional psychoanalytic approaches. The three volumes of Attachment and Loss (1969, 1973, 1980) provide a modem synthesis that goes well beyond the modesty of Bowlby's original claims. Nevertheless, Ainsworth's (1969) observation that "In effect what Bowlby has attempted is to update psychoanalytic theory in the light of recent advances in biology" (p. 998) still rings true. Bowlby's (1969/1982) synthesis of psychoanalytic thought and ethological research was very compatible with the ethology of the 1950s and 1960s period. Patterns of infant-adult attachment were approached from a comparative cross-species perspective as evolved species-typical behavioral adaptations. Bowlby was careful to distinguish between "teleological assumptions" under which the purposes of behavior are assumed and "teleonomy" under if which the contingencies facilitating the survival value of behavioral adaptations may be demonstrated. Bowlby attributed the evolutionary origins of attachment behavior to predatory selection pressures. This conceptualization of human attachment was articulated within the framework of biopsychosocial systems theory (Bowlby, 1969/1982; Bischof, 1975) that invites comparisons with levels of organization and analysis that we have identified as characteristic of the ethological approach.

If one reviews the methods and practices of present-day adherents of the ethological theory of attachment, there is found a mismatch between those conceptualizations and objectives of modem ethology (as we have elaborated them) (e.g., Ainsworth, Blehar, Waters, & Wall, 1978; Bretherton & Waters, 1985; Sroufe & Waters, 1977). In a striking contrast to the cricket song example, these contributions are characterized by the paucity of research on ontogeny, including mechanisms of causation, function, and evolution of attachment. Considerations of genetic, neurophysiological, neuroendocrine, functional analyses, the latter including such molar processes as perception, preverbal, nonverbal and verbal communication, and learning, and evolutionary processes of attachment are missing or are dealt with superficially.

In contemporary ethology, Darwinian formulations such as "adaptations for the good of the species" have given way to considerations of evolutionary strategies of ultimate causation and conditional probabilities in proximal development that are derived from theory and empirical evidence from both experimental and field ethology, population genetics, evolutionary biology, behavioral ecology, and developmental psychobiology. Among the researchers of human attachment, these developments have received but scant attention. We noted in an earlier section that Bowlby (1969/1982) was careful to distinguish between teleological and teleonomic assumptions. Admittedly, "adaptive" is a troublesome term incurring problems of teleology in its use, if ecologic-teleono mic contingencies of survival value are not specified. Moreover, given the biological history of *Homo sapiens*, various modes of adaptation may be outcomes of specific experiences rooted in learning and tradition as of genetically programmed processes. At some level of analysis, however, the modem view holds that conditional responses are an outcome from the coaction. of these processes (probablistic epigenesis). Even so, analyses of these processes in a given ecological setting are required. Lack of sensitivity to these issues is noteworthy among human developmentalists investigating attachment under the aegis of ethology.

Contemporary ethology is neutral about the relative contributions of laboratory and field research. The consensual view holds that the problems of interest to researchers are to be found in nature. A laboratory is a tool that allows the investigator an opportunity to test specific hypotheses under controlled conditions and investigate experimentally puzzling aspects of behavioral development. In turn, laboratory solutions are evaluated in terms of their putative biological/ ecological origins, thereby allowing researchers to explore the fitness of behavioral adaptations found in nature. By comparison, the application of the Strange-Situation laboratory procedure for assessing attachment has dominated the methodological landscape in the human-development approach to attachment under the conceptions of ethology. The relation of these laboratory assessments to the ecological dimensions of attachment have not been pursued systematically or with discipline (Lamb, Thompson, Gardner, Chamov, & Estes, 1984).

The treatment of functional aspects of behavior is limited. For example, Waters' and Deane's (1985, p. 42) statement that "questions about what is learned during the attachment relationships, about the course of attachment after infancy, and about individual differences beyond security and anxiety have received little attention," is likely to be shared by any ethologists interested in molar and ecological dimensions of early socialization.

The conceptualizations and research in modem ethology are characterized by testing hypotheses stemming from evolutionary processes of inclusive fitness, parental investment, and kin selection. Response to predation is just one measure of parental investment. Two decades ago, Bowlby (1969/1982) attributed the evolutionary origins of attachment to predatory selection pressure, a view that is still widely held by researchers of human development and by authors of texts of child development (e.g., Sroufe & Cooper, 1988). In contrast, from the perspective of contemporary ethology, the most plausible ultimate explanation of the origins of attachment is that behaviors denoting attachment increase the inclusive fitness of the individual whose mode of reproduction is characterized by intricate patterns of parental investment (Petrovich & Gewirtz, 1985; Petrovich, Gewirtz, & Hess, 1986).

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