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A Review the Literature and Data in Comparative Psychology, Animal Cognition, Ethology, Ontogenesis, and Elements of Cognitive Neuroscience as they Relate to Animal Inquisitiveness (2nd Edition)

Wojciech Pisula

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Foreword

Today, a decade seems like a whole era for science. With the number of research papers published in reputable, peer-reviewed journals growing each year, it is tempting to focus on the most recent findings, leaving aside older papers, some of which treat the issues of interest differently. This attitude is especially apparent in young researchers and students, who seem to believe that anything of any import for science (with a handful of notable exceptions, such as the theories of Nicolaus Copernicus and Charles Darwin) happened within the past few years. This approach is further reinforced by the algorithms of digital knowledge databases that tend to sort entries in a way that gives preference to the most recent publications. But it only takes a moment's reflection to understand how flawed this oapproach is. After all, scientific knowledge is a system of knowledge accumulated by successive generations of researchers and thinkers. Ignoring, forgetting or intentionally leaving out the knowledge accrued at any of the stages of scientific progress may be detrimental to the creation of new information in science.

Another problematic aspect of modern science is that it is often done in isolation from more general systems of knowledge, i.e. without the scientist aiming to frame her findings within the conceptual system of philosophy, including the philosophy of science. As rightly pointed out by Laplane et al. (2019), there are many tangible benefits of scientists' engagement with philosophy, some of which are directly related to the specific issues studied in a given discipline. This is why in this book I will attempt to analyze empirical findings within a wider, somewhat philosophical context.

It has been ten years since the first edition of this little monograph. During that time we saw many new insights into animal and human exploration, and what is commonly known as curiosity. Some definitions have changed. There has been a shift of focus towards the topics studied in neuroscience. The current edition has been supplemented with new information both from the author's own research and reported by other scientists. Have these changes significantly affected our knowledge about human and animal curiosity? I take full responsibility for my choices. I selected research I considered most relevant to the concept of this book. I did my best not to succumb to the pressure of the current moment and tried to include slightly older studies and papers that have contributed to this area of knowledge. Ultimately, it is for the readers to judge whether, based on the outcome of my efforts, they are able to form a balanced picture of this area of knowledge about human and animal behavior.

Chapter 1.

Introduction and Short History of Research within Animal Psychology

Animal behavior has been the subject of human interest since the dawn of man. The nature of that interest, however, has been changing over time. Initially, discovering the animals' behavioral patterns was essential for man's survival in a hostile and challenging environment. With this knowledge man was able to hunt effectively and to protect himself from predators.

The significance of animals from the human point of view changed as our control over the environment increased. Their previous uses were supplemented by new ones. A good example of such change was the domestication of many animal species. The dog is a prime example of this process, albeit an untypical one. The phenomenon of domestication is quite complex. Domestication of animals kept as a source of food (meat, milk) or skin can be interpreted in terms of counteracting the shortage of game (caused by diminishing hunting grounds) and taking advantage of economic opportunity. However, the attitude towards animals as living creatures has not changed. They still are perceived in material terms. The dog is an example of a species whose domestication cannot be explained by the same factors as the domestication of pigs or cattle. Clearly, man must have noticed dogs' other assets: intelligence, alertness, ability to survive in difficult situations. For the first time the benefit was not the animal's meat or skin, but its behavior: humans started to appreciate and learned to take advantage of such important abilities of animals as learning and attachment. From

then on the motivation to discover the rules of animal behavior took on a new, more profound character. The animal became man's partner (albeit not his equal) in everyday work and leisure.

The utilitarian motives for learning animals' behavioral patterns used to be and still are of primary importance, but there are also others. Apart from consciousness, the attributes often quoted as being exclusive to men are self-awareness and the urge to understand the relationships to our environment. Animals, with their varied and often complex behavior, have undoubtedly been among the stronger stimuli driving man's quest for knowledge. The result was that animals were often included in religious belief systems. The attempts aimed at explaining animal behavior without reference to metaphysics followed a different path.

The attitude towards animals and their psychology always tended towards one of two extremes. In antiquity they were symbolized by the ideas of Aristotle, who interpreted the structure of the natural world in terms of quest for perfection, and Plato, who emphasized the gulf between the human and animal world. The two opposing trends continued through centuries, as evidenced by St. Francis of Assisi and his love of animals on the one hand, and Renè Descartes, who claimed that the soul present in humans is absent in animals, making them more akin to machines on the other. And indeed, in the 18th century that followed, dominated by the preoccupation with engineering and machinery, the influence of Descartes' philosophy meant that animals were regarded as machines, neither having a soul nor experiencing even the most basic psychological sensations, pain included. Fascination with machines centered on their internal mechanisms, i.e. that which made them pieces of machinery. In the 18th century, this fascination coupled with the view that animals experienced no psychological sensations, paved the way for such practices as live vivisections performed in order to demonstrate the workings of the animals' „mechanisms" (e.g. the heart, diaphragm, lungs, etc.).

This was the state of affairs when the theory of evolution (Darwin, 1859) burst onto the scene. Its impact was revolutionary. Where there was once a chasm separating the animal and human kingdoms, there was now a scalable distance, greater or smaller depending on the species. Thus, if it had previously been acceptable to conduct a comparative analysis of the phylogenetic development of the heart or

skeleton, it was now equally reasonable to compare behavior, and consequently – psychology. Darwin himself published the first modern monograph in comparative psychology (back then referred to as zoopsychology) titled "The expression of the emotions in man and animals" (1872). The incredible success of the idea that "Nature takes no leaps" (*Natura non facit saltus*) laid the foundations for animal psychology. Those practicing the new discipline were interested in finding relationships between psychological processes in humans and animals. Their reasoning was as follows: if the continuity of morphological, anatomical or physiological development could be demonstrated, then in all probability the same held true for psychological processes. They were therefore looking for similarities between human and animal behavior. If there are analogies between the construction of a nest by a bird and the construction of a house by a man, and if the functions of the former are similar to those of the latter, then it only takes one short step to assume that the underlying psychological processes are analogous. This approach to the study of animals was strongly opposed by some researchers. One of them was C. L. Morgan, who proposed the following argument against the anthropomorphic interpretation of animal behavior: „In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in psychological scale." (Morgan, 1894, p. 53). The two parallel schools of animal behavior analysis were founded on the distinction between approval and rejection of Morgan's cannon.

J. Loeb's principle of forced movements (Loeb, 1918) was the prime example of the mechanistic view of animal behavior influenced by the philosophy of Descartes. Using models of animals with simple anatomy (flatworms, annelids), Loeb demonstrated that a significant part of their behavior was generated by simple reflexes occurring in response to environmental stimuli and, more importantly, controlled peripherally, with no involvement of the central nervous system. He referred to these simple, directional responses as tropisms, and he was looking for evidence of their operation in higher organisms.

The answer to the shortcomings of zoopsychology (criticized for its anthropomorphism) and experimental psychology was to be animal ethology. Ethologists (ethos meaning habit in Greek) made animal habits the scope of their research. K. Lorenz, N. Tinbergen, K. von Frisch,

R. Hinde and I. Eibl-Eibesfeldt came to the conclusion that the behavior of animals must be studied in their natural habitat, where its biological meaning could be deduced. Any interference with the behavior of a single animal or group distorts the significance of a given behavior, making it more difficult to interpret and rendering useless the most precise measurements and analyses. Ethologists record the forms of behavior typically exhibited by a given species in its proper environment. The primary research technique is observation. There is a strong emphasis on the evolution of behavior. Ethology broadened our knowledge by contributing such ideas as chains of actions, key stimuli, or conflict between drives.

Initially, in order to avoid the mistakes of zoopsychologists, ethologists rejected the realm of psychological phenomena, focusing on "objectively measurable" behavioral factors. With time, however, it became clear (Lorenz, 1982) that the cognitive processes underlying or regulating animal behavior along with other factors would be the core subject of ethology and comparative psychology. Lack of objectification of results and standardization of experimental conditions, as well as disregard for the concepts of general psychology (including the achievements of the psychology of learning) provoked mounting opposition to the ethological school and led to the foundation of a new paradigm, namely the ethoexperimental approach.

This avenue of research was continued in the work of experimental psychologists, who developed a new branch of psychology: behaviorism. The work of behaviorists (Skinner, 1938; Tolman, 1949) embodied the ambition to achieve strict control of experimental conditions, reproducibility of results and mathematization of data analysis. Experimental psychologists usually based their studies on animals on selected forms of behavior, artificially generated through instrumental conditioning, e.g. pressing a lever, running in a running wheel, etc. They paid little attention the particular species on which they were experimenting, implicitly assuming universal significance of all processes under investigation. The use of artificially generated forms of animal behavior was coupled with a nearly total disregard for the biological significance of a given behavior and for individual differences. Experiments were conducted in a laboratory, and their only aspect going beyond its confines were the researchers' conclusions. Obviously, the conclusions were formulated in a universal manner, but

the criticism leveled at the aforementioned interpretative limitations prompted a significant change in the approach to research on animals. Objections aside, we cannot ignore the great achievements of behavioral psychologists (e.g. their contribution to the theory of learning), and their impact on the development of psychology.

The publication in 1935 of the principles of animal psychology by N. R. F. Maier and T. C. Schneirla was an attempt to avoid the basic dispute about the nature of animals, i.e. whether their psychological functions were comparable to human ones. The authors presented their own analysis, trying to assume an unbiased and objective approach, without favoring either option. The monograph still makes for interesting reading, although it should be pointed out that both the followers of the mechanistic school and the proponents of the cognitive approach have rejected the ideas of Meier and Schneirla.

Beginning in the 1930s, the theory of continuous phylogenetic development of higher psychological processes became the cornerstone of progress in animal behavior research. Its prominence was due to the famous research of W. Köhler (1926) on insight learning in chimpanzees completing problem-solving tasks. With the resistance to the notion that thinking is not a privilege reserved to human beings, Köhler's study was quoted as evidence of thinking in animals as often as to support the idea that thinking and related phenomena occur only in anthropoid primates.

The founder of modern ideas about cognitive processes in animals was L. V. Krushinsky. Working in the Soviet Union, back then dominated by dogmatic Pavlovianism, he had to come a long way to develop his own, original theoretical and methodological framework. The key notion of his system is extrapolation, defined as the ability to predict physical events, especially the direction of movement of biologically significant objects (Krushinsky, 1990). One classic example is predator chasing its prey, when the escaping animal suddenly changes direction, often disappearing from the predator's field of vision. By analyzing data from countless experiments, Krushinsky was able to distinguish a number of important patterns. For instance, he concluded that within-class differences in vertebrates are greater than between-class differences. Extrapolation abilities in corvids are superior to most mammals, while tortoises, generally regarded as extremely unintelligent, perform no worse than average mammals. It took nearly twenty years

for Krushinsky's monograph to be discovered by the English-speaking world. Its publication in English came too late (1990) and failed to make the impact it would have made had it been available in the early 1980s. The ideas of Krushinsky are present in numerous publications, but direct quotes and citations are few and far between.

The turning point was the publication of D. Griffin's seminal work (Griffin, 1984). Griffin undertook a radical critique of the reductionist and mechanistic approach by re-interpreting a number of animal behaviors that could suggest the presence of cognitive processes. His main thesis concerned methodology, or, to use T. S. Kuhn's terminology, paradigm. Griffin argued that strict adherence to Morgan's principle lead to an error in reasoning which consisted in denying facts that could be evidence of thinking and consciousness in animals. To underestimate the complexity of the organization of phenomena is a mistake as serious as to overestimate it. Griffin advocated the introduction into animal psychology of concepts from cognitive psychology, such as consciousness, representations and thinking, and their verification within its framework on similar terms as in human psychology. The key to his analytical method was the use of the term „other minds". Besides its strictly descriptive function, the significance of this term lies in the fact that it expresses the overall position towards the problem of mind. The key is to truly abandon the anthropocentric perspective in which the human mind is the frame of reference for all comparisons. The study of other minds is the process of learning other, sometimes alternative, and sometimes completely distinct evolutionary solutions.

Griffin's approach suffers at times from the so-called pendulum effect. Developed in opposition to behavioral psychology on the one hand, and classic ethology on the other, animal cognitive psychology may seem somewhat naive and not entirely free from the restrictions of anthropomorphism. It should be pointed out that there is nothing in Morgan's principle that prohibits the study of mental phenomena in animals. What it posits, however, is that one should verify hypotheses related to lower-level structures before proposing one that refers to the mind. Criticism aside, there is no doubt that the publication of Griffin's monograph was the turning point in the study of cognition in animals.

One of the important themes in the new cognitive ethology/psychology of animals was the nature of cognitive/neural representation.

C. R. Gallistel (1990) defined four *sine qua non* conditions which must be satisfied if the claim of the existence of a representation is to be valid. Thus, representations exist if:

1) There is a mapping from external entities or events to mental or neural variables that serve as representatives of those entities.

2) There is a formal correspondence between relational and combinatorial operations involving these neural or mental variables and relations and combinatorial processes involving the things denoted by them.

3) The mapping process and the combinatorial processes are together such that the combinatorial processes in the representing system generate valid anticipations of events and relations in the represented system.

4) The capacity of the neural or mental operations to generate generally correct anticipations of external events and relations is exploited by the mechanisms that generate behavior adapted to those events and relations.

This version of the defining conditions of cognitive or neural representations is considered overly restrictive by some commentators (Shettleworth, 1998). Nevertheless, it exemplifies the way of thinking typical for present day animal psychologists and ethologists of cognitive persuasion.

A separate issue is the demarcation of research domains essential for understanding the evolution of mental processes. We can say with a high degree of certainty that those include: exploratory behavior, play, counting and numerical operations, individual recognition of others and oneself, communicating in a learned language and formulation of the theory of mind. An exhaustive review of the state of knowledge in each of those domains is outside the scope of this text. There are, however, those elements that are central to our overall understanding of the subject.

Both play and exploration are forms of behavior that elude analysis. Typically, ethologists have been looking for repetitive and therefore relatively stereotyped behavior patterns. Play and exploration, however, are instigated by a wide range of stimuli (no specific stimulus-behavior relationship), occurring irregularly, and varying in performance.

Particularly noteworthy is the relationship between exploration, play, and behavior referred to as intelligent. Curiosity, play, and intelligence together form an inseparable triad in the evolution of vertebrates. Interestingly, a popular belief that play is only observed in mammals, and to a very limited degree in birds (Fagen, 1981), is currently undergoing revision. For example, M. Kramer and G. M. Burghardt (1998) found that some behaviors demonstrated by turtles would be difficult to interpret as anything other than play.

The study of intellectual abilities in animals seemed to have come to an abrupt stop early in the 20th century with the demise of Clever Hans, the counting horse. However, the subject came back into the focus of animal behavior researchers towards the end of twentieth century. There is no doubt that a number of animal species have the ability to estimate (measure?) time, volume or incidence (probability of occurrence). What is unclear is the nature of the process that leads to the observable results. There is no question that most laboratory vertebrates (e.g. rats) can tell the difference between three and five objects. It is less obvious whether the animal makes its judgment based on some primitive mechanism for quantity estimation, limited to a certain number of elements, or whether it is actually counting. The problematic question is this: does arithmetic require some form of understanding of mathematical properties of numbers? Probably not. Quantities can be denoted (Shettleworth, 1998) with labels, i.e. "one", „two", „three," and, for example, „many". The ultimate criterion for judging arithmetic competence would be the ability (or lack thereof) to manipulate numbers (addition, subtraction). This particular ability seems to be very rare, but recent studies show that it is found in primates, and perhaps also in other animals. M. D. Hauser (2000) demonstrated that in rhesus monkeys spontaneous calculation and use of arithmetic operations is rare. The efficiency of number manipulation is increased dramatically by training. Currently, the key issue in the study of mathematic abilities in animals is to uncover the nature of number representation.

The results obtained in studies on the development of communication in a learned language in chimpanzees are ambiguous. On the one hand, research conducted by Allen and Beatrice Gardner (1969) on teaching sign language to chimpanzees seemed to confirm the ability of these animals to use a learned language at a level comparable to simple human speech. On the other hand, many authors emphasized

the imitative nature of the chimpanzees' communication and their inability to communicate spontaneously (meaning they are unlikely to chat about the weather). In a summary of the above controversies, Sara J. Shettleworth (1998) concluded that there is no definitive answer to the question whether members of other species can be taught to communicate using a system similar to human language. Nevertheless, there is a growing body of data that show the belief in the gulf between linguistic abilities of men and other primates to be false. The question why members of other species do not make use of often significant capabilities at their disposal remains open.

Another hotly contested issue among animal psychologist is the ability of some animals to form the so-called theory of mind. D. Premack and G. Woodruff (1978) defined theory of mind as the process of attributing mental states to oneself and others. D. Griffin (1984) devoted a lot of attention to the phenomenon of deception in animals. Naturally, what I refer to here is deceitful behavior, such as hiding attractive food from peers, and not mimicry. In a review of research on behaviors that could be indicative of theory of mind, Sara J. Shettleworth (1998) concludes that it would be difficult to find evidence of a general ability to formulate theory of mind. The view that individual species appear to have this ability within a limited set of activities (foraging, courtship, etc.) has recently been gaining in popularity (Tomasello, Call, Hare, 2003).

The history of scientific interest in the research on exploration and curiosity dates back, as most ideas in comparative psychology, to Charles Darwin. He was the very first person to emphasize the significance of curiosity in the formation of higher psychical faculties. H. Jennings (1906) included in his immense book on the behavior of lower organisms extensive examples of activities that he described as trial movements, and which today we could call exploratory. For instance: „When stimulated, the earthworm frequently responds by moving the head first in one direction, then in another, often repeating these movements several times. It then finally follows up those movements which decrease stimulation" (Jennings, 1906, p. 247). Jennings also quoted S. J. Holmes (1905, p. 108), who stated „The lives of most insects, crustaceans, worms... show an amount of exploration that in many cases exceeds that made by any higher animals. Throughout the animal kingdom there is obedience to the Pauline injunction, "Prove

all things, hold fast to that which is good". Presumably, these authors understated, that the intensity of trial movement correlates with the complexity of animals' sensory systems. It is their undeniable commitment however, to emphasize the role of exploration even in simple organisms.

In the middle of the twentieth century, two major events shaped the study of exploratory behavior. These were the works by Daniel Berlyne (1962) and Harry Fowler (1965). Throughout the twentieth century, interest in the research on exploration in animals was oscillating to reach its final peak at the beginning of the twenty first century, and that time the interest was clearly associated with the cognitive approach to animal behavior (Pisula, 2007).

Today, research uses animal exploration as an indicator of anxiety, novelty preference, as well as habituation (Hughes, 2007). The present approach is a combination of behavioral, neurobiological, and cognitive paradigms. These studies emphasize the concept of multi-level analysis of the object under investigation, from strictly biochemical processes, through brain-level phenomena, to the behavior of the organism as a whole.

The present confusion with the use of names denoting disciplines of science is so complex that it is often not enough to mention which field of research one represents. This is especially true of comparative psychology, which is an interdisciplinary science. It is positioned on the crossroads of physiology (physiological psychology), behavioral ecology, sociobiology, and general psychology. E. O. Wilson (1975) in his monograph, which aspired to be the new and total synthesis of behavioral sciences, speculated on the future development of disciplines focused around the central aspects of behavior

It might seem that the grim prognosis for comparative psychology could soon become reality. A symptom of this process is the evolution of journals publishing papers on comparative psychology. For years, the leading periodical was the „Journal of Comparative and Physiological Psychology". In 1974, the American Psychological Association shut down "JCPP", replacing it with two new journals: „Behavioral Neuroscience" and „Journal of Comparative Psychology". The former focuses on publishing articles in neurophysiology which take into account behavioral variables. As such, its subject matter is physiological psychology proper. Thus the journal of choice for comparative

psychologists should be the latter. However, they tend to publish their work in journals which make no mention of the comparative method in their names. The reason is that psychology is mainly concerned with proximate causes of behavior. It analyses environmental stimuli in terms of behavioral control and describes hypothetical psychological mechanisms underlying specific behaviors. References to ultimate causes (evolutionary, environmental) in psychological accounts play an auxiliary role and have little bearing on the value of a research study or a particular theory. As the name suggests, comparative psychology is also the focus of „International Journal of Comparative Psychology," published since 1987 by the International Society for Comparative Psychology. Its primary goal is to present articles on the evolution and development of behavior, the use of the comparative approach for the analysis of behavior control processes and verification of the validity of psychological and evolutionary theories. It should be noted, though, that comparative psychology is also prominent in other scientific journals publishing articles on animal behavior. These include: „Animal Cognition", „Animal Behavior", Behavioral Processes", „Animal Learning and Behavior", Behavioral Neuroscience", „Journal of Ethology", „Ethology", „Journal of Experimental Psychology: Animal Behavior Processes", „Journal of Applied Animal Welfare Science", „Comparative Cognition and Behavior Reviews", the recently established "Animal Behavior and Cognition," as well as others, often with narrower specializations. Thus E. O. Wilson's prediction that comparative psychology would gradually disappear as a separate sub-discipline is turning out to be accurate. The reason, however, is not that research or interest in comparative analysis is on the decline, but rather that it attracts more attention from psychologists, neuroscientists, and behavioral biologists. Comparative psychology is undergoing integration into the general field of behavioral science. L. C. Morgan's (1894) vision of psychology as a comprehensive discipline, defined not by narrow specializations but by the issues under investigation, is being realized over a century later. Comparative research has paved the way for the development of an important branch of the science of human and animal behavior.

Chapter 2.

Remarks on The Methods: The Four „Whys" and The Theory of Integrative Levels

Ethel Tobach (1995) pointed out that comparative psychology suffered from the lack of paradigms that were agreed upon by most psychologists. Additional damage has been done by the acceptance of the modern version of genetic determinism developed in the seventies (see Wilson, 1975; Dawkins, 1982, 1989). In North America, discussion of different approaches to the evolution and development of behavior has been ongoing for more than forty years. Europe seems to be reticent about these issues, having adopted sociobiological-determinist views (see writings by Dawkins, 1982, 1989). After almost forty years of sociobiological dominance in the field, it is hard to imagine in comparative psychology models alternative to genetic determinism. I believe that it is now time to rethink the way comparative psychologists think. The main purpose of this chapter is to compare two approaches/paradigms to the study of animal behavior: the traditional, biological model and an alternative, holistic model. The traditional, biological model is exemplified by the formulations of Mayr (1961), Tinbergen (1963), Dewsbury (1992), and Alcock (2009). The alternative, holistic model is based on the concept of Levels of Integration (Greenberg and Tobach, 1984).

Mayr (1961) proposed two categories of explanations in the biological approach to behavior: proximate and ultimate. Proximate causation refers to factors acting directly on the individual in its day-to-day life, or, in other words to the control of behavior. Ultimate causation refers to births and deaths of generations and therefore to evolutionary processes. In a similar vein, Tinbergen (1963) distinguished four types of answers to the question "Why animals behave as they do?":

- *In terms of causation, which* includes an analysis of the whole collection of external and internal factors that cause organisms to behave as they do.
- *In terms of development, which* refers to developmental processes underlying the onset of given behaviors, including learning, brain maturation and other processes related to age.
- *In terms of survival value,* based on the likelihood of survival and/or reproduction success associated with given behaviors.
- *In terms of evolutionary history,* focusing on the origins of species-specific behaviors; e.g. why do starlings sing and dogs bark.

Tinbergen's formulation is considered to be so important that many authors of animal behavior books begin their writings with a description of Tinbergen's four questions (see Colgan, 1989; Krebs and Davies, 1991; McFarland, 1993; Goodenough, McGuire, and Wallace, 1993). Sherman and Alcock (1992), in editing their selection of animal behavior papers, highlighted their treatment of behavioral mechanisms with a paper describing the implementation of Tinbergen's framework (Holekamp and Sherman, 1989). This paper is an analysis of male ground squirrel dispersal. A type of analysis termed "multilevel" is used in the paper. The findings are summarized in Table 1 to correspond with Tinbergen's four questions. The significance of Tinbergen's Four Whys was emphasized by Jensen (1997), Cuthill (2005), and more recently by Barrett et al. (2013) and Strassmann (2014). Importantly, these authors stress the fact that Tinbergen's approach remains valid and applicable in today's research on animal behavior and that its impact goes beyond the contribution made to ethology in the seventh decade of the twentieth century.

Table 1. Summary of Results Obtained by Holekamp and Sherman (1989).

Level of analysis	Summary of Findings
Physiological mechanisms	Dispersal by juvenile males is apparently caused by organizational effects of male gonadal steroid hormones. As a result, juvenile males are more curious, less fearful, and more active than juvenile females.
Ontogenetic processes	Dispersal is triggered by attainment of a particular body mass (or amount of stored fat). Attainment of this mass or composition apparently also initiates a suite of locomotory and investigative behaviors among males.
Effects on fitness	Juvenile males probably disperse to reduce chances of nuclear family incest.
Evolutionary origins	Strong male biases in natal dispersal characterize all ground squirrel species, other ground-dwelling sciurid rodents, and mammals in general. The consistency and ubiquity of the behaviors suggest that it has been selected for directly across mammalian lineages.

J. Alcock's (2009) popular book on animal behavior adopts a similar perspective, through a synthesis of the approaches of Mayr and Tinbergen. He suggests that animal behavior should be analyzed within the following framework:

1. Proximate causation
   a) Genetic-developmental mechanisms
      - Effects of heredity on behavior
      - Genetic-environmental interactions during development that produce sensory-motor mechanisms
   b) Sensory-motor mechanisms
      - Detection of environmental stimuli: Operation of the nervous system
      - Adjustment of internal responsiveness: Operation of hormonal systems
      - Carrying out responses: Operation of skeletal-muscular systems

2. Ultimate causes
   a) Historical pathways leading to the behavior, (origin of behavior and its alteration over time)
   b) Past effects of natural selection in shaping current behavior. (Past and current utility of the behavior in reproductive terms).

Alcock also uses the term "multilevel analysis" to describe this framework. It is necessary to stress this point here because it will be the focus of the criticism below. This way of thinking is being developed today by J. Bolhuis and L. Giraldeau (2005) in their contemporary textbook about animal behavior.

Dewsbury's (1992) review of problems studied by ethology and comparative psychology made an important point about weaknesses inherent in these approaches. He realized that most researchers who were not satisfied with Tinbergen's approach looked for possible relationships between the levels of analysis, or problems, fields and so on, of analysis. Tinbergen, contrary to the assertions of many authors, treated his questions as equal. Dewsbury developed a different way of asking questions about animal behavior. He attempted to deal with controversies around specific problems in that particular area of study, proposing an interrelationship between the levels involved. Figure 2.1 presents the details of Dewsbury's conceptualization.

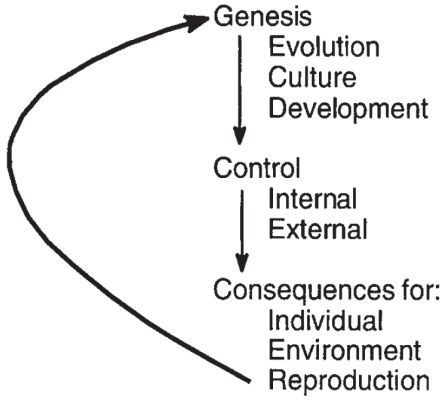

Figure 2.1. Pathway of processes shaping development of behavior.

Certainly, Dewsbury was looking for a structural way of integrating elements of the system. In this sense, his proposal seems to be efficient and mature. However, certain features common to all described systems make them rigid and unproductive. These are:

- Overstating the role of reproductive success in behavior, or in other words, understating the significance of processes unrelated to reproduction and selection.
- Labels used for level description and the lack of structure.

For biologists, the theory of evolution is as important as Newton's and Einstein's concepts for physicists. The idea of behavior evolution goes back to Darwin's (1872) monograph, and is regarded as an important organizing concept (Mayr, 1978). Wilson (1975) proposed that we should analyze all aspects of behavior in terms of their value for reproductive success. All models presented earlier in this paper follow this way of thinking. The weakness of such approaches in predicting behavior has been sufficiently demonstrated (Tobach, 1978). Evolution has been central for comparative psychology since Romanes (1892). The model presented in this chapter, however, takes a non-reductionist approach.

Labels used to describe the levels of analysis may be helpful in organizing our thinking. As was pointed out by Tobach (1965), labels reflect different approaches to an area of study. However, labels may also limit our thinking. Labels reflect our knowledge and our understanding. When the knowledge changes, we should consider changing labels as well (Feibleman, 1954). The biological models described above differ in the number of words and terms they use. They do not differ, however, in the content that they cover, all being fundamentally trapped within a "behavior → survival → reproduction → behavior" cycle.

Moreover, these models do not allow us to determine the relationship between listed areas of study. What is the function of a given process and the mechanism responsible for it? This is an obvious result of the reductionism built into these systems. Since gene transmission is the key to understanding both functions and mechanism of the evolution of behavior, there is no need to look for other aspects of behavior. Though Alcock (2009) and Dewsbury (1992) write about multilevel analysis, they do not describe the nature of the relationship between the levels. They seem to list the issues to be studied with no