

## **Role of Development in Evolutionary Change: A View from Comparative Psychology**

**Robert Lickliter and Susan M. Schneider**  
*Florida International University, U.S.A.*

Evolution has come to be increasingly discussed in terms of changes in developmental processes rather than simply in terms of changes in gene frequencies. This shift is based in large part on the insight that since all phenotypic traits arise during ontogeny as products of individual development, a primary basis for evolutionary change must be variations in the patterns and processes of development. Comparative psychology has a unique role to play in defining and describing these developmental dynamics, in large part because its specific aims and purposes are not well represented in other sub-disciplines within the life sciences. These include an empirical concern with the developmental and ecological dynamics contributing to behavioral and psychological functioning (especially in terms of degrees of flexibility or malleability) and the significant role of behavior in the evolutionary process (particularly in generating novel phenotypes). Comparative psychologists have provided converging evidence supporting the view that shifts in behavior brought about by changes in the environment and the resulting changes in the activity of the organism can lead to variations within and across generations in morphology and physiology, providing the engine for generating evolutionary change.

The link between development and evolution has emerged as an important theme in the life sciences in the beginning of the 21<sup>st</sup> century. It was not always this way. For the better part of the 20<sup>th</sup> century, evolution was commonly defined as “a change in the genetic composition of populations” (see Ayala & Valentine, 1979; Curtis & Barnes, 1989; Dobzhansky, 1951; Mayr, 1982). This definition of evolution was often taken to assume that (a) the instructions for building organisms reside in their genes, and (b) genes are the exclusive vehicle by which these instructions are transmitted from one generation to the next. Given these two assumptions, it was a logical next step to propose that since genes contained the necessary information for phenotypic traits, the role of development in evolution was minimal (see Maynard Smith, 2000; Mayr, 1997, for recent examples). From this view, development was thought to be internally determined, set on course at conception and specified by a genetic composition selected over evolutionary time. As a result of this type of thinking, evolutionary biology came to focus on population genetics during much of the last century, moving away from its earlier concerns with embryology and developmental biology (Gilbert, 1994; Gottlieb, 1992).

The last several decades have seen this gene-centered focus gradually accommodating a broader and more integrative view of evolution. This integrative effort has involved moving beyond the notion of genes as the fundamental cause of phenotypic traits and characters, thereby allowing for the consideration of a variety of extragenetic factors that also contribute to the emergence and maintenance of phenotypic traits (e.g., Gilbert, Opitz, & Raff, 1996; Goodwin, 1994; Jablonka & Lamb, 1995; Newman & Muller, 2000; Rossiter, 1996). Thanks to recent advances in molecular and developmental biology, we now know that the expression of genes is routinely affected or modified not only by other genes, but also by the lo-

cal cellular as well as the extracellular environment of the developing organism (reviewed in Davidson, 2001; Gerhart & Kirschner, 1997; Gilbert, 2000; Gottlieb, 1998; Johnston & Edwards, 2002), including cell cytoplasmic factors, hormones, and sensory stimulation (so called immediate-early gene expression, Clayton, 2000; Hughes & Dragunow, 1995; Tischmeyer & Grimm, 1999). Genes thus cannot be characterized as occupying a privileged position in the development of an organism, as they are themselves participants in the developmental process, which includes influences and interactions taking place at many hierarchically arranged levels, including nucleus–cytoplasm, cell–cell, cell–tissue, and organism – organism (Gottlieb, 1991, 1992; Sole & Goodwin, 2001). As a result of this insight, the relevance of development to evolution has received increasing attention over the last several decades and evolution has come to be increasingly discussed in terms of changes in developmental processes rather than simply in terms of changes in gene frequencies (e.g., Burian, 2000; Griesemer, 1999; Oyama, Griffiths, & Gray, 2001; Robert, 2004). This shift is based in large part on the insight that since all phenotypic traits arise during ontogeny as products of individual development, a primary basis for evolutionary change must be variations in the patterns and processes of development.

### **Links Between Developmental and Evolutionary Biology**

One of the most rapidly growing fields within biology, evolutionary developmental biology, is concerned with how developmental processes affect evolutionary change and how developmental mechanisms themselves evolve. Evolutionary developmental biology (often referred to as *evo-devo*) involves a partnership among evolutionary, developmental, and molecular biologists and in its most general sense, attempts to integrate developmental processes operating during ontogeny with those operating across generations (e.g., Arthur, 1997; Hall, 1999, 2003; Hall & Olson, 2003; Raff, 2000). This focus on developmental dynamics has resulted in a growing appreciation that development contributes to evolution in at least two major ways. First, it constrains phenotypic variation in such a way that the traits and characters presented to the filter of natural selection are not random. In other words, developmental processes and resources limit the range of the possible in terms of phenotypic form. This is the *regulatory* function of development. In addition to this regulatory function, development has an even more far-reaching effect in influencing evolution. Development provides variants in traits and characters that may lead to enduring alterations of the phenotype. This production of phenotypic novelties is the *generative* function of development and as we discuss in what follows, has significant implications for evolutionary change (Alberch, 1982; Gottlieb, 2002; Wcislo, 1989; West-Eberhard, 2003).

The renewed interest in the relationship between development and evolution (see Goldschmidt, 1940; Gould, 1977; Schmalhausen, 1949; Waddington, 1941; Whyte, 1965, for earlier examples) is redefining several assumptive bases of evolutionary theory. For example, the emerging appreciation of the regulatory and generative nature of development has called into question whether the natural selection of genetic mutations can be a sufficient causal explanation to account for evolution and its outcomes. Contrary to this assumptive base of the neo-Darwinian

synthesis of the last century, a growing number of evolutionary theorists are proposing that the introduction of phenotypic variation upon which natural selection acts is the result of a wide range of epigenetic processes, involving internal *and* external factors contributing to individual ontogeny (e.g., Arthur, 2004; Pigliucci, 2001; Rossiter, 1996; West-Eberhard, 2003). Variations in morphologies, physiologies, and behaviors resulting from modification in developmental processes can place their possessors in different ecological relationships with their environments, and if these phenotypic variations provide slight advantages in survival and reproduction, then competitors without the novel phenotype will eventually decrease in frequency in the population. The novelty-generating aspects of evolution are thus primarily the result of the developmental dynamics of living organisms, situated and competing in specific ecological contexts, and not simply the result of random genetic mutations (see Lickliter & Honeycutt, 2003; Oyama et al., 2001, for further discussion).

### **Role of Comparative Psychology in Evolutionary Studies**

Comparative psychology has a unique role to play in defining and describing these developmental dynamics, in large part because its specific aims and purposes are not well represented in other sub-disciplines within the life sciences (Greenberg & Haraway, 1998; Lickliter, 2004). These aims include an empirical concern with both the developmental and ecological dynamics contributing to behavioral and psychological functioning (especially in terms of degrees of flexibility or malleability) and the significant role of behavior in the evolutionary process (particularly in generating novel phenotypes). As briefly reviewed below, the work of comparative psychologists has provided converging evidence supporting the view that *shifts in behavior* brought about by changes in the environment and the resulting changes in the activity of the organism can lead to variations within and across generations in anatomy, morphology, physiology, and ultimately to changes in gene frequencies (for examples see Gottlieb, 2002; Wcislo, 1989).

In a key paper linking development and evolution, Johnston and Gottlieb (1990) provided a useful example of how new phenotypes may arise due to an enduring change in behavior before changes in gene frequencies. They describe a scenario in which a population of rodents whose normal diet consists of soft vegetation encounters a new food source of relatively hard but highly nutritious seeds. As the animals learn to sample and eventually increase the representation of seeds in their diet, a number of developmental effects of their new diet become evident, including possible changes in body size and composition, fecundity, age of sexual maturation, and indirect changes in morphology. For example, as the diet changes from soft vegetation to harder seed items, the mechanical stresses exerted on growing jaw tissues during development will change. Given that patterns of bone growth are known to be partly determined by forces exerted on the growing bone (Frost, 1973), the skeletal anatomy of the jaw will likely be different in the animals that experience hard vs. soft diets early in life. Such changes in diet have, in fact, been shown to affect the jaw and skull of rats (Bouvier & Hylander, 1984). In this scenario, behavioral change in members of a population (a preference for a new diet of hard seeds) leads to specific anatomical changes (modification of the jaw

and teeth). Such changes can endure across generations, and as long as the new diet remains available, may eventually lead to changes in gene frequency as a result of long-term behavioral or geographic isolation among variants within the population.

### **Behavior as a Leading Edge of Evolutionary Change**

Whereas the importance of behavior as an agent of evolutionary change is not a new idea (Baldwin, 1896; Bateson, 1988; Gottlieb, 1987; Hardy, 1965; Morgan, 1896; Plotkin, 1988; Wyles, Kunkel, & Wilson, 1983), it has yet to be fully incorporated into evolutionary theory. Toward this goal, Gottlieb (2002) has recently provided a succinct overview of the theory that evolution (defined as enduring transgenerational phenotypic change) can occur at the behavioral, anatomical, and physiological levels before it occurs at the genetic level. In essence, this theory proposes that changes in development that result in a novel behavioral shift that recurs across generations can facilitate new organism-environment relationships. These new relationships, which can include “invasion” of novel environments, can bring out latent possibilities for morphological or physiological change. Eventually, a change in gene frequencies may also occur as a result of geographically or behaviorally isolated breeding populations. Thus, changes in behavior can be the first step in creating new phenotypic variants on which natural selection can act (Gottlieb, 1992, 2002). In this view of evolutionary change, genetic change is often a secondary or tertiary consequence of enduring transgenerational behavioral changes brought about by alterations of normal or species-typical development. This scenario introduces a plurality of possible pathways to evolutionary change, complementing genetic factors such as mutation, recombination, and drift.

Shifts in behavior that are brought about by alterations in species-typical development can arise at different stages of the life cycle, but are most likely to occur during early development. This point was promoted by several developmental and evolutionary theorists over the last century (e.g., deBeer, 1940; Denenberg, 1964; Goldschmidt, 1940; Gottlieb, 1992; Johnston & Gottlieb, 1990; Kuo, 1967; Waddington, 1975), who despite their different backgrounds and emphases recognized the significance of embryonic and neonatal periods of development to the generation of phenotypic novelties. These early periods of development are a time of rapid morphological, physiological, and behavioral change, and modifications in experience during this time can initiate a host of physical and behavioral novelties, some of which can (given the availability of appropriate developmental conditions) persist across subsequent generations. An illustration of this scenario is the dramatic finding that modified early experience in one generation can predictably influence phenotypic outcomes in subsequent generations, even in the absence of the original experiential modification. Differences in physical (body weight, endocrine responses) and behavioral (fearfulness) measures have consistently been observed between groups of rats whose mothers (Denenberg & Whimby, 1963; Francis, Diorio, Liu, & Meany, 1999; Whimbey & Denenberg, 1967) or grandmothers (Denenberg & Rosenberg, 1967) were handled or not handled as infants. Despite its obvious importance to both developmental and evolutionary concerns, these types of transgenerational effects on both physiological responsiveness (in particu-

lar, the development of the hypothalamic adrenocortical system) and behavioral responsiveness (including curiosity, novelty seeking, and emotional regulation) remains poorly understood. Comparative psychology has much to contribute in this area, particularly to exploring how previous developmental outcomes and current experiences in specific contexts combine to influence these transgenerational processes (see Honeycutt, 2006; Garipey, Rodriguiz, & Jones, 2002; Lickliter & Ness, 1990, for examples and discussion).

### **A Developmental View of Species-Typical Behavior**

In this light, comparative research with birds and mammals has provided several examples of how normally occurring experience, particularly prenatal experience, can play an essential role in the development and maintenance of species-typical perception and behavior (i.e., Fifer & Moon, 1995; Gottlieb, 1997; Lickliter, 2005; Pedersen & Blass, 1982; Ronca & Alberts, 1994; Smotherman & Robinson, 1990). The term “species-typical” is used here to refer to those behaviors commonly observed across members of a population. It thus refers to the behavioral phenotypes that are reliably found across individuals and across generations, but does not imply notions of innate, instinctive, or “hard-wired” behavior (see Schneirla, 1956). The perspective that features of species-typical behavior could be a consequence of experience that occurred prenatally was raised by Zing-Yang Kuo (1921) early in the last century and several comparative and developmental theorists subsequently elaborated on and provided empirical support for this idea, including Lehrman (1953, 1970), Schneirla (1956, 1965), Gottlieb (1968, 1971a), and Miller (1988, 1997), among others.

From this framework, species-typical behavioral development is understood as an historical and contingent process, the result of specific, reliable, and repeatable transactions and relationships that take place within and between complex levels of integration both inside and outside the developing organism (Gottlieb, 1991; Lickliter, 2000; Oyama, 1985). Species-typical behavioral phenotypes are thus generated during individual ontogeny due to particular aspects of the temporal and spatial arrangements of organisms and their contexts reliably occurring at times when the organism is in particular developmental states, having had a particular developmental past (see Oyama, 1985, 1993, for further discussion). This thoroughly historical and contingent view of species-typical behavior represents a radically different view from that assumed by traditional notions of innate, instinctive, or other internally determined characterizations of the regularities of species-typical behavior. From a developmental perspective, behavioral phenotypes are generated, constrained, maintained, and reorganized through the activities of an historical organism engaged with its surround.

The reliable and repeatable features of stimulation and experience occurring in an organism’s surround (its *developmental ecology*) have been termed the “ontogenetic niche” by West and King (1987), defined as the set of ecological and social circumstances inherited by members of a species. This ontogenetic niche is available both prenatally and postnatally and provides diverse but dependable resources and influences for the developing organism. These extragenetic factors are part of each organism’s inheritance, and each ontogenetic cycle depends on the

availability of a set of these developmental resources, reconstructed in each generation (Avital & Jablonka, 2000; Oyama, 1985; Weber & Depew, 2001).

The recurrence from generation to generation of the specific resources and interactions that make up a given organism's ontogenetic niche serves as a primary basis for the development and maintenance of its species-typical behavior (see Haraway & Maples, 1998; Kaufman, 1975; Miller, 1997; West, King, & White, 2003, for similar views). In addition, significant alterations or modifications in the normally available resources and interactions of an organism's ontogenetic niche are likewise a primary basis for the generation of *novel* behaviors. Behavioral changes brought on by alterations in normal prenatal and postnatal rearing environments can lead to new organism-environment relationships, including changes in diet, habitat use, or reproductive behaviors (including parenting). These behavioral shifts can be maintained across generations if such changes or alterations in the developmental rearing environment persist, allowing for a cascade of possible changes in morphology and physiology. For example, the phenotypic consequences of invading "novel" environments have been studied experimentally in fruit flies (*Drosophila*) by rearing them in darkness for some 800 generations (Mori, 1986). Numerous changes in behavior (phototaxis, daily emergence rhythms, olfaction) and morphology (the structure of compound eyes, length of head bristles) were observed in the dark-reared flies as compared to controls, highlighting the complex relationship between changes in behavior and morphology and suggesting an important but poorly understood pathway for generating evolutionary change, including speciation.

### **Significance of Early Development in the Induction of Novel Phenotypes**

In keeping with the long-standing links between embryology and evolutionary biology (i.e., deBeer, 1940; Driesch, 1908; Harrison, 1937; Waddington, 1941), we see the study of early development, particularly prenatal development, as of fundamental importance to research in this area. However, despite over a century of behavioral embryology documenting the motor behavior of the early embryo and fetus as well as the ability of the embryo or fetus to detect and respond to sensory stimuli (see Hamburger, 1963; Kuo, 1967; Gottlieb, 1973; Oppenheim, 1982, for overviews), relatively little is known regarding the specific nature of the sensory stimuli typically available *in ovo* or *in utero* or its particular effects on the emergence, maintenance, and transformation of physiological and behavioral organization during early development (but see Gottlieb, 1971a, 1997; Lickliter, 1993; Rogers, 1995; Ronca & Alberts, 1995; Smotherman & Robinson, 1986; Vince, 1973, for examples from birds and mammals). Although there is widespread appreciation that the prenatal and early postnatal environment of avian and mammalian species is rich in tactile, vestibular, chemical and auditory sensory stimulation (Freeman & Vince, 1974; Smotherman & Robinson, 1986) and that sensory systems capable of responding to some or all of these inputs are already developed and functional before birth or hatching (Alberts, 1984; Bradley & Mistretta, 1975; Gottlieb, 1971b; Lecanuet & Schaal, 1996), the specific details of how the sensory capabilities of the young organism and the stimulative features of its prenatal and early postnatal rearing environment coact to influence the emergence

of such basic processes as selective attention, perception, learning, or memory have received relatively little systematic research attention. These basic processes are a primary source of behavioral plasticity and novelty during early development and likely contribute to the kinds of shifts in behavior that can lead to enduring transgenerational phenotypic change.

As discussed in more detail below, findings from the study of birds and mammals have demonstrated that the features of available prenatal and early post-natal sensory stimulation (such as amount, intensity, or the timing of presentation, and the sources of stimulation) coact with specific organismic characteristics (such as the stage of organization of the sensory systems, previous history with the given properties of stimulation, and the current state of arousal of the young organism) to contribute to the developmental course of emerging capacities for species-typical perceptual preferences, learning, and memory (Lickliter, 1995, 2005; Spear, 1984; Spear & McKenzie, 1994). Changes in these basic processes can set up a trajectory of experiential events that can result in modifications to typical patterns of species identification, habitat selection, diet preference, and other key aspects of the organism-environment system. Such phenotypic variations provide the opportunity for natural selection to filter out those novelties that are less successful and promote those that provide some reproductive advantage. Simply put, individual ontogenies are the source of variation necessary for evolutionary change.

### **Learning, Development, and Evolution**

In this light, learning capacities and the behaviors they generate are an obvious and effective means of adjusting and modifying the functional fit between developing organisms and their changing physical and social environments. Learning is a type of developmental plasticity and as such plays a critical role in both developmental and evolutionary processes (see Avital & Jablonka, 2000; Schneider, 2003; Shettleworth, 1998, for further discussion). This conclusion applies across the basic categories of learning. An associative learning example is “upside down” flamingo feeding, an operant behavior that presumably developed through enhanced foraging opportunities and was followed by structural modification of the bird’s bill (Gould, 1985; Wcislo, 1989). Similarly, Johnston and Gottlieb’s (1990) example of a diet change from soft vegetation to harder seeds in rodents, described earlier, highlights the link between learning, behavioral plasticity, and morphological change.

Operant learning enables successful foraging in many young vertebrates. The neonatal and juvenile periods are of special interest because these skills are so critical to growth and survival. As far back as 1913, Shepard and Breed reported that newly hatched chicks would peck at grain without any apparent learning; however, the development of accurate pecking appeared to follow operant learning principles (see also Balsam, Graf, & Silver, 1992; Cruze, 1935). More recently, researchers have demonstrated how young vertebrates learn from consequences and associated antecedent stimuli to avoid noxious foods and detect palatable prey (e.g., Kono, Reid, & Kamil, 1998). Examples of learning-dependent feeding and hunting have also been reported in invertebrates (Papaj & Prokopy, 1989; Papini & Bitterman, 1991; Wilcox & Jackson, 1998) and highlight the importance of asso-

ciative learning to the successful utilization of locally available ecological resources (as well as the possible exploitation of new niches or habitats). For example, it is now recognized that social learning based on observation applies to the acquisition of foraging skill in several invertebrate species, most notably the social insects (Hammer & Menzel, 1995). A concern with how such learning skills coact with changes in species-typical rearing experience has a long tradition in comparative psychology (see Kuo, 1967; Mason & Lott, 1976).

In regards to non-associative learning, Gottlieb (1993) has shown that by manipulating the available sensory stimulation available to mallard ducklings immediately following hatching, he could affect both their overall arousal levels and their malleability to learn non-conspecific maternal calls (a chicken maternal call). He found that ducklings' malleability to learn to prefer the chicken maternal call over their own species-specific mallard maternal call was significantly affected by the presence or absence of tactile stimulation. Mallard ducklings denied tactile stimulation from broodmates following hatching (a normally reliable aspect of their postnatal environment) did not learn to prefer the chicken maternal call over the mallard maternal call, whereas ducklings allowed normal levels of postnatal tactile experience strongly preferred the chicken call over the mallard maternal call following extended auditory exposure. These outcomes appeared to be determined by the ducklings' level of arousal during exposure to the chicken call. Ducklings denied normal postnatal tactile experience demonstrated higher levels of behavioral arousal (as indexed by distress vocalizations and time spent awake) than did ducklings not deprived of tactile contact. Birds not permitted tactile contact slept less and were highly aroused before, during, and after playbacks of the chicken call. In contrast, socially reared ducklings slept more and were less aroused than the isolates, suggesting elevated arousal interfered with the usual (normal) degree of malleability following hatching. In sum, ducklings that experienced normal levels of tactile contact with siblings were highly malleable, whereas those deprived of tactile contact were not.

Lickliter and Lewkowicz (1995) likewise showed the importance of prenatal tactile and vestibular stimulation from broodmates to the successful emergence of species-typical perceptual responsiveness to maternal cues in bobwhite quail chicks. In this study, quail embryos incubated in physical isolation from other eggs in their clutch (but allowed normal auditory experience) during the late stages of prenatal development failed to show typical patterns of postnatal responsiveness to both maternal auditory and visual stimulation seen in communally incubated embryos. In addition, embryos denied normal levels of tactile and vestibular stimulation from broodmates failed to demonstrate prenatal auditory learning of an individual bobwhite maternal call, a behavior reliably seen in communally incubated embryos.

These differences in perceptual and behavioral malleability across groups of ducklings or quail receiving different amounts of tactile contact from siblings suggest that the normally occurring prenatal and early postnatal rearing environment provides the embryo and hatchling with a suitable range and timing of sensory stimulation, thereby supporting an effective level of arousal and attention for species-typical perceptual learning and development (see Radell & Gottlieb, 1992, for further discussion). Deviations above or below this window of stimulation can

modify the embryo or neonate's arousal level and negatively affect the ability to attend and process the available sensory information present in the young organism's immediate rearing environment. What fosters malleability (in this case, the presence of siblings and the effects of their stimulation on the young organism's arousal levels) are the simultaneous coactions of internal and external parameters associated with the normal rearing environment. In other words, the structure of the organism and the structure of its developmental ecology together form a relationship of mutual influence on the developmental resources readily available to support the emergence, maintenance, and transformation of early behavior. This normally available and replicable system of resources and constraints provides a reliable order and organization (and under unusual conditions a range of variation) in the developmental ecology of embryos and neonates, helping to explain both the generation of normal, species-typical behavior *and* the generation of novel behavior within members of a given population (see West, King, & Freeberg, 1994, for a similar argument).

### **Sources of Phenotypic Plasticity**

Of particular importance to our concern with the links between development and evolution is the fact that such variability across individuals (the grist for the mill of natural selection) can be generated by genetic *and* nongenetic means. These means are varied, including random mutation, drift and other well recognized genetic processes; they also include less well studied extragenetic processes, such as maternal cytoplasmic constituents, mRNA, and chromatin-modifying enzymes (chromatin is the protein-DNA complex involved in fitting the genome into the cell nucleus), all known to influence changes by which the fertilized egg cell transforms into a complex organism during embryonic development and in later life allows cells to respond to hormones, growth factors, and other regulatory molecules (Jablonka & Lamb, 1998). In mammals, where the embryo develops within the body of the female, such epigenetic factors also include maternal uterine effects (Vom Saal & Dhar, 1992).

For example, several studies have demonstrated that when a female rodent embryo develops in a uterine environment in which most adjoining embryos are male, their prenatal exposure to the relatively high level of testosterone produced by their male siblings results in later maturation and the display of more aggressive and territorial behavior as adults than that displayed by other females (Clark & Galef, 1995; Clark, Karpiuk, & Galef, 1993). These testosterone-exposed females themselves go on to produce litters in which the proportion of male offspring is greater than the normal 1:1 sex ratio, and as a result their daughters also develop in a testosterone rich uterine environment, again demonstrating how extragenetic factors are at play in the transgenerational expression of behavioral phenotypes (see Jablonka, 2001; Gottlieb, 1998; West et al., 1994, for other examples of nongenetic phenotypic transmission). Contrary to the gene-centered view of evolution promoted by the neo-Darwinian synthesis of the last century, changes in extragenetic factors can also lead to significant and enduring changes in phenotypic development. Such alterations in development can result in variations in morphol-

ogy, physiology, or behavior within a population, providing the engine for generating evolutionary change.

Although such phenotypic plasticity was historically considered to be genetically determined (e.g., Mayr, 1942; Via & Lande, 1985), in recent years a growing number of developmental and evolutionary biologists have emphasized the necessity of considering the complex interactions between genetics, development, and ecology in order to understand the range of morphological structures, shifts in behavioral repertoires, and other instances of phenotypic plasticity seen across plants and animals (e.g., Duffy, Clobert, & Moller, 2002; Gilbert, 2001; Nijhout, 2003; Schlichting & Pigliucci, 1998). That being said, many continue to frame the concept of phenotypic plasticity only in terms of the potential “responses” of a genome to different environmental conditions. For example, West-Eberhard (1989, p. 249) argues that “phenotypic plasticity is the ability of a single genotype to produce more than one alternative form of morphology, physiological state, and/or behavior in response to environmental conditions”. Pigliucci (2001, p. 1) defines phenotypic plasticity as “the property of a given genotype to produce different phenotypes in response to distinct environmental conditions.” Scheiner (1993, p. 35) proposes “phenotypic plasticity is the change in the expressed phenotype of a genotype as a function of the environment.” These definitions all serve to illustrate an implicit assumption still common in discussions of the link between development and evolution, namely that although genetic effects can be modified by epigenetic interactions or environmental conditions, these “modifiers” are not on equal causal footing with genetic factors (see Hall, 2003, for a well developed example).

Nearly all contemporary developmental and evolutionary biologists acknowledge the importance of both genetic and environmental factors to understanding phenotypic development; however, most versions of this “interactionism” continue to embrace a causal framework comprised of components representing nature (genes) and those that represent nurture (all else). In this framework, genes continue to be characterized by many as playing the primary or determinative role in the form and nature of phenotypic characteristics and non-genetic or environmental factors are typically delegated to the role of activating or triggering the various developmental instructions presumed to be encoded in the organism’s genome (see Crawford & Krebs, 1998; Rosenberg, 1997; Smith-Gill, 1983, for examples). As a result, many continue to view the environment as essentially supportive or disruptive to normal or species-typical outcomes and therefore less than equal partners with genetic factors involved in phenotypic development.

Genes are clearly critical to all development. However, the passing on of a genome cannot serve as a sufficient explanation for the achievement of any phenotypic outcome, although it is certainly a necessary one (Moore, 2002; Morange, 2001). Genetic and non-genetic factors constitute a dynamic system within which these components coact to construct traits and characters. Thus, it is not biologically meaningful to discuss gene activity and its influences without also referring to the molecular, cellular, organismal, and environmental context within which genes are activated and expressed (see Coen, 1999; Wahlsten & Gottlieb, 1997; Wolf, 1995, for further discussion). As argued in detail elsewhere (Lickliter & Honeycutt, 2003), a dynamic and contingent approach to phenotypic development

undermines the notions that (a) genes can determine the production of phenotypes and (b) that genetic and environmental influences on development can be effectively separated or partitioned. Simply put, genetic and environmental factors are not separable developmentally (see Johnston & Edwards, 2002). As pointed by West et al. (1994) in their work on cowbird song development, it is the correlated nature of genetic *and* environmental inheritance that must be more fully explored to provide a developmental perspective on how both phenotypic stability and plasticity are generated in response to the internal and external conditions encountered by the developing organism.

### **Conclusions and a Look to the Future**

Several decades of findings from comparative psychology (and the related field of developmental psychobiology; see Michel & Moore, 1995) add to the growing evidence from the biological sciences that changes or variations in phenotypic traits arise through the modification of developmental processes. Individual ontogenies are the source of variation necessary for evolutionary change and how we understand evolution will depend, at least in large part, on how we understand development (Gottlieb, 2002; Oyama et al., 2001; Robert, 2004). This hard won insight suggests several key roles for how comparative psychology can contribute to evolutionary studies in the 21<sup>st</sup> century.

First, comparative psychologists can continue to provide systematic investigation of the developmental and ecological dynamics contributing to behavioral plasticity or malleability. This focus is exemplified by several decades of research on the various neural, hormonal, and behavioral consequences of early rearing experiences. Starting with the pioneering work of Hymovitch (1952), Levine (1956), and Cooper and Zubek (1958), a large body of research from comparative psychology and developmental psychobiology has explored the influence of early experiential alterations on later exploratory behavior and problem-solving abilities (see Renner & Rosenzweig, 1987, for a review). Expanding on this research tradition is critical to a fuller understanding of the mechanisms responsible for shifts in behavior and psychological functioning due to changes in species-typical environments, resulting in changes in the activity of the organism and leading to potential variations within and across generations in anatomy, morphology, or physiology (see Garipey et al., 2002, for a recent example). The observed behavioral changes reported in enriched rearing and early handling experiments (i.e., enhanced exploratory behavior, increased problem-solving abilities, resistance to stress) are the types of behaviors that could support the seeking out and utilization of new habitats, leading to a host of other potential phenotypic novelties and setting the stage for possible evolutionary change. In this light, Gottlieb (1997) points out that animals that have had considerable variation in social and physical experiences early in life are more likely to seek out variation later in life (see also Neuringer, 2004), showing greater levels of exploratory behavior and novelty seeking than animals having more limited early experience. This sort of behavioral plasticity can increase the likelihood of particular individuals utilizing or migrating to new habitats, where they could encounter different types of functional demands. Although many changes in functional demands would be transient, others could be long last-

ing and persist across generations, revealing latent morphological or physiological variability not expressed in the original environment. How these processes work and the underlying biology involved remains poorly understood, and comparative psychology can provide a developmental and ecological perspective to the ways and means of such transgenerational processes and their effects. This approach stresses the organism-environment system as the primary unit of developmental analysis (see Wagman & Miller, 2003) and expands the scope of traditional evolutionary inquiry to include inherited environmental effects (Jablonka, 2001; Ros-siter, 1996).

Another related task for comparative psychology is to provide more detailed empirical evidence for the role of behavior as a leading edge in the evolutionary process. Changes in behavior brought about by changes in prenatal and postnatal rearing environments have been well documented in comparative psychology (e.g., Kuo, 1967; Lickliter, 2005; Michel & Moore, 1995; Renner & Rosenzweig, 1987) but how such changes are significant to evolutionary issues has received little empirical or conceptual attention (but see Johnston & Gottlieb, 1990; Gottlieb, 1992, 2002). Experimental demonstrations of how novel behavioral phenotypes lead to genetic, morphological, or physiological alterations can help further explicate the specific biological and psychological mechanisms involved in the behavioral initiation of evolutionary change. This will require a multidimensional, process-oriented approach that includes a variety of levels of analysis beyond the behavioral, including the environmental regulation of gene expression and cellular function, the effects of sensory stimulation on neural and hormonal responsiveness, and the direct and indirect effects of a developing organism's biological, ecological, and social organization, to name but a few examples.

Such efforts can complement and extend work from evolutionary developmental biology and contribute to the larger project of reintegrating developmental and evolutionary theory in the 21<sup>st</sup> century. By explicitly not making a distinction between genetic and environmental sources of phenotypic traits, a comparative developmental approach provides a perspective that moves beyond outdated notions of genetically *or* environmentally determined phenotypic development. This more integrated developmental approach to evolution, now evident in some quarters within both the biological and psychological sciences, provides a valuable conceptual framework to address the complex task of incorporating what has been the "black box" of development into contemporary evolutionary theory.

## References

- Alberch, P. (1982). The generative and regulatory roles of development in evolution. In D. Mosakowski & G. Roth (Eds.), *Environmental adaptation and evolution* (pp. 19-36). Stuttgart, Germany: Fischer-Verlag.
- Alberts, J. R. (1984). Sensory-perceptual development in the Norway rat: A view towards comparative studies. In R. Kail & N. S. Spear (Eds.), *Comparative perspectives on memory development* (pp. 65-101). Hillsdale, NJ: Erlbaum.
- Arthur, W. (1997). *The origin of animal body plans: A study in evolutionary developmental biology*. Cambridge, UK: Cambridge University Press.
- Arthur, W. (2004). *Biased embryos and evolution*. Cambridge, UK: Cambridge University Press.

- Avital, E. & Jablonka, E. (2000). *Animal traditions: Behavioral inheritance in evolution*. Cambridge, UK: Cambridge University Press.
- Ayala, F. J., & Valentine, J. W. (1979). *Evolving: The theory and processes of organic evolution*. Menlo Park, CA: Benjamin/Cummings.
- Baldwin, J. M. (1896). A new factor in evolution. *American Naturalist*, **30**, 441-451.
- Balsam, P. D., Graf, J. S., & Silver, R. (1992). Operant and Pavlovian contributions to the ontogeny of pecking in ring doves. *Developmental Psychobiology*, **25**, 389-410.
- Bateson, P. P. G. (1988). The active role of behaviour in evolution. In M. W. Ho & S. Fox (Eds.), *Process and metaphors in evolution* (pp. 191-207). New York: Wiley.
- Bouvier, M., & Hylander, W. L. (1984). The effects of dietary consistency on gross and histologic morphology in the cranio-facial region of young rats. *American Journal of Anatomy*, **170**, 117-126.
- Bradley, R. M., & Mistretta, C. M. (1975). Fetal sensory receptors. *Physiological Reviews*, **55**, 352-382.
- Burian, R. M. (2000). General introduction to the symposium on evolutionary developmental biology: Paradigms, problems, and prospects. *American Zoologist*, **40**, 711-717.
- Clark, M. M., & Galef, B. G. (1995). Parental influence on reproductive life history strategies. *Trends in Ecology & Evolution*, **10**, 151-153.
- Clark, M. M., Karpuk, P., & Galef, B. G. (1993). Hormonally mediated inheritance of acquired characteristics in Mongolian gerbils. *Nature*, **364**, 712-716.
- Clayton, D. F. (2000). The genomic action potential. *Neurobiology of Learning & Memory*, **74**, 185-216.
- Coen, E. (1999). *The art of genes: How organisms make themselves*. Oxford, UK: Oxford University Press.
- Cooper, R. M., & Zubek, J. P. (1958). Effects of enriched and restricted early environments on the learning ability of maze bright and dull rats. *Canadian Journal of Psychology*, **12**, 159-164.
- Crawford, C., & Krebs, D. L. (1998). *Handbook of evolutionary psychology: Ideas, issues, and applications*. Hillsdale, NJ: Erlbaum.
- Cruze, W. W. (1935). Maturation and learning in chicks. *Journal of Comparative Psychology*, **19**, 371-409.
- Curtis, H., & Barnes, N. S. (1989). *Biology* (5<sup>th</sup> Ed.). New York: Worth Publishers.
- Davidson, E. H. (2001). *Genomic regulatory systems: Development and evolution*. New York: Academic Press.
- deBeer, G. (1940). *Embryos and ancestors*. Oxford, UK: Clarendon Press.
- Denenberg, V. H. (1964). Critical periods, stimulus input, and emotional reactivity: A theory of infantile stimulation. *Psychological Review*, **71**, 335-351.
- Denenberg, V. H., & Rosenberg, K. M. (1967). Nongenetic transmission of information. *Nature*, **216**, 549-550.
- Denenberg, V. H., & Whimbey, A. E. (1963). Behavior of adult rats is modified by the experiences their mothers had as infants. *Science*, **142**, 1192-1193.
- Dobzhansky, T. (1951). *Genetics and the origin of species* (3<sup>rd</sup> Ed.). New York: Columbia University Press.
- Driesch, H. (1908). *The science and philosophy of the organism*. London, UK: Black.
- Duffy, A. M., Clobert, J., & Moller, A. P. (2002). Hormones, developmental plasticity and adaptation. *Trends in Ecology & Evolution*, **17**, 190-196.
- Fifer, W. P., & Moon, C. (1995). The effects of fetal experience with sound. In J.P. Lecanuet, W. P. Fifer, N. A. Krasnegor, & W. P. Smotherman (Eds.), *Fetal development: A psychobiological perspective* (pp. 351-366). Hillsdale, NJ: Erlbaum.

- Francis, D., Diorio, J., Liu, D., & Meaney, M. J. (1999). Nongenomic transmission across generations of maternal behavior and stress responses in the rat. *Science*, **286**, 1155-1158.
- Freeman, B. M., & Vince, M. A. (1974). *Development of the avian embryo*. London: Chapman and Hall.
- Frost, H. M. (1973). *Bone remodeling and skeletal modeling errors*. Springfield, MA: Thomas.
- Gariepy, J. L., Rodriguiz, R. M., & Jones, B. C. (2002). Handling, genetic, and housing effects on the mouse stress system, dopamine function, and behavior. *Pharmacology, Biochemistry, & Behavior*, **73**, 7-17.
- Gerhart, J., & Kirschner, M. (1997). *Cells, embryos, and evolution*. Oxford, UK: Blackwell Scientific.
- Gilbert, S. F. (1994). Dobzhansky, Waddington, and Schmalhausen: Embryology and the modern synthesis. In M. B. Adams (Ed.), *The evolution of Theodosius Dobzhansky* (pp. 143-154). Princeton, NJ: Princeton University Press.
- Gilbert, S. F. (2000). *Developmental biology* (6<sup>th</sup> edition). Sunderland, MA: Sinauer.
- Gilbert, S. F. (2001). Ecological developmental biology: Developmental biology meets the real world. *Developmental Biology*, **233**, 1-12.
- Gilbert, S. F., Opitz, J. M., & Raff, R. A. (1996). Resynthesizing evolutionary and developmental biology. *Developmental Biology*, **173**, 357-372.
- Goldschmidt, R. (1940). *The material basis of evolution*. New Haven, CT: Yale University Press.
- Goodwin, B. (1994). *How the leopard changed its spots*. New York: Scribner.
- Gottlieb, G. (1968). Prenatal behavior of birds. *Quarterly Review of Biology*, **43**, 148-174.
- Gottlieb, G. (1971a). *Development of species identification in birds: An inquiry into the prenatal determinants of perception*. Chicago, IL: University of Chicago Press.
- Gottlieb, G. (1971b). Ontogenesis of sensory function in birds and mammals. In E. Tobach, L. Aronson, & E. Shaw (Eds.), *The biopsychology of development* (pp. 67-128). New York: Academic Press.
- Gottlieb, G. (1973). Introduction to behavioral embryology. In G. Gottlieb (Ed.), *Behavioral embryology* (pp. 3-45). New York: Academic Press.
- Gottlieb, G. (1987). The developmental basis of evolutionary change. *Journal of Comparative Psychology*, **101**, 262-271.
- Gottlieb, G. (1991). Experiential canalization of behavioral development: Theory. *Developmental Psychology*, **27**, 4-13.
- Gottlieb, G. (1992). *Individual development and evolution: The genesis of novel behavior*. New York: Oxford University Press.
- Gottlieb, G. (1993). Social induction of malleability in ducklings: Sensory basis and psychological mechanism. *Animal Behaviour*, **45**, 707-719.
- Gottlieb, G. (1997). *Synthesizing nature – nurture: Prenatal roots of instinctive behavior*. Mahwah, NJ: Erlbaum.
- Gottlieb, G. (1998). Normally occurring environmental and behavioral influences on gene activity: From central dogma to probabilistic epigenesis. *Psychological Review*, **105**, 792-802.
- Gottlieb, G. (2002). Developmental-behavioral initiation of evolutionary change. *Psychological Review*, **109**, 211-218.
- Gould, S. J. (1977). *Ontogeny and phylogeny*. Cambridge, MA: Harvard University Press.
- Gould, S. J. (1985). *The flamingo's smile*. New York: Norton.
- Greenberg, G. & Haraway, M. M. (1998). *Comparative psychology: A handbook*. New York: Garland Publishing.

- Griesemer, J. R. (1999). Reproduction and the reduction of genetics. In P. J. Beurton, R. Falk, & H. Rheinberger (Eds.), *The concept of the gene in development and evolution* (pp. 240-285). Cambridge, UK: Cambridge University Press.
- Hall, B. K. (1999). *Evolutionary developmental biology* (2<sup>nd</sup> Ed.). Boston: Kluwer.
- Hall, B. K. (2003). Unlocking the black box between genotype and phenotype: Cell condensations as morphogenetic (modular) units. *Biology and Philosophy*, **18**, 219-247.
- Hall, B. K. & Olson, W. M. (2003). *Keywords and concepts in evolutionary developmental biology*. Cambridge, MA: Harvard University Press.
- Hamburger, V. (1963). Some aspects of the embryology of behavior. *Quarterly Review of Biology*, **38**, 342-365.
- Hammer, M., & Menzel, R. (1995). Learning and memory in the honeybee. *Journal of Neuroscience*, **15**, 1617-1630.
- Haraway, M. M., & Maples, E. G. (1998). Species-typical behavior. In G. Greenberg & M. M. Haraway (Eds.), *Comparative psychology: A handbook* (pp. 191-197). New York: Garland Publishing.
- Hardy, A. C. (1965). *The living stream*. London: Collins.
- Harrison, R. (1937). Embryology and its relations. *Science*, **85**, 369-374.
- Honeycutt, H. (2006). Studying evolution in action: Foundations for a transgenerational comparative psychology. *International Journal of Comparative Psychology*, **19**, 170-184.
- Hughes, P., & Dragunow, M. (1995). Induction of immediate-early genes and the control of neurotransmitter-regulated gene expression within the nervous system. *Pharmacological Review*, **47**, 133-178.
- Hymovitch, B. (1952). The effects of experimental variations on problem solving in the rat. *Journal of Comparative and Physiological Psychology*, **45**, 313-321.
- Jablonka, E. (2001). The systems of inheritance. In S. Oyama, P. E. Griffiths, & R. D. Gray (Eds.), *Cycles of contingency: Developmental systems and evolution* (pp. 99-116). Cambridge, MA: MIT Press.
- Jablonka, E., & Lamb, M. J. (1995). *Epigenetic inheritance and evolution*. New York: Oxford University Press.
- Jablonka, E., & Lamb, M. J. (1998). Epigenetic inheritance in evolution. *Journal of Evolutionary Biology*, **11**, 159-183.
- Johnston, T. D., & Edwards, L. (2002). Genes, interactions, and development. *Psychological Review*, **109**, 26-34.
- Johnston, T. D., & Gottlieb, G. (1990). Neophenogenesis: A developmental theory of phenotypic evolution. *Journal of Theoretical Biology*, **147**, 471-495.
- Kaufman, I. C. (1975). Learning what comes naturally: The role of life experience in the establishment of species-typical behavior. *Ethos*, **3**, 129-142.
- Kono, H., Reid, P. J., and Kamil, A. C. (1998). The effect of background cuing on prey detection. *Animal Behaviour*, **56**, 963-972.
- Kuo, Z.-Y. (1921). Giving up instincts in psychology. *Journal of Philosophy*, **18**, 645-664.
- Kuo, Z.-Y. (1967). *The dynamics of behavior development: An epigenetic view*. New York: Random House.
- Lecanuet, J. P., & Schaal, B. (1996). Fetal sensory competencies. *European Journal of Obstetrics, Gynecology and Reproductive Biology*, **68**, 1-23.
- Lehrman, D. S. (1953). A critique of Konrad Lorenz's theory of instinctive behavior. *Quarterly Review of Biology*, **28**, 337-363.
- Lehrman, D. S. (1970). Semantic and conceptual issues in the nature-nurture problem. In L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), *Development and evolution of behavior: Essays in memory of T. C. Schneirla* (pp. 17-52). San Francisco, CA: Freeman.

- Levine, S. (1956). A further test of infantile handling and adult avoidance learning. *Journal of Personality*, **25**, 70-80.
- Lickliter, R. (1993). Timing and the development of perinatal perceptual organization. In G. Turkewitz & D. A. Devenny (Eds.), *Developmental time and timing* (pp. 105-123). Hillsdale, NJ: Erlbaum.
- Lickliter, R. (1995). Embryonic sensory experience and intersensory development in precocial birds. In J. P. Lecanuet, W. P. Fifer, N. A. Krasnegor, & W. P. Smotherman (Eds.), *Fetal development: A psychobiological perspective* (pp. 281-294). Hillsdale, NJ: Erlbaum.
- Lickliter, R. (2000). An ecological approach to behavioral development: Insights from comparative psychology. *Ecological Psychology*, **12**, 319-334.
- Lickliter, R. (2004). The aims and accomplishments of comparative psychology. *Developmental Psychobiology*, **44**, 26-30.
- Lickliter, R. (2005). Prenatal sensory ecology and experience: Implications for perceptual and behavioral development in precocial birds. *Advances in the Study of Behavior*, **35**, 235-274.
- Lickliter, R. & Honeycutt, H. (2003). Developmental dynamics: Towards a biologically plausible evolutionary psychology. *Psychological Bulletin*, **129**, 819-835.
- Lickliter, R., & Lewkowicz, D.J. (1995). Intersensory experience and early perceptual development: Attenuated prenatal sensory stimulation affects postnatal auditory and visual responsiveness in bobwhite quail chicks. *Developmental Psychology*, **31**, 609-618.
- Lickliter, R., & Ness, J. W. (1990). Domestication and comparative psychology: Status and strategy. *Journal of Comparative Psychology*, **104**, 211-218.
- Lloyd Morgan, C. (1896). Of modification and variation. *Science*, **4**, 733-739.
- Mason, W. A., & Lott, D. F. (1976). Ethology and comparative psychology. *Annual Review of Psychology*, **27**, 129-154.
- Maynard Smith, J. (2000). The concept of information in biology. *Philosophy of Science*, **67**, 177-194.
- Mayr, E. (1942). *Systematics and the origins of species*. New York: Columbia University Press.
- Mayr, E. (1982). *The growth of biological thought*. Cambridge, MA: Harvard University Press.
- Mayr, E. (1997). *This is biology: The science of the living world*. Cambridge, MA: Harvard University Press.
- Michel, G. & Moore, C. (1995). *Developmental psychobiology: An integrative science*. Cambridge, MA: MIT Press.
- Miller, D. B. (1988). Development of instinctive behavior: An epigenetic and ecological approach. In E. M. Blass (Ed.), *Handbook of behavioral neurobiology*, Vol. 9, *Developmental psychobiology and behavioral ecology* (pp. 415-444). New York: Plenum Press.
- Miller, D. B. (1997). The effects of nonobvious forms of experience on the development of instinctive behavior. In C. Dent-Reed & P. Zukow-Goldring (Eds.), *Evolving explanations of development* (pp. 457-507). Washington, DC: American Psychological Association.
- Moore, D. S. (2002). *The dependent gene: The fallacy of nature vs. nurture*. New York: W. H. Freeman.
- Morange, M. (2001). *The misunderstood gene*. Cambridge, MA: Harvard University Press.
- Mori, S. (1986). Changes of characters of *Drosophila melanogaster* brought about during the life in constant darkness and considerations on the processes through which these changes were induced. *Zoological Science*, **3**, 945-957.

- Neuringer, A. (2004). Reinforced variability in animals and people: Implications for adaptive action. *American Psychologist*, **59**, 891-906.
- Newman, S. A., & Muller, G. B. (2000). Epigenetic mechanisms of character origination. *Journal of Experimental Zoology*, **288**, 304-317.
- Nijhout, H. F. (2003). Development and evolution of adaptive polyphenisms. *Evolution & Development*, **5**, 9-18.
- Oppenheim, R. W. (1982). The neuroembryological study of behavior: Progress, problems, perspectives. *Current Topics in Developmental Biology*, **17**, 257-309.
- Oyama, S. (1985). *The ontogeny of information*. Cambridge, UK: Cambridge University Press.
- Oyama, S. (1993). Constraints and development. *Netherlands Journal of Zoology*, **43**, 6-16.
- Oyama, S., Griffiths, P. E., & Gray, R. D. (2001). *Cycles of contingency: Developmental systems and evolution*. Cambridge, MA: MIT Press.
- Papaj, D. R., & Prokopy, R. J. (1989). Ecological and evolutionary aspects of learning in phytophagous insects. *Annual Review of Entomology*, **34**, 315-350.
- Papini, M. R., & Bitterman, M. E. (1991). Appetitive conditioning in *Octopus cyanea*. *Journal of Comparative Psychology*, **105**, 107-114.
- Pedersen, P. E., & Blass, E. M. (1982). Prenatal and postnatal determinants of the first suckling episode in albino rats. *Developmental Psychobiology*, **15**, 349-355.
- Pigliucci, M. (2001). *Phenotypic plasticity: Beyond nature and nurture*. Baltimore, MD: The Johns Hopkins University Press.
- Plotkin, H. C. (1988). *The role of behavior in evolution*. Cambridge, MA: MIT Press.
- Radell, P., & Gottlieb, G. (1992). Developmental intersensory interference: Augmented prenatal sensory experience interferes with auditory learning in duck embryos. *Developmental Psychology*, **28**, 795-803.
- Raff, R. A. (2000). Evo-devo: The evolution of a new discipline. *Nature Reviews: Genetics*, **1**, 74-79.
- Renner, M. J., & Rosenzweig, M. R. (1987). *Enriched and impoverished environments*. New York: Springer.
- Robert, J. S. (2004). *Embryology, epigenesis, and evolution: Taking development seriously*. New York: Oxford University Press.
- Rogers, L. J. (1995). *The development of brain and behaviour in the chicken*. Wallingford, UK: CAB International.
- Ronca, A. E., & Alberts, J. R. (1994). Sensory stimuli associated with gestation and parturition evoke cardiac and behavioral responses in fetal rats. *Psychobiology*, **55**, 270-282.
- Ronca, A. E., & Alberts, J. R. (1995). Maternal contributions to fetal experience and the transition from prenatal to postnatal life. In J. P. Lecanuet, W. P. Fifer, N. A. Krasnegor, & W. P. Smotherman (Eds.), *Fetal development: A psychological perspective* (pp. 331-350). Hillsdale, NJ: Erlbaum.
- Rosenberg, A. (1997). Reductionism redux: Computing the embryo. *Biology and Philosophy*, **12**, 445-470.
- Rossiter, M. C. (1996). Incidence and consequences of inherited environmental effects. *Annual Review of Ecology and Systematics*, **27**, 451-476.
- Scheiner, S. M. (1993). Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology & Systematics*, **24**, 35-68.
- Schlichting, C. D., & Pigliucci, M. (1998). *Phenotypic evolution: A reaction norm perspective*. Sunderland, MA: Sinauer.
- Schmalhausen, I. I. (1949). *Factors of evolution*. Philadelphia, PA: Blakiston.
- Schneider, S. M. (2003). Evolution, behavior principles, and developmental systems: A review of Gottlieb's Synthesizing nature-nurture: Prenatal roots of instinctive behavior. *Journal of the Experimental Analysis of Behavior*, **79**, 137-152.

- Schneirla, T. C. (1956). Interrelationships of the “innate” and “acquired” in instinctive behavior. In P. P. Grasse (Ed.), *L'Instinct dans le comportement des animaux et de l'homme* (pp. 387-452). Paris, France: Masson.
- Schneirla, T. C. (1965). Aspects of stimulation and organization in approach/withdrawal processes underlying vertebrate behavioral development. *Advances in the Study of Behavior*, **1**, 1-71.
- Shepard, J. F., & Breed, F. S. (1913). Maturation and use in the development of an instinct. *Journal of Animal Behavior*, **3**, 274-285.
- Shettleworth, S. J. (1998). *Cognition, evolution, and behavior*. Oxford, UK: Oxford University Press.
- Smith-Gill, S. J. (1983). Developmental plasticity: developmental conversion versus phenotypic modulation. *American Zoologist*, **23**, 47-55.
- Smotherman, W. P., & Robinson, S. R. (1986). Environmental determinants of behaviour in the rat fetus. *Animal Behaviour*, **34**, 1859-1873.
- Smotherman, W. P., & Robinson, S. R. (1990). The prenatal origins of behavioral organization. *Psychological Science*, **1**, 97-106.
- Sole, R., & Goodwin, B. (2000). *Signs of life: How complexity pervades biology*. New York: Basic Books.
- Spear, N. E. (1984). Ecologically determined dispositions control the ontogeny of learning and memory. In R. Kail & N. E. Spear (Eds.), *Comparative perspectives on the development of memory* (pp. 325-358). Hillsdale, NJ: Erlbaum.
- Spear, N. E., & McKinzie, D. L. (1994). Intersensory integration in the infant rat. In D. J. Lewkowicz & R. Lickliter (Eds.), *The development of intersensory perception: Comparative perspectives* (pp. 133-161). Hillsdale, NJ: Erlbaum.
- Tischmeyer, W., & Grimm, R. (1999). Activation of immediate early genes and memory formation. *Cellular and Molecular Life Sciences*, **55**, 564-574.
- Via, S., & Lande, R. (1985). Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution*, **39**, 505-522.
- Vince, M. A. (1973). Some environmental effects on the activity and development of the avian embryo. In G. Gottlieb (Ed.), *Behavioral embryology* (pp. 285-323). New York: Academic Press.
- Vom Saal, F. S., & Dhar, M. G. (1992). Blood flow in the uterine loop artery and loop vein is bidirectional in the mouse: implications for transport of steroids between fetuses. *Physiology and Behavior*, **52**, 163-171.
- Waddington, C. H. (1941). The evolution of developmental systems. *Nature*, **147**, 108-109.
- Waddington, C. H. (1975). *The evolution of an evolutionist*. Edinburgh, UK: Edinburgh University Press.
- Wagman, J. B., & Miller, D. B. (2003). Nested reciprocities: The organism-environment system in perception-action and development. *Developmental Psychobiology*, **42**, 317-334.
- Wahlsten, D., & Gottlieb, G. (1997). The invalid separation of the effects of nature and nurture: Lessons from animal experimentation. In R. J. Sternberg & E. Grigorenko (Eds.), *Intelligence, heredity, and environment* (pp. 163-192). New York: Cambridge University Press.
- Wcislo, W. T. (1989). Behavioral environments and evolutionary change. *Annual Review of Ecology & Systematics*, **20**, 137-169.
- Weber, B. H., & Depew, D. J. (2001). Developmental systems, Darwinian evolution, and the unity of science. In S. Oyama, P. E. Griffiths, & R. D. Gray (Eds.), *Cycles of contingency: Developmental systems and evolution* (pp. 239-253). Cambridge, MA: MIT Press.
- West, M. J., & King, A. P. (1987). Settling nature and nurture into an ontogenetic niche. *Developmental Psychobiology*, **20**, 549-562.

- West, M. J., King, A. P., & Freeberg, T. M. (1994). The nature and nurture of neophenotypes: A case history. In L. A. Real (Ed.), *Behavioral mechanisms in evolutionary ecology* (pp. 238-257). Chicago, IL: University of Chicago Press.
- West, M. J., King, A. P., & White, D. J. (2003). The case for developmental ecology. *Animal Behaviour*, **66**, 617-622.
- West-Eberhard, M. J. (1989). Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology & Systematics*, **20**, 249-278.
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. New York: Oxford University Press.
- Whimbey, A. E., & Denenberg, V. H. (1967). Experimental programming of life histories: The factor structure underlying experimentally created individual differences. *Behaviour*, **29**, 296-314.
- Whyte, L. L. (1965). *Internal factors in evolution*. London, UK: Tavistock Publications.
- Wilcox, R. S., & Jackson, R. R. (1998). Cognitive abilities in Araneophagic jumping spiders. In R. P. Balda, I. M. Pepperberg, & A. C. Kamil (Eds.), *Animal cognition in nature: The convergence of psychology and biology in laboratory and field* (pp. 411-434). San Diego, CA: Academic Press.
- Wolf, U. (1995). The genetic contribution to the phenotype. *Human Genetics*, **95**, 127-148.
- Wyles, J. S., Kunkel, J. G., & Wilson, A. C. (1983). Birds, behavior, and anatomical evolution. *Proceedings of the National Academy of Sciences, USA*, **80**, 4394-4397.

*Received February 1, 2005.*

*Revision received May 10, 2005.*

*Accepted May 12, 2005.*