A model for understanding the evolution of mammalian behavior

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A MODEL FOR UNDERSTANDING THE EVOLUTION OF MAMMALIAN BEHAVIOR

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Abstract
Unlike reptiles, who are born with species-specific morphology and behavior that hardly changes as they grow into adults, mammals are born with a class-specific neonatal phase that renders the morphology and behavior of each species different from the physiology and behavior of their species-specific adulthood. Mammals must undergo a transformation phase, called youth, between the neonate and the adult. This youthful metamorphic and meta-behavioral phase is necessary while the mammal is remodeling from sucking milk to munching grass or hunting meat. During its youthful phase a mammal is not simply growing linearly into its adult form and behavior but is a hybrid trying out different patterns of neonatal and adult micro-motor pieces of behavior that change almost daily in frequency as pieces of neonatal behavior inactivate and adult behavioral motor pieces begin to activate. The offsets of neonatal behavior and the onsets of species-specific adult behavior drive the youthful mammals into varied combinations of behavior sequences, that, since they are hybrids of two very different systems, don't look functional and are often unusual enough to amuse an observer. Such random hybrid combinations of micromotor pieces of behavior are commonly called play. But, then, play is not a unitary drive as many researchers have assumed but the consequence of youths hybridizing between neonatal and adult behaviors that are waning and waxing in intensity and frequency at each successive stage of youthful ontogeny. During the youthful period, any random combination of motor sequences that are useful for any reason can be remembered, repeated, and learned, so the youthful phase of mammalian ontogeny has potential for learning. A fixed neonatal system of physiological adaptations and complex behaviors is built into the neonate and might be modified for the worse by learning at this stage of its ontogeny. At a mammal's species-specific adult stage it is presumably well adapted to a stable niche. So, again, at this phase of ontogeny learning might be unnecessary. However, during its youthful transition phase a mammal is shifting between two systems of physiology and behavior designed to fit two very different stable environments. Thus its abilities and motives are in constant flux and trial and error learning is perhaps its best means of adjusting to almost daily changes in its own physiology and behavior. The environment of many adult mammals has been changing fast, during the past two and a half million years of successive glaciations and melting with new niches opening and old niches disappearing or degrading. Learning provides a way of coping with swiftly changing environments, and the fastest and most efficient means of providing adult mammals some more learning ability, and a somewhat less fixed and invariable species-specific behavior system would have been a selection for extending the youthful learning phase of mammalian ontogeny into adulthood. An extension of the youthful phase into the adult phase would likely have also loosened the typical species-specific sequences that would have been, in ancestral adults, a fixed system of invariable sequences that fit them to a formerly stable environment. A number of mammalian species and even some orders, such as Primates, probably Cetaceans, and including many Carnivores have, by an evolutionary process of neoteny, retained into adulthood some of their youthful phase of ontogeny. Such an adaptation provided these more neotenic adults a more open system of learning that could modify remnants of ancestral species-specific behavior to better fit adults of that species to a swiftly changing environment. We hypothesize an interesting phenomenon in mammalian phylogeny: that a number of mammalian species have been modified over the past several million years by selection for the metamorphic phase of ontogeny extended into the adult phase. Mammalian phylogeny appears to be recapitulating a reversal in the usual direction of ontogeny.
1. PROBLEMATIC NATURE OF YOUNG MAMMAL BEHAVIOR

The ontogeny of mammal behavior can be characterized as a "closed," fixed-action pattern system of neonatal behaviors (Eibl-Eibesfeldt, 1975), followed by an "open" juvenile behavior system of mixed elements from many different functional contexts (Bekoff, 1972), until a final, more or less "closed" adult system of behavior is reached. Mammals display some behavioral discontinuities with reptilian forms, such as the "lactation complex" (Count, 1973). As another example of a discontinuity with earlier forms we have singled out play. While both neonatal and adult behavior are highly functional in mammals, the juvenile phase displays behaviors, called "play," that can be described as ontogenetically changing, complex, and unpredictable combinations of motor patterns that do not seem immediately functional. Because of its apparent non-functionality, juvenile play is one of the strangest ontogenetic phenomena to arise during evolution and has become the center of study in young mammal behavior.

Early theorists of young mammal behavior tended to focus attention on simple unitary motives in order to explain the uniqueness of play--unique because it is apparently only seen in mammals (and some birds) (Fagen, 1981). Spencer (1898) suggested that young mammals behave "playfully" out of an excess of energy. Or is play an "instinct" as Groos (1898) first suggested, or is there a drive for play in particular groups of mammals such as Bekoff (1974a) argued for in canids? Later writers became dissatisfied with unitary causal explanations and insisted that there must be more than one motive or drive at work in order to explain the ever-changing nature of this complex behavior (Baldwin and Baldwin, 1977). Furthermore, Meyer-Holzapfel (1956) maintained that the motivational system of young mammals must somehow be qualitatively different from that of adults. Most recently, Burghardt (1984) has, among many interesting observations, suggested a respite from boredom as yet another possible unitary motive for juvenile play: "Could not the earliest play be related to what we colloquially refer to as escaping boredom?" (Burghardt, 1984, p. 33).

One can discern three distinct schools of opinion on the topic of play. In addition to the motivationists, who, as we have seen in the preceding paragraph, tend to posit unitary motives to explain play, many recent investigators of juvenile behavior focus on either its motor patterns (descriptivists) or its adaptive value (adaptivists). Descriptivists (e.g., Hole and Einon, 1984) study the structure of behavior, how it seems unique to youthful ontogeny, what motor patterns juveniles of particular species display and in what sequences at what phases of ontogeny. Adaptivists consider what proximate adaptive function is served by the juvenile incomplete or imperfect display of neonatal and adult behavior. Is it practice for adulthood (Egan, 1976), or, in mammals such as carnivores and primates, is the function motor training, socialization, or cognitive training (Bekoff and Byers, 1981)? Is any benefit in fitness from play immediate or deferred till adulthood (Martin, 1984, p. 88)? Some studies carefully balance data and theory in order to examine youthful behavior from all points of view (e.g., Fentress, 1983). Too rarely has the subject of youthful behavior been examined in an ultimate evolutionary context, as by Burghardt (1984).
Whatever the approach toward the development of a theory of young mammal behavior, certain major questions must be answered satisfactorily;

1. Since the seemingly nonfunctional play, curiosity, and learning of the poly-behavioral juvenile phase is practically unique to mammals and some birds (Fagen, 1981), what is its phylogeny?

2. From what earlier forms of behavior did it arise, and why?

3. Why is juvenile behavior recognizably similar in most mammals even though the structure of the animals and their motor displays are so diverse?

4. Since behavior, even in the same species, changes considerably during the youthful phase of ontogeny, how can we define juvenile behavior when its motor description differs not only between species but within species at different ontogenetic stages?

5. How could such a motley patchwork of changing behaviors ever have been adaptive enough to have evolved into the youthful phase of many mammals?

6. The rat (Rattus norvegicus) continues to play as an adult according to Pellis and Pellis (1987), whereas the golden hamster (Meso-cricetus auratus) no longer plays as an adult (Goldman and Swanson, 1975). Why do adults of some species not play, or play only rarely, when in other species adults continue to play even though the frequency may decrease compared to that of juveniles?

7. What is the relation of play to non-play in youthful behavior?

8. Is play fundamentally different from other youthful behavior or is the concept of "play" simply an arbitrary construct which impedes understanding.

For reasons which this chapter will explain, the authors tend to think of play as an arbitrary construct that can impede understanding. Consequently, we would have put "play" in quotations throughout the chapter except that it is easier to warn the reader of our bias and use the term according to convention.

One of the difficulties in discussing young mammal behavior is the very popular yet vague and variously defined concept of play that has been used to describe some of its aspects. There are few clear criteria for when different mammals can be said to be at play or not at play. Some researchers, for example, count social play but not nonsocial play, or play with objects but not exploratory play. Muller-Schwarze (1984) tries to develop some criteria using definitive motor patterns common to a group of species; such a motor pattern in ungulates is identified as "interactive miming." It might be harder to isolate a definitive motor pattern in the play of primates. In addition, there are some problems with the comparability of measurements of play. The motor patterns involved in the play of different orders of mammals often differ so much that
descriptivist comparisons are all but impossible. Field studies of mammals at play are not strictly comparable to captive animal studies (Muller-Schwarze, 1984). He also points out that since play changes in character with ontogeny, measurements of play behavior or time spent in play at different stages of ontogeny, even in the same species, are hardly comparable.

A recent subject for debate among writers on play, which reflects the field's quicksand of often incomparable empirical observations based on conflicting definitions and a plethora of plausible but almost un-testable adaptive hypotheses, is the question of whether the field of play behavior suffers from too much or too little theory, too much or too little observational data. Fagen (1981), for example, suggested that the amount of observational data on play has overwhelmed theory. The real difficulty, according to Chalmers (1984), is that data and theory need to be more carefully related. Descriptivists who intend to study play operationally by carefully measuring and timing motor elements cannot ignore theory, since they must first recognize play in the study animals before it can be analyzed. Too often observers simply accept recognition of play as intuitive or accept inter-observer agreement as a guarantor of objectivity rather than, perhaps, a consequence of anthropomorphism (Hess, 1964; Fagen, 1981, pp. 64-65). Probably humans spend more time in play, both as children and adults, than any other species of mammal. It hardly seems surprising, then, that human researchers would emphasize play to the exclusion of the rest of juvenile behavior.

In most mammals non-playful juvenile behavior has been estimated to occupy over 90% of their total time. Fagen (1981, p. 273) has said that moat young mammals spend between 1% and 10% of their total time in play, with the exception of primates, which have been found by various investigators to spend from 0% to as much as 50% of their time in play (Muller Schwarze, 1984, p. 148). Muller-Schwarze adds that "more mammals are closer to 1% than to 10%." According to Muller-Schwarze (1984, p. 153), young caribou (Rangifer tarandus) begin to play 2 days after birth, from which time the amount of play increases daily until play reaches its full duration and complexity at about 10 days. Play begins at about 6 days and peaks at about 2.5 months in black-tailed deer (O. hemionus columbionus). The average time spent in play among young caribou was 0.3% (Muller-Schwarze and Muller-Schwarze, 1983). Young black-tailed deer average about 3.3% of their time in play (Muller-Schwarze, 1984), whereas pronghorns (Antilocapra americana) average about 0.7%. Young Norway rats play for 0.4% of their total time (Muller-Schwarze, 1984).

As a result of a more and more exclusive focus on play, the field of young mammal behavior may be losing a sense of the larger context of the ontogeny of mammal behavior as a whole, a sense of how play is related to the other 90% of the juvenile's behavior. If we look at how juvenile behavior is related not only to adult behavior (the conventional direction of study) but how it is related to neonatal behavior as well, we may find new insights into this unique, strange, and complex phenomenon. Few investigators are attentive to infant motor patterns in the youthful behavior they are observing, since in studying play the focus has traditionally been on its similarities to, and the development of, adult behavior patterns. Fagen (1981) wondered why more neonatal behaviors have not been observed in play, and Burghardt (1988) axiomatically rules out the likelihood of any neonatal behavior patterns in mammalian play: "Behavior patterns largely
evolved by neonatal endotherms (sucking, gaping, thermoregulation) should rarely be found in play, although they may be found in adults in ritualized forms, particularly in courtship," (p. 139).

On the contrary, we think neonatal behaviors do not simply vanish when juvenile play/learning behavior begins and then surface again as ritualized adult behavior. Chevalier-Skolnikoff (1974), for example, observed in young stumptail macaques [Macacca arctoides) the ontogenetic development of several communicative facial expressions including "friendly puckered lips, mutual mouth nibble or kissing," "play-face" (play-soliciting expression of open or gaping mouth, eyelids down and eye contact avoidance, ears back), and "threat expression" (open-mouthed stare, eyes wide and eye contact sought, ears forward), each composed of motor units of the neonate suckling/rooting complex dismembered from their original neonatal feeding context and in succeeding weeks during the juvenile phase reassembled into social expressions that later serve as ritualized gestures of adult communication. If we are ever to discover the motive, structure, function, and evolution of young mammal behavior, it seems best to avoid a narrow focus on play in order to explore the process of mammalian ontogeny as a whole system.

2. DEVELOPING A HYPOTHETICAL MODEL MAMMAL

2.1. Introduction

We commonly think of mammals as niche-adapted. We can usually locate them geographically giving limits to their range and within that range we can locate them ever more precisely because of their behavioral as well as morphological specializations. Behavioral studies of animals are conventionally divided into three categories—feeding, avoiding hazards, and reproduction. Those who study behavior therefore see these animals in their niche with a specialized feeding complex of morphology and behavior for finding the specific food, procuring, ingesting, digesting it, and a specialized hazard-avoiding complex such as homeothermy, fur, alarm systems, or fight-or-flight apparatus, etc., and a specialized reproducing complex for finding the specific mate, procuring, processing, birthing, and parental care. We assume that species-specific morphologies have to be accompanied by appropriate behavior that orients the structures within the niche and that these behaviors are as adaptive in the Darwinian sense as are the more obvious structures of the animal's morphology. Therefore the study of behavior implies an interest in its phylogeny.

This simple model of the evolution of form and behavior becomes more complex when we consider that all mammals change form and behavior throughout their lives (ontogeny). The animal starts as a fertilized egg with a morphology and a behavior appropriate to that egg's niche. At every stage the animal has to be a fit organism, has to feed and avoid hazards differently from the adult, yet effectively, as it develops to the reproductive or even the post-reproductive period. Death itself is probably timed by selective forces. We commonly think of the animal as simply
"developing" as it grows larger from egg to adult, and we commonly think of the adult as the specialist, assuming that the young animal is at first unspecialized and grows progressively more specialized until it is fully functional adult. But these common sense views are mistaken. Ontogenetic growth is not linear progression; rather, the maturing mammal undergoes complex redefinition at distinct stages, often adding or subtracting whole organ systems, necessitating a concomitant reintegration of the whole organism at each stage. The embryonic forming, functioning and discarding of the placenta in eutherian mammals is an obvious example.

Ontogeny does not recapitulate phylogeny. The mere fact of a mammal's increasing size during ontogeny changes its adaptive relationship with its environment. The niche changes with ontogenetic time and the organism has to change niches. The nerves, muscles, and bones don't simply extrapolate linearly from one stage to another, but rather at every successive stage of ontogeny each behavior in an animal's changing behavioral repertoire must be reintegrated with all the others to produce a functional organism that can survive the present as well as the next stage.

Nature can select mutations that act at any phase of a mammal's ontogeny. In spite of definitive arguments that natural selection can and has operated on features expressed early in ontogeny by Garstang (1922), Hardy (1951), do Beer (1958), and Gould (1977), Haeckel's (1866) so-called "biogenetic law," even though discredited, still influences the direction of thinking in biology and psychology. Because natural selection does operate to adapt and fine-tune adults to their specialized niches by the addition of mutations, and because adult mammals have indeed evolved new highly species-specific structures and behaviors (Eisenberg (1982), it is easy to forget that earlier phases of ontogeny, such as the neonatal, for example, have also been under selection, as the often elaborate systems of species-specific care-soliciting patterns in infants attest.

If ontogeny doesn't recapitulate phylogeny morphologically, and since structure and behavior are intrinsically related, then behavioral ontogeny in the descendant doesn't necessarily recapitulate the behavioral ontogeny of the ancestor. Mammalian neonates are specialized for soliciting feeding by mother, parents, or other adults, and for finding, preparing, and suckling the teat. The complete system of organs and behaviors needed for this specialized synthesis of neonatal and parental behavior was newly evolved in mammals. If the neonate has evolved a complex (care-soliciting system, then new traits are not necessarily stacked onto the end of ontogeny, onto the adult species-specific form, as Haeckel (1866) argued and many biologists still maintain for somewhat different reasons. (Stebbins, 1974; Zuckerkandl, 1970). Mammals did not originate simply because more specialized mutations selected for parental behavior were added onto adult reptiles. Selection significantly modified their early ontogenetic stages.

Insects provide a dramatic illustration of this process. The caterpillar's legs don't grow into butterfly legs either phylogenetically or morphologically. Nobody is fooled by the fact that in both ontogenetic stages the legs appear on the ventral surface, nor do we necessarily think that, phylogenetically, caterpillars came before butterflies, nor do we think that caterpillars are any less specialized than butterflies. Neither do we imagine that caterpillar behavior simply matures or grows linearly into butterfly behavior. It is easy to see that linear growth is not an adequate model
of ontogenetic change in the frog when we consider its tadpole form morphologically and behaviorally specialized to a watery niche and after metamorphosis its adult form adapted to a semi-terrestrial niche.

Mammalian ontogenetic changes are not as visible as are those of such animals, yet mammals do express two distinct stages and they do remodel or metamorphose between those stages. In this paper we would like to explore those two stages—the neonate and the adult—and, in particular, the youthful metamorphic phase between them. Textbook explanations of the development of behavior often presume linear growth and/or progressive specialization, which we, and some other animal behaviorists (e.g., Bateson, 1984), do not accept. In order to avoid the assumptions of unspecialized precursors progressively developing adult specializations, we are going to construct a hypothetical "primitive" mammal. Our mammal (Fig. 1) starts as a neonate, which is quite distinct from its species specific adult stage. It must metamorphose rather than "develop" between these two very different stages during its youth.

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Figure 1, Ontogenetic model of mammalian behavior.

2.1.1. The Model Neonate Mammal

Our hypothetical model of a neonate is a highly specialized form—exquisitely adapted to a stable environment, exquisitely adapted in the sense that it is a system of functional complexes specialized both morphologically and behaviorally. In fact, it is so highly specialized that it need not learn. For the model adapted neonate, learning would not be adaptive. In a neo-Darwinian sense, both play and learning would be maladaptive for the model adapted neonate because they waste energy by expending it on alternatives to
innate functional behavior.

2.1.2. The Model Adult Mammal

The hypothetical model adult is exquisitely adapted in both structure and behavior to a particular niche in a stable environment. However, its highly adapted adult form and behavior is distinct from its highly adapted neonatal form and behavior. Nor does our model adult share the juvenile's problem of keeping a changing form and behavior selectively adapted to the species-specific niche. In the highly specialized adult mammal model, systems of courtship, predation, escape, territoriality, parental behavior, etc., can be thought of as reasonably stereotyped closed systems so long as the environment remains constant. Learning and play would, as in the neonate, be maladaptive, wasting energy, unless the environment changed.

We are supposing that natural selection structures morphology and behavior for both the adult and neonate phases of ontogeny that would fit our model mammal—the same animal at different stages of ontogeny in the same habitat—to two quite different survival strategies. These two discrete ontogenetic stages, neonate and adult, would represent the most efficient and competitive uses of form and behavior to capture energy in their respective niches. What happens in between—the youth and its behavior—begins evolutionary history as a metamorphic form. The youthful metamorph that might be overlooked as a mere consequence of natural selection for the neonate, perhaps only an epiphenomenal afterthought without phyletic history, will unfold in the remainder of this chapter as a phenomenon of considerable evolutionary significance.

2.1.3. The Model Youthful Metamorphic Mammal

Our hypothetical model neonate has to be changed into a model reproductive adult. It has to metamorphose from a dependent form to an independent form. It has to rebuild the morphology from the neonate's niche to adult's niche. It has to survive as the neonatal behavior wanes and the adult behavior waxes. In other words, it has to survive as the stereotyped neonatal form and behavior is pulled apart and the adult form and behavior is assembled. It has to live in the house as it is being rebuilt (Fig. 2). It will display behaviors that seem functionless, which will be loosely termed "play." For, in order to survive this remodeling day by day, it will have to constantly readapt its changing bits and pieces of behavioral motor patterns to its environment, i.e., learn swiftly and easily.
2.2. The Neonate

The problem with being a mammalian neonate, or any neonate, is the increased probability of starvation or of encountering environmental hazards such as predation compared to its adult form. If one assumes that the adult size is adapted to feed efficiently, hide, escape, or fight off predators efficiently, then it is hard to imagine that a miniature adult can be adapted to the same niche, i.e. the vulnerability of the smaller organism would necessarily be increased.

Most of the animal world compensates for the vulnerability of its young with increased egg production. Mammals and birds have not only evolved a complex system of parental care but as its complement they possess an unusually complex system of neonatal behavior. Other animals as well, such as social insects, fish, amphibians, and reptiles, have experimented with various degrees of neonatal specialization and/or parental behavior.

The display of care-soliciting behavior similar to that of a mammalian or avian neonate is less frequent in the rest of the animal world, but analogous or perhaps homologous behavior can be seen in reptiles such as alligators. Neonatal behavior in a reptilian species may last for only a few days or weeks immediately before, during, and after hatching. For example, Garrick (1977)
described the crying of un-hatched or nest-bound alligators. The parent, in response to repeated "care-soliciting" cries from the nest, characteristically breaks away the mud with which it had covered the eggs after laying them, and which had become a hard crust prison as well as protection over the nest. Some species are incapable of breaking out without parental aid. The mother may remain close to her neonates, driving away possible predators for some days or weeks, while the newly hatched reptiles may cry in the event of hazards. However, the young alligators from birth must effectively hunt their own food, such as insects and tadpoles.

The ancestors of birds and mammals may well have had a rudimentary care-soliciting/parental care system similar to that of some reptiles today. Reptilian neonatal behavior, even though it may somewhat resemble mammalian care soliciting, represents at best a rudimentary portion of the mammalian neonatal system, what Count (1973, p. 125) refers to as "primitive familialism." The point we wish to emphasize here is that the complex interactive system of care soliciting and reciprocal care giving in mammals, together with the feeding of the infant on the mother's milk, represents a discontinuous event (Count, 1973, p. xii), a quantum leap, in evolutionary history.

Birds have also developed a specialized neonatal phase. Some birds feed the neonate crop milk, and some juvenile parallels between birds and mammals such as play, learning, and curiosity have been documented (Fagen, 1981). We will not, however, discuss birds again, not because we don't think young bird behavior interestingly similar but because we do not think neonatal and juvenile avian behaviors are necessarily homologous in every particular to young mammal behaviors, although the general theory of neonatal and juvenile evolution may be analogous. Also, whenever we mention mammals we refer to eutherians. We think that the ontogeny of monotremes and marsupials is also tantalizingly similar to eutherians and that much of what we say about eutherians may apply to them as well.

Neonatal mammals are unique in their food source, their food approach pattern, their sucking form of feeding (with specialized mouth, lips, palate, tongue, muscles of the neck, face, and throat, for effective suckling), their set of digestive enzymes (e.g., lactase), and their complex repertoire of social signals (to obtain food by inducing facilitating postures and motor patterns in another organism that stimulate chemical changes in that organism). It seems clear that those structures and behaviors are built into the neonate.

Similarly, feeding by the neonate comprises a functional sequence of motivations and specialized motor patterns. The teat has to be prepared, which the neonate can do by nuzzling, kneading with forepaws, bumping with head (depending on species) to start the flow and stimulate the hormones that cause milk production, and then sucking. And each of these stereotyped sequences is composed of micro-motor units which can be recognized and measured. For instance, Brake et al. (1979, 1982) and Hall and Williams (1983) divide infant rat suckling into measurable frequencies and intensities and into recognizable categories: "bursts," "treadles," and "rhythmic sucking."

Neonatal feeding behavior is not an incipient form of adult feeding (Hall and Williams, 1983) but a unique system that adapts infant mammals to their parental care niche. If a newborn is to
survive, it needs to successfully search out and begin to suckle a teat as soon after birth as possible. Such immediate and accurate behavior could not be left to trial-and-error learning, nor could its motivation be allowed to depend on external stimulation by some chance environmental releaser. Rather there must be motivation sufficient to stimulate the performance of these crucial behaviors right away in order to elicit the necessary maternal behavior on the part of the adult (e.g., if a neonate does not begin suckling the mother sheep within 15 min of birth, she cannot recognize it and will let it starve). Such behavior must be functionally perfect the first time, and every time thereafter, and is built into the newborn animal's nervous system. Not only would all specialized morphological structures have developed in the embryo ready to fulfill the newborn's needs at birth, but since the newborn's reward system for performing the behavior would have been built into the behavior, the performance of the behavior would be its own reward. Display and reward would have to be looped into the same internal motivational system in the neural tissue that nature selected. Hall and Williams (1983, p. 223) refer to this sort of neonatal behavior as "prepotent," and in their study of neonatal feeding in rat pups they state: "Five-day-old pups will continue suckling for hours even though they receive no milk. Suckling is thus initially a highly prepotent behavior that is exteroceptively dominated and is not dependent on nutritional state or nutritive consequences. Only after several weeks of age do these factors begin to participate in the control of pups' nipple attachment." "In the normal litter situation rat pups suckle for large portions of their day (70-80% in 5-day-olds; e.g., Plaut, 1974), yet during most of the time they receive no milk." "Pups' limited intake control via suckling might best be viewed as an adaptation of infancy which allows pups to take advantage of changing milk availability and maximize growth" (Hall and Williams, 1983, p. 246).

There is another unique characteristic of the mammalian neonate. It is a highly adapted intra-specifically dependent form, whereas in much of the animal kingdom, even the egg is an independent form. Relative to mammals, the reptilian ancestor is assumed to have had not only a precocious neonate, but one which was socially independent at birth. Care-soliciting in most species of alligators already referred to notwithstanding, mammal neonates have evolved a system of care soliciting so intricate that, together with the related "lactation complex" (Count, 1973), it seems almost discontinuous with care-soliciting/parental care systems of earlier vertebrates. Indeed, no other care-soliciting/parental care systems in the animal kingdom seem as intricate, with the possible exception of those of the social insects.

Care soliciting is commonly defined as a group of behaviors requesting feeding, protection, retrieval, or comfort. They are often displayed as, species-specific vocalizations and are most prevalent in neonates. Attracting attention to its discomforts is an adaptive behavior for a dependent mammal that needs to elicit care and protection from parent or group. Since the mammalian mother has the only food that a neonate can ingest, care-soliciting is a class-common behavior even though it is displayed by some motor patterns that are more or less specific to each species. For example, in some species, such as in domestic cows, the mother initiates infant feeding by presenting without needing to be solicited by the neonate (Broom and Leaver, 1977). In other species, maternal presenting is sometimes initially elicited and maintained at necessary levels of motivation by the care-soliciting behavior of the infant. Rosenblatt (1965, 1970) showed this to be the case in Norway rat mother-infant interactions. Care-soliciting signals may be precise
in neonates so that they will receive the appropriate response by the parent. Zippelius and Schleidt (1956) and Sewell (1968) found that neonates in many species of murid and cricetid rodent species emit ultrasonic calls between 30 and 60 kHz when cooled in the laboratory. Such calling elicits appropriate orienting toward the sound, pup-retrieving, and nest-building responses by the parent (Allin and Banks, 1972; Noirot, 1974). Broom et al. (1977) found that Mongolian gerbil (Meriones unguiculatus) pups care-solicit with ultrasonic calls whose sound level, complexity, and duration change with age and thermoregulatory needs.

The neonate is a very different animal from the adult, but it is difficult to argue quantitatively that it is any less complex and specialized morphologically or behaviorally than the adult. In a moment we will argue that the youthful metamorph is, in more than a manner of speaking, a hybrid between the neonate and adult forms, and thus, it might be argued, less specialized than either the adult or the neonate (Coppingor el al., 1985). The neonate is as niche-adapted as the adult, for its innate behaviors are just as well adapted to its socially dependent niche.

We can see why nature might select internally motivated innate behavior for newborn mammals. Although it may be argued that no behavior is totally innate, these early behaviors compose a fairly closed system that needs minimal environmental stimulation for smooth functioning. In the evolution of mammals, the selection processes have produced a highly specialized neonate. In marked contrast to what we have been saying here, the literature often treats the neonate as if it were a primitive, or even degenerated or deteriorated (Burghardt, 1984, pp. 34-35), animal that continues growth and complexity to maturation, with its ontogeny recapitulating phylogeny. But as we have argued, mammalian evolution has added a highly specialized unique stage to early ontogeny, thereby creating one of the most specialized and complex feeders in the animal world: the neonate. In addition, mammals also exhibit one of the most unique and complex social forms ever developed: the youthful metamorph.

2.3 The Youthful Metamorph

The crucial problem with our theoretical mammal is that the neonate, with a closed system of fixed-action patterns, has to metamorphose into the adult, with a whole different set of fixed-action patterns to serve different functions. Insects do this by creating a separate and discrete stage of morphology, the pupa, in which metamorphic remodeling can take place. However, in the ontogenetic system of insects, the adult is necessarily smaller than the larva, whereas in mammals the adult is larger than the larval neonate. The neonate must change form while continuing to avoid hazards, feed, and grow. The problem is that the neonate has a set of innate stereotyped hazard-avoiding and feeding behaviors that cannot simply "develop"—grow linearly and progressively—into its adult hazard-avoiding and feeding behavior. Crying for attention while hiding from predators is not a very effective defense for an adult. Bumping the teat with the head is not useful in eating grass.

Drewett (1978) and Hall and Williams (1983, p. 238) "the suckling behavior of infant rats is different from later ingestive behavior, and is therefore unlikely to be the immature form of the
adult ingestive behavior system." Hall and Williams (1983, pp. 244-245) go on to demonstrate that

"an ingestive system exists in rat pups that is present at birth and is more like the adult system for ingestion than is suckling. This type of ingestion in the pup is similar to adult feeding in several ways: (1) in its motor patterns for consumption, (2) in its ability to support appetitive learning, (3) in its physiological controls, and (4) in at least some of its neural substrates as indicated by response to pharmacological manipulations. This is, of course, in contrast to the suckling behavior of pups younger than 10 days of age which bears none of these relationships to adult ingestion. ... Pups' independent ingestion is perhaps more usefully conceptualized as a hidden forerunner to later ingestion that will only reveal its presence if tricked in the right manner. This feeding behavior is not normally suppressed or inhibited in infants, it is just not normally elicited."

Because of the necessity and constraints of growth, metamorphosis must be more or less gradual. The neonate must lose all its functional stereotyped innate hazard avoiding and feeding behaviors and at the same time gain a new adult set of innate functionally stereotyped hazard-avoiding and feeding behaviors. We do not use the concept "metamorphosis" here as a synonym for "development." Metamorphosis has been used throughout this chapter to differentiate juvenile ontogeny from the developmentalist assumptions of linear growth from an incomplete young precursor to a fully specialized and functional adult. Bateson (1987, p. 16) describes some discussions of development in which "everything that happens between conception and adult life is treated as though it were all relevant to understanding the same kind of developmental problem— namely, how adult behaviour is assembled." Bateson (1987, p. 17) chastises these developmentalist assumptions and insists that "by no means everything found in the young animal is a precursor of adult structure or function," affirming that "many aspects of its [the developing animal's] morphology, physiology and behaviour meet needs that are peculiar to its age."

When fragments of adult behavior begin to be expressed in the metamorphosing youth they seem loosely organized, easily elicited, and more labile in form than the more stereotyped, more crisply performed displays of either the neonatal or the adult stage. Let us consider the following example of gradual onsets during metamorphosis. The Norway rat expresses the several separate motor units of self-grooming behavior as a pup in the same ontogenetic order as will later be displayed in its stereotyped adult grooming sequence (Richmond and Sachs, 1980). The activation of each new motor pattern (muzzle grooming, face grooming, ear grooming, haunch grooming, tail grooming) is separated by several days from the expression of the next motor pattern in the rat pup's behavioral ontogeny. Each of these motor units, as it is expressed, seems to be separately motivated and can thus be displayed individually or as an element in a mixed string of any motor behaviors in the pup's repertoire from almost any functional context. The resulting behavior seems "playlike" to observers, because it is nonfunctional and appears maladaptive relative to either the neonatal or the adult niche. When a more mature stage in the rat pup's ontogeny is reached, these steps in grooming become assembled into more predictable patterns until, finally, they become one stereotypically sequenced system of self-grooming behavior.
The ontogenetic onset of grooming behavior in the Norway rat can serve as a model for the onsets of other adult behavior complexes in other species. Leyhausen (1973) and Martin (1984), for example, discuss the ontogenetic onset of predatory behavior in juvenile cats, reporting a similar overall ontogenetic scheme (activation of separate units that can be combined and recombined "playfully" with other motor units, and only later in ontogeny firming up into stereotyped sequences) which has been generalized for predatory mammalian ontogeny by Fentress (1983).

We hypothesize that this general scheme for the onsets of adult behavior is the inverse of that for the much less studied ontogenetic offsets of mammalian neonatal behavior. A neonatal behavior will decay during ontogeny by first showing a progressive loosening of the formerly invariable sequence of the neonatal fixed-action pattern. This loosening of the sequence will be followed by a later-metamorphic period when the remaining motor elements can be displayed mixed with other behavioral elements in any order of composition. Finally, for one motor element after another the motivational propensity required for its display abates, or is suppressed by onsets of other neural structures (Peiper, 1963), until its frequency of display may become so low in late metamorphosis that we no longer see that behavior in the repertoire.

As phylogenetically selected neonatal fixed-action behavior patterns begin to be deactivated during ontogeny, some motor units will be offset, inactivated, or reduced in motivational intensity before others. In this case, the neonatal behavior system may continue to motivate whatever fragments of behavior that are left as portions of the once functional complex are inactivated. For example, care soliciting, or begging for attention, can continue to be performed during youth, even if it receives no positive and considerable negative external reinforcement. Poirier (1970) describes how young Nilgiri langurs (Presbytis johnii) take rather severe punishment for many months, sometimes as long as a year, as the mother weaning them rejects their advances with not very gentle nips and cuffs.

Though a care-soliciting neonate is likely to receive the care it needs from an adult with species-typical parental behavior, the neonate is not performing the behavior so that it will get care but because the motivation remains intense and the behavior is often repeated even after care is given. The behavior itself is apparently rewarding (Eibl-Eibesfeldt, 1975). Once started, a care-soliciting signal may continue, for such insistent and persistent signals are more likely to assure parental attention. It is adaptive for the infant to stay sufficiently motivated at all times for almost any environmental change or discomfort stimulus to elicit care-soliciting, and thus avoid ever being alone out of the notice of parent or group.

The metamorphosing mammal youth does not simply develop linearly from amorphous neonatal behaviors into progressively more specialized adult behaviors. Rather, a complete reorganization of behavior must take place during metamorphosis. Motor pattern frequencies measured daily during metamorphosis show differing behavioral compositions, a series of ontogenetic snapshots of a profound remodeling process.
This is an important point to emphasize, since much of the literature on the development of mammalian behavior (and particularly on the development of human behavior) often assumes that the neonate is a precursor form that grows progressively into the complex adult form. Indeed, this may be true of most reptiles, as Burghardt (1984, pp. 32-33) writes in differentiating between mammal and reptile neonates: mammalian neonates "have food, heat, shelter and protection provided by parent," whereas reptilian neonates "must provide for all their own resources" so that "behaviours necessary for survival need to be highly functional at birth." However, we must emphasize that whereas reptilian neonatal behaviors are probably precursors of later adult behaviors, the neonatal mammal's behaviors are not linear precursors of its adult behaviors but must undergo thorough remodeling during metamorphosis. The disorganizing neonatal system and the organizing adult system together drive an ontogenetically changing mix of motor fragments, which we call metamorphic behavior.

Just as in the profound remodeling of skeletal bones during mammalian ontogeny, so well explained for facial bones by Enlow (1968, 1975), there are no behavioral motor patterns or configurations that remain stable, that do not change or undergo profound re-composition or remodeling during youth from neonate to adult. Inverse allometries of offsets and onsets of motor patterns, together with variations in degree of motivation among these patterns, occur as the neonatal system is disorganizing at the same time as a quite different adult system is being organized. A linear diagram (such as a straight-line connection) is commonly used to illustrate ontogenetic change in feeding from sucking milk as a neonate to grazing or predating later in ontogeny. However, Chalmers (1984, p. 130, diagram a), for example, questions the linear diagram as too simple a device to represent the ontogeny of behavior from neonate to adult, and suggests instead a more complex illustration of offsets and onsets of some motor patterns during the ontogenetic process (1984, p. 130, diagram b). But even a complex offset/onset diagram does not begin to do justice to the complexity of ontogenetic behavior remodeling, for we would have to include in the diagram the organization of motor patterns and their sequencing. With notable exceptions (e.g., Hall and Williams, 1983; Pellis, 1984, 1988; Pellis and Pellis, 1987, 1988), animal behaviorists have not investigated mammalian metamorphosis considering all three parameters of adult onsets, neonatal offsets, and their changing organization and sequencing.

Leyhausen (1973) addressed some of the complexity of motor unit adult onsets, including his proposal of a model of differences in motivational propensity or energy, in different species of felids at different stages of juvenile metamorphosis. A motivation may develop to a different degree later in ontogeny than it had earlier. Neonatal and adult motor elements and their concomitant motivations, whichever happen to be present in the youth's repertoire at a particular stage of ontogeny, produce a heterogeneous display of motor patterns vacillating between functional contexts. We must remember that even in the infant, several behavior complexes selected for adult functioning, wholly different from that of the neonate, are becoming activated piece by piece, so that as ontogeny progresses, sequences of motor units become less random. Yet these complexes will remain less than stereotyped and mixed with motor elements from other functional contexts until all the motor units and motivations of which the behavioral complexes are composed are fully activated.
According to Pellis and Pellis (1987, 1988), play fighting in young, as well as adult, rats shows fundamental differences in both targets and tactics from the targets and tactics of serious fighting. "During play-fighting, the nape of the neck is attacked, whereas, during serious fighting the lower dorsum is attacked" (Pellis and Pellis, 1988). "Other muroid rodent species also exhibit a division between the targets of playful and serious fighting" (Pellis and Pellis, 1987, p. 238). Play fighting in muroid species seem to be pieced together from parts of both adult and neonatal functional behaviors. "The nape is an important body area during social investigation, being frequently nosed and allogroomed, and is even grasped by the male with the mouth when mounting during sexual encounters. In the Djungarian hamster, the pups nuzzle and lick the mother's mouth in the week preceding weaning. In sexual encounters, adult males lick the female's mouth before mounting" (Pellis, 1988). Furthermore, "similar intermediate forms of play-fighting may be found in the exaggerated forms of greeting and social investigation present in many species of rodents. For example, the social ground squirrels kissing, a form of greeting thought to be important for maintaining social recognition, is often exaggerated during the juvenile phase into 'mouth-wrestling'" (Pellis, 1988).

For all these species, then, the targets attacked and defended during play-fighting are areas of the body which are otherwise contacted during friendly social interactions (i.e., contact-promoting). Thus, in these species the opponents compete over access to amicable targets during play-fighting. This is in marked contrast to those species ... in which the opponents compete over access to agonistic targets during play-fighting, that is, those targets attacked during serious fighting (Pellis, 1988).

The difference in targets of attack provides strong evidence that play-fighting is not merely an immature or inhibited form of adult aggression, as has been suggested by some researchers. Furthermore, this target difference provides evidence against the commonly held view that with the onset of sexual maturity the division between playful and serious fighting becomes indistinct, as one merges into the other. ... On the contrary, this differential targeting persists well into adulthood .... supporting the view that adult rats continue to play. The difference between play-fighting and serious fighting is often more apparent in the golden hamster, which ceases to play altogether in early adulthood (Pellis and Pellis, 1987, p. 239).

Until the motor elements are all activated and their differential motivations are optimally tuned to operate functional systems of adult species-specific behavior by the end of metamorphosis, the youth is also motivated by remnants of the internal neonatal system yet has at its disposal only bits and pieces of both neonate and adult behavior complexes, neither of which are complete enough to provide full functional behavior. Perhaps motivations for some individual motor patterns remain or become activated while the rest of the component motor patterns of a functional complex are unexpressed, in which case the result would be a strangely nonfunctional-looking mix of play-like behaviors.
Metamorphosing youthful behavior looks maladaptive when compared to either neonatal or adult behavior because it does not appear appetitively or consummatorily functional for either context, and it is just this nonfunctional heterogeneous appearance that is the commonly agreed on defining characteristic of play (Bekoff and Byers, 1981; Martin and Caro, 1985; Burghardt, 1988).

2.3.1. Play

We have seen that neonatal offsetting and adult onsetting are proceeding at the same time with opposite trajectories. Furthermore, we know that we must add to the neonatal offsets and adult onsets a third parameter—changing motivational intensities for each motor pattern expressed that organize these patterns into sequences. When all three changing parameters are perceived as one behavioral ontogeny, we can begin to understand the complexity of metamorphic behavioral remodeling. Without an awareness of species-specific differences in all three parameters of behavioral ontogeny that vary almost daily throughout the youthful metamorphic phase, the difficulty of describing or defining juvenile metamorphic behavior in one species of mammal, let alone all species, can seem overwhelming. Without precise studies of these three changing parameters for each species, it will remain all too easy to dismiss from serious consideration a given instance of juvenile behavior as just another example of unpredictable play.

Pellis (pers. commun.) explained how his investigations of juvenile play in the deermouse (Peromyscus maniculatus) revealed an underlying structure of developing adult functional behavior:

In some of our rodents, such as the deermouse for instance, juvenile play is indistinguishable from the maturation (piece by piece) of male sexual behavior. When the early components are observed in isolation in younger juveniles, the behavior looks playful. The most parsimonious explanation would be that we are seeing the gradual maturation of sexual behavior, not a distinctly motivated behavioral activity.

Investigation into the play behavior of juveniles of a different species revealed a quite different underlying structure (Poliis, pers. commun.):

In the captive otters I studied (Pellis, 1983, 1984), object play started at the onset of each activity period (i.e., after a period of rest/sleep) with forepaw manipulations while rolling on the ground (supine and lateral), but then progressed to gripping and pulling the objects, and then finally the animals adopted a crouched sitting posture, with chewing and fragmenting as in eating! Therefore, over the course of 2-3 hour activity period "object-play" changed dramatically in form, seeming to progress through the various motivational phases of predation—locating, handling, fragmenting, and eating..
Nonrandom combinations of innate units of motor patterns are programmed by successive ontogenetic patterns of differential motivational propensities associated with each motor unit in the juvenile's repertoire of motor units at that particular phase of ontogeny. In this way different behavioral combinations of motor units—different kinds of play—become characteristic of youths at different ages. When we isolate a play pattern from other behaviors of the juvenile, it is easy to forget the whole three-parameter system of juvenile behavior that is under constant genetic and environmental control during metamorphosis.

For us, then, play is a consequence of the metamorphic period. Play is but a term for the protean nature of the neonatal to adult metamorphosis. Play is a combination and recombination of whatever pieces of neonatal fixed-action patterns remain and whatever adult motor patterns are expressed thus far in ontogeny. According to this model, play is not a unitary drive (Leyhausen, 1973) nor, contrary to what has been suggested by Egan (1976) and Crowell-Davis et al. (1987), is play simply practice for adulthood. Rather it is the recognizable consequence of the metamorphic behavioral synthesis. Play is an epiphenomenon of the evolution of the mammalian neonatal system and its subsequent reorganization into the adult behavioral system.

This is not to argue that evolutionary adaptation has not taken place on the metamorphic form, for we will soon hypothesize that selection for components in this stage of ontogeny has become, for a number of orders and species, an important aspect of mammalian phylogeny. But play as the waxing and waning of ontogenetic stages explains not only the uniqueness of mammals, but the uniqueness of each species of mammal, and the uniqueness of each age within a species.

In addition, redefining play as a consequence of a metamorphosis explains why play has no phyletic history. The search for play behaviors in reptiles (see Burghardt, 1984, pp. 9-11 for review) reveals only strained instances such as recorded by Lazell and Spitzer (1977). According to Burghardt's description, reptiles do not have discrete ontogenetic stages, but rather are born as little, albeit incomplete, adults and as such literally grow up; thus we would not expect them to play.

One implication of play as a consequence of metamorphosis is that it will be different for each mammal species depending on the rate at which a disintegrating neonatal form and behavior coexists (merges) with an integrating adult form and behavior. Play is therefore specific to each species, yet the similarity that we see between species at play results from the fact that all infants are "care-soliciting suckers" that have to be remolded into adults. Moreover, each motor pattern has its own motivation that is changing in degree during the metamorphosis, the effect of which is to disorganize no longer adaptive neonatal motor sequences and organize other motor patterns into highly probable sequences of adult functional behavior (Leyhausen, 1973). But this not only argues against play being a unitary drive but argues also against play being strictly comparable across species boundaries.

Does play provide physiological tuning and toning that enhances juvenile survival? Of course. Is it practice for deferred adult functional performance? It could be, provided that it were selected for in a particular species. Is it a unitary drive? Again, it could be, provided that it was selected for
in a species. Was any of the above the original adaptive advantage of play? We think not.

It is hard to separate "practicing to be adult" from differential onset of innate motor patterns. Crowell-Davis et al. (1987) argued that sex differences in play in colts and fillies are "consistent with theories of play being practice for adult behavior." Their point was that a colt's later reproductive success is dependent on fighting skills and they observed more interactive play in colts than in fillies. However, it might be argued that colts are metamorphosing into stallions and thus have those motor patterns to play with, whereas fillies do not. Neither fortuitous perfecting of physiological abilities for the adult stage nor the possible selection for play as a unitary drive constrains us to believe that play arose as an adaptation for practicing adulthood.

Observations by Rasa (1971) on social object play in elephant seals (Mirounga angustirostris) followed a similar line of reasoning. She said that the propensity of these animals for differentially manipulating overhead objects of different colors and shapes is evidence for an emerging innate schemata of prey. Similarly, she noted that social play among pups is reminiscent of adult territorial and aggressive motor patterns, which led her to conclude that "young elephant seals are therefore equipped genetically with a variety of responses to animate and inanimate objects . . . these behaviors are practiced out of their usual context with inadequate stimulus objects and are thought to aid in the animal's physical and mental development and coordination." No doubt this is true, but if the young seal's behavior is as genetic as she supposes, it is the genetic onsets of certain motor components together with their precise degrees of motivation that will result in functional fixed-action patterns later in life, i.e., the juvenile phase is a genetically controlled maturation within the limits of a particular environment. Young seals would not learn what they do without the innate components.

A number of writers on youthful mammal behavior have reported the gradually organizing adult motor patterns of the dominance hierarchy that become more and more sequenced during ontogeny until play fighting becomes real fighting (Bekoff, 1972, 1974b; Fox, 1978; Poole, 1978; Fentress, 1983). Here is the way Hole and Einon (1984) describe the rough-and-tumble play characteristic of early ontogeny in rodents: "animals engage in prolonged ventral-ventral contact, one attempting to hold down the other on his back, while the one held down struggles to get free and to attain the on-top position. There is some degree of reciprocity, either within or across bouts, so that a given animal 'dominates' roughly as much as it is 'dominated'." Later in youthful ontogeny, rodents no longer engage in rough-and-tumble play but begin "not-very-serious-fighting" play in which the motor patterns look more like adult fighting. Finally, Meaney and Stewart (1981) report that the play of laboratory rats later in youthful ontogeny becomes more and more like adult dominance-aggression.

Leyhausen (1973, p. 244) stated that "the instinctive movements of predation (lying in wait, crouching, stalking, pouncing, seizing, "angling") are performed independently of one another by the playing cat, in varied combinations with each other and with activities derived from instinctive systems other than predation." Since many adult motor patterns are performed in stereotyped sequences, the interspersing of other instinctive systems in non-functional, i.e., non-rewarding, displays that disrupt any sequence makes it hard to argue that the motivation for play is merely
practice for adulthood.

Pellis et al. (1988) found that predatory play with mice in the adult cat can best be described as "an artifact of the interaction of attack and defense p. 20. . . . Only those cats that vacillate between defense and attack are typically viewed as being playful. ... As Wolgin (1982) noted, it is the superimposition of approach and withdrawal that creates the illusion of playfulness, i.e., exaggerated and seemingly out-of-context movements, repeated performance of behavior patterns lacking apparent goal direction, and disordered sequencing of motor patterns" (p. 35). . . . Our findings show that such 'playful' characteristics can arise without having to invoke separate motivational states for predatory play and for serious predation. . . . The interaction of two behavioral systems, attack and defense, can account for a wide range of responses towards prey, including avoidance, play and killing" (p. 37).

Most writers on play, whether descriptivists, adaptivists, or evolutionists, tend to report onsets of adult behaviors; rarely do they note offsets of neonatal behavior. However, there are some writers who do. Tyler (1972, p. 170) charts changes in the orientation of play in foals from mother to other foals over the 8-week period following parturition. Feinstein and his students at Hampshire College (pers. commun.) are documenting the overlap of neonate vocalizations, their disintegration, and the onset of adult vocalizations in dogs. Interestingly enough, domestic dog pups will sound the care-soliciting call for retrieval long after the offset of the fixed-action pattern for retrieving by the mother. The onset in pups (12 days) of deep offensive growling overlaps puppy care-soliciting alarm calls long before and long after either stereotyped system is functional. It would be hard to call these behaviors play because of the context in which they appear, but they have a nonfunctional heterogeneous appearance. Food begging in dogs and wolves, although not strictly neonatal, starts as care-soliciting in the very young, then is play soliciting with siblings, appeasement gestures in the sub-adult, and ritualized greeting as an adult.

In discussing ontogenetically transitory adaptations of the lactation complex, Count (1973) suggests that "an ad hoc suctorial apparatus is no more anomalous than an ad hoc mammary apparatus. Both of them survive their primary functions and acquire a tissue of secondary functions or significance whose persistence does not depend upon the exercise of the primary function." Count terms "survivals of such ingredients from an earlier ontogenetic state into a later one" as "reverberances," and in referring to one of these reverberances writes: "The lips are long; they [lips] can be erected outward, in deviant plane from the surface of the bone over which they are draped. Monkeys, apes and man can purse and can kiss—and they do. May I further suggest—orbiter—that we have just reviewed incidentally some antecedents and prerequisites for the articulatory end of speech." Is the mammalian metamorphic phase characterized by what many researchers have called nonfunctional play really nonfunctional or, as Count (1973) suggests, can it be antecedent to a new form of behavior?

2.3.2. Learning

Animals must at every stage of their ontogeny be adapted to their environment (Galef, 1981).
Theoretically, in a constant environment it is hard to imagine how the juvenile can be adapted. The juvenile has not attained adult size, shape, or behavior; it is hard to imagine any natural environment that could be isomorphic with the daily remodeling required of a metamorphosing shape and behavior. As we have seen, some authors assume that "practice makes perfect," which presupposes that juveniles are not adapted. In any case, juveniles display apparently nonfunctional behaviors which, according to neo-Darwinist assumptions, should long since have been selected against. The youthful phase of mammalian ontogeny looks maladaptive to a biologist. How can it persist, sometimes for years?

Mammals in youthful metamorphic phase have one advantage over their adult and neonate stages—they are more flexible learners. Parental care and/or social organization may make up for some of the deficits in specific adaptation. Our favorite in this regard is the elephant seal pup whose mother leaves the 300-lb mass of blubber suddenly and permanently. The pup has never been in the water, does not "know" how to swim, does not "know" what food looks like (let alone how to catch it), and finds nothing but rejection and aggression from surrounding adults (Rasa, 1971). Although this example may be thought extreme, it might not be far from the mean for most mammals. And the elephant seal pup, like other metamorphosing mammals, has to learn and practice not for the future, but to survive its metamorphosis.

Thus we would like to argue now that the metamorphic mammal needs to "learn" more than neonates or adults, and also that it has some attributes that may make it the "best" learner. In our model mammal the neonate and the adult typically had closed or fixed-action behavioral systems. Natural selection operated to adapt morphology and behavior to a specific environmentally stable niche—the neonate to the nest and parent, the adult to its "natural" habitat. In both cases, then, learning would be maladaptive, wasting precious energy on movement that was by necessity less than perfect. The metamorphic youth, however, far from seeming perfect, is composed of a jumble of overlapping offsets and onsets requiring the youth to continuously adapt its changing form and behavior to its environment.

Neonates and adults of our model animal not only do not learn; they probably cannot. Animal trainers do not work with neonates and "you can't teach an old dog new tricks." We have postulated here a stereotyped system of fixed-action patterns, which simply means that once the initial behavior in a sequence is activated, the probability of each succeeding event is high. Our model mammal is, of course, an abstraction, but looking for learning in real mammalian neonates is about as difficult as looking for play in reptiles. Even in human neonates, for example, it is hard to find clear examples of learning for the first 2 months (Sameroff, 1983). However, learning in mammals is probably not different in kind from learning in reptiles (Burghardt, 1984), although the degree of difference is very large. It is this leap in degree—this discontinuity in play and learning between reptile and mammal—and how it may be related to the ontogeny and phylogeny of mammalian behavior that we are interested in understanding.

We would like to hypothesize that the evolution of learning in mammals is fundamentally the same as that of play. Like play, learning in mammals is a consequence of their metamorphosis. Like play, learning is, as is all behavior in the metamorphosing mammal, the result of the
combining and re-combining of whatever neonatal behaviors remain and whatever adult behaviors are expressed thus far. Learning as well as play is a synthesis of neonatal and adult behaviors in sufficient variety of loose pieces and unexpected combinations to provide raw material that may be reinforced, remembered, and thus may permanently modify subsequent behavior, which is the definition of learning. Learning differs from play only in that the play/learning mammal remembers those combinations that are fortuitously functional for it at that stage of ontogeny.

Neither the neonate nor the model adult would be likely to make facile learners because the elements of their behavior are connected into stereotyped sequences. Such invariable sequences would preclude the possibility of bits of behavior being easily rearranged into new, possibly more functional combinations. On the other hand, the youthful metamorphosing mammal probably has a much larger motor repertoire than either the neonate or the adult. The mammalian metamorphosis is under a genetic control that gives juvenile mammals separate pieces of behavior with which to tinker rather than the complete constructions given to the adult or neonate. Juveniles are granted separate notes and motivations with which to play a variety of tunes rather than a few stereotyped neonatal or adult fixed-action patterns.

In order for learning to take place, an animal would need to have the structures necessary to perform a certain range of motor units, and separate motivations for displaying each motor unit (Leyhausen, 1988, pp. 238-239), so that diverse combinations of motor units could result. And, finally, occasional environmental reinforcement would be needed so that useful combinations would be remembered. Species with a greater variety of "play"--a greater number of small, separately motivated motor elements producing greater behavioral variance--should learn better than species with more restricted play patterns. Nevertheless, learning probably occurs in most, if not all, metamorphosing mammals. Whether the learning is subtle or startling depends on the variance in the behavioral repertoire during metamorphosis, and the degree of variance depends on the behavioral characteristics of each particular species. The youthful behavior of rats or rabbits will have to be examined more carefully than that of monkeys, apes, humans, or dolphins in order to find evidence of unmistakable learning.

Learning is a potential of metamorphic mammals because of the genetically programmed open system of behaviors that instigate the mixed motor patterns to make learning in the wild possible. When the Japanese macaque, Imo, discovered a useful combination of motor units that programmed potato washing, she was a late infant/early juvenile. She was not much older when she learned a variation on the former program, this time to float rice grains on still-water pools, which served to separate food from the heavier grains of sand with which it was mixed. The diffusion of novel behavioral programs was carefully observed to spread quickly among youthful peers (and some mothers learned it with their infants), but the rest of the adults could not learn nearly as well (Itani, 1958; Miyadi, 1958; Kawai, 1965). The discoveries of new and useful motor pattern combinations such as those proto-cultural inventions of Imo are not mysterious or inexplicable phenomena, for learning is made likely during the youthful phase (Leyhausen, 1973, pp. 240-241).

Primates are not the only mammals that learn during their youthful phase. Caro (1980) found,
for example, that kittens that play with birds rather than mice develop different predatory phenotypes. However, metamorphic learning is not necessarily deferred learning for the adult phase as many writers tend to assume. Play may be related to immediate learning so that the youth can survive its own metamorphosis. Play appears nonfunctional only because we categorize and separate some metamorphic behavior from its larger context, thus rendering the intrinsic relation of youthful behavior to learning more difficult to discern.

After the onset of a particular motor pattern but before the onset of others, there is a high probability of that motor pattern being utilized in varied sequences in combination with almost all other patterns in a youth's repertoire at that particular phase of ontogeny. Whatever use that motor pattern, in any combination, can be to the youth is likely to be repeated, remembered and learned during play or investigation. Even metamorphic behavior that looks repetitive and not very random, such as play fighting in young rats, contains considerable variation on which some learning could take place. Pellis and Pellis (1987, p. 240) found that in young rat play fighting "the topography of each 'behavior pattern' is highly variable, with subtle modifications to contextual variables, such as orientation and posture." Even subtle wrestling configurations that gain it some mechanical advantage could be remembered by the young rat and repeated in new contexts. In displaying each motor pattern in many different sequences and social situations, a young mammal is learning the use and social effect of that motor pattern almost as though it were a tool being manipulated.

Thus metamorphic behavior provides a learning situation and makes a high degree of operant conditioning not only possible but likely. However, metamorphic learning is limited temporally to combinations made likely because of differential motivational propensities associated with specific offsets/onsets scheduled during the ontogeny of its species. In this way learning, like play, is species-specific and ontogenetically specific, i.e., specific stages during the metamorphic phase of particular species may be said to constitute critical or sensitive periods for certain kinds of learning.

Metamorphic behavior as the ontogenetic bridge between the newly evolved neonatal system and a very different system of adult behavior in mammals may have provided a discontinuous evolutionary leap in the degree of learning, as well as play, between reptilian and mammalian forms. When we understand that quite unlike the fixed-action pattern behavior of our model neonates and adults that lack behavioral variance, the youthful metamorph enjoys behavioral variance that could lead to some learned responses to its immediate needs. The more youthful metamorphic variance the greater the potential range of learning that could occur. We are now in a position to understand the part that evolution may have played in fortuitously providing youthful mammals with an optimal or open phase for learning.

Play/learning could and surely did become newly adaptive (an "exaptation" as Gould and Vrba, 1982, would term it) for some species of mammals after it had appeared as the byproduct of youthful metamorphosis. In fact, as Leyhausen (1973), Gould (1977), and Geist (1978) suggest, the evolution of mammals, including humans, shows a trend toward selection for the youthful play/learning phase carried into the adult phase. The possibility that play/learning has become an
exaptation makes it easier to see why play and learning, although not unitary drives, may be selected for. If play/learning is more than an artifact of metamorphosis, e.g., if in a particular species there has been exaptation of the original youthful metamorphic phase, then that exaptation is to change. The metamorphic stage of mammalian ontogeny is unique in the animal world because it is a stage adapted to nothing but change.

2.4. The Adult

Our model of highly stereotyped adult behavior seems to fit some, but not all, adult mammals. Different orders of carnivores, for example, as well as primates, especially in more recent radiations, display an adult behavior system that looks metamorphic and, in fact, often includes play and learning. We will argue in this section that some, perhaps many, adult mammals have indeed become adapted to changing environments by selection for youthful metamorphic behavior. Significant change in the behavior of a new or modified mammalian species could be the consequence of a relatively small genetic regulatory change. Sudden discontinuities can happen in the evolution of behavior, according to Bateson (1984), who suggests two possible evolutionary scenarios. We think that many evolutionary discontinuities in adult mammal behavior have been accomplished by another evolutionary process called neoteny.

We use the term "neoteny" as Kollmann (1885) defined it originally and as Gould (1977, p. 227) recently redefined it: a phylogenetically selected, genetically induced deceleration of physical and behavioral allometry resulting in the offspring retaining into adulthood a character—or often a whole package of behavior and morphology (Bemis, 1984)—that would have been thought juvenile, or even infantile, in the ancestral stock (de Beer, 1958; Geist, 1971; Gould, 1977).

Any actual heterochronic evolutionary process is no doubt much more complicated than we can suggest in this short chapter. Neoteny is a cumulative process during which some traits, perhaps advantageous behavioral ones, are under intense selection while other features of the neotenic package, such as certain structural traits not involved in the behavior, are only being selected indirectly as epiphenomenal characters of a more general evolutionary trend. Over many generations such epiphenomenal characters may be selected against or modified in different directions from the neotenic package as a whole. A macro-evolutionary process owing to the selection of regulatory mutations at a high level of genetic organization may initially provide a neotenic rough draft that is continually being edited by selection at other levels of organization. After a few generations neotenic strains may no longer retain the full package of more youthful form and behavior. In time, a species that evolved by means of a neotenic process may appear more and more like the product of a typical mosaic evolution, except for the more youthful behavioral advantage that was selected for.

This hypothesis of a neotenic extension of the youthful metamorphic phase into the sexually mature adult stage has implications for an understanding of extended learning and play throughout the life history of some species of mammals, such as primates, including humans, for whom evidence of a systemic neotenic process of evolution has been offered (Bolk, 1926; de Beer, 1958;
Montagu, 1962; Gould, 1977). Moreover, it is not unreasonable to suppose that the behavior of adults in many species of mammals at the present time consists of fragments of motor patterns that were selected for some ancestral stereotyped sequence that has been lost, leaving its remnants as modern tools with which it can now play and learn, and which may be selected for or against in the future.

For example, African hunting dogs (Lycaon pictus) have evolved a predatory sequence that includes a play-like rallying period before the chase (Estes and Goddard, 1967). The collared peccary (Tayassu tajacu), too, has integrated play into its adult behavior (Byers and Bekoff, 1981; Byers, 1983). Circular playgrounds about 2 m in diameter are trampled bare by the play of both juveniles and adults, with 64% of play bouts actually initiated by adults. Apes, humans, and domestic mammals appear not only to play frequently as adults but also to continue to learn and to display care-soliciting dependency behaviors as adults. These strange "adults" show signs of having evolved by a selection for youthful metamorphic behavior.

Nevertheless, neoteny has not occurred in all mammalian species, for in some species of mammals the adult phase looks rather similar to our posited model. We can argue empirically that some, perhaps many, adult forms in stable environments are niche-adapted by means of relatively "stereotyped, closed systems of behavior, i.e., their feeding behaviors are products of highly specialized dentition, mouth parts, digestive and eliminative systems. Equally highly adapted in those adults are their locomotor systems that facilitate contact with food, avoid hazards, and, of course, enable complex reproductive functions including response to climactic and environmental signals, species recognition, mating behaviors, and maternal/paternal behavior. The adult's teeth, digestive system, and locomotive apparatus provide the limits to the kinds of food it can contact and ingest. Of course cows can't forage at the top of trees or puncture or tear flesh efficiently; bats don't munch grass. Morphology, physiology, and, ultimately, genetics govern the range of any behavior and, in this simplified sense, set innate limits.

Furthermore the feeding of some adults, like their other behaviors generally, is a stereotyped behavior made up of component motor patterns. Typically there is an arousal that is internally and/or externally motivated and an orientation stage followed by an approach pattern, a manipulation or preparation, and an ingestion. For an adult predator this is search and find, orient, eye, stalk, chase, grab-bite, crush- or kill-bite, and ingest. Each of these motor patterns can be so stereotyped that a good field naturalist can identify the predator by the condition of the kill (Wade and Bows, 1982). The same would be true of an herbivore where the naturalist could look at the damaged plant and identify the browser. Moreover, the behavior of many mammals is stereotyped enough to allow their identification by examination of the slurry or mush of their stomach content, or even their scat. Their functional sequences of behaviors comprise a number of separate motor patterns each of which is species-specific. Of course, each of these macro-motor patterns (eye/stalk/chase/bite) may comprise a number of micro-motor patterns depending on the degree of specificity a researcher would care to investigate.

However, our model adult adapted by highly stereotyped behavior to a stable environment was posited as an illustrative abstraction. In reality, adult mammals of different species display such
diverse adaptive strategies that generalizations about this phase of ontogeny are quite difficult. As we had modeled adult mammalian behavior, it was a fairly closed system adapted to a stable environment. Mammalists may well feel that whether or not adult behavior is a closed system must remain open to debate. At the very least we observe tremendous variation between species and even within species in different or changing environments. Certainly a mammalogist has a much more difficult time creating an ethogram than an ornithologist or herpetologist. Let us now proceed to question our model adult built on the assumption that the adult is highly adapted, fitted by form and stereotyped behavior to its exclusive niche in a stable environment. We will need to explain how neotenic selection for metamorphic behavior into adulthood could have become adaptive during mammalian evolution.

The model adult is highly vulnerable to environmental instability, the possible loss of the particular niche to which it is adapted, indeed, many niches have changed radically, particularly in the last few million years. During the multiple ice ages of the Pleistocene, for example, the climatic fluctuation was six times normal (Kerr, 1981) and the growing and melting glaciers opened, closed, or changed formerly stable habitats. For mammals, whenever the environment becomes destabilized, a unique opportunity arises. Instead of trying to keep pace by changing the adult form to match the rapidly changing niche, the mammals already have an ontogenetic form that is adapted to its own rapidly changing niche. Consequently, selection for metamorphic learning and against a closed system of ancestral stereotyped behavior almost perfectly adapted to one stable environment may well have taken place (Leyhausen, 1973).

Once the metamorphic phase with play/learning was introduced to mammalian ontogeny it could become available for selection to act on. Learning could swiftly replace ancestral habitat-specific behavior in the adult phase of the ontogeny of any mammalian species by heterochronic selection that retarded development enough to retain youthful behavior throughout life and never attain the complete ancestral adult stereotyped behavior. Extending the metamorphic phase into the adult period would serve to attenuate fixed-action patterns and induce more and more learning in the adult. Consequently, real adult mammals do not always have the closed systems of stereotyped behavior that we temporarily posited for the model adult. In a fast-changing environment we might have imagined that model mammals with closed behavior systems would simply have gone extinct. That only some mammalian species did in reality become extinct during the fluctuating environment of the Pleistocene is understandable when we see how relatively quickly mammals can replace a stereotyped habitat-specific behavior with a more open system of learned behavior. If the metamorphic play/learning phase could be selected to replace the old stereotyped adult system with a new, more open adult system, then learning could become more important in the adult stage.

The evolutionary process of extending youthful learning and blurring adult stereotyped behavior in many mammalian species may have proceeded until some species of mammals appear to care-solicit and play/learn throughout life history. Species of domesticated mammals often continue to display throughout life what in their wild ancestors would have been called juvenile behavior (Zeuner, 1963; Ratner and Boice, 1975; Geist, 1978; Clutton-Brock, 1981; Price, 1984). And in many wild species youthful metamorphic behavior, including neonatal motivations, do not
disappear altogether since some mammals are observed at play, however rarely, even as adults. Geist (1971) gave a model for this in mountain sheep (Ovis canadensis). It seems reasonable to assume that if youthful metamorphic play/learning becomes extended by selection into adult behavior, so will more remnants of neonatal behavior be displayed by adults.

As immediately adaptive as youthful metamorphic learning may be to the young mammal, it could also be adaptive in the adult phase in the case of a swiftly changing--metamorphosing--environment. In a changing environment such as the Pleistocene, this metamorphic animal that can adjust to changing environments may have the advantage over the stereotyped adult. Since, as we have seen, the metamorphic form is already adapted to its maladaptation, selection could change ontogeny, delaying or simply abandoning the adult habitat-specific form. One of the most efficient ways to have abandoned some ancestral stereotyped adult behavior and replaced it with a new, more open system of learned behavior was by selecting for retarded development (neoteny), thus keeping the animal in the youthful metamorphic phase for a longer time or permanently. Selection for retardation of a whole basket of youthful metamorphic behavior could happen fast with relatively few regulatory mutations (King and Wilson, 1975; Gould, 1977) compared to the traditional concept of point-by-point mutation and selection adapting the adult by adding on new stereotyped behavior. Neotenic selection for youthful learning, to one degree or another, represented for a mammalian species the swiftest and most profound re-adaptation with the least genetic investment.

If range expansion or migration by means of swift phenotypic variation became advantageous to a species, as it probably would have to many a species during the geological and climatic disruptions of the Pleistocene (Coppinger and Smith, 1983), then a neotenic retardation of the youthful behavior phase could have been selected. This more metamorphic species could add, through the interaction between its genetically retarded youthful metamorphic potential and its new environment, one or more learned combinations of micro-motor pieces of behavior to replace previously fixed-action elements with newly functional sequences. Leyhausen (1973, pp. 210-214, 227-228), for example, describes how advanced felids can replace the more primitive stereotyped "neck-shape taxis" of the typical predatory sequence with a learned alignment and orientation toward the nape of the prey's neck just before crush-bite; "This learned orientation is an entirely new mechanism, not a modification or adaptation of the innate neck-shape taxis, which persists unaltered. The cat henceforth has the choice of either way of orienting its killing bite."

Because bone fossilizes and behavior does not, natural selection for behavior rather than structure may need emphasis here. The more retarded the youthful metamorphic phase of an evolving species, the greater the potential range of learned patterns to replace innate adult elements in ancestrally stereotyped sequences. Some species, including humans, have a youthful metamorphic phase that is more retarded than that of any felid. Humans retain lifelong youthful behavior, with concomitant multi-phenotypic adaptivity. A retarded metamorphic phase in humans could at first have made their adult behavior slightly more flexible to allow a range expansion. Or it could have been that a somewhat more neotenic species greater range of possible phenotypes that were shaped by the environment during the developmental phase of successive generations gave that species an adaptive advantage in a fluctuating environment. Another
behavioral advantage of a metamorphic phase retarded into adulthood that could also have been selected for is the more social and generally less aggressive behavior of the juvenile phase that might have allowed larger, more closely cooperating groups of new semi-adult hominids to occupy the same space (Coppinger and Smith, 1983). As a behaviorally adaptive retardation became selected for over many generations, the new youthful "adults" finally could have become exapted to lifelong migration with lifelong youthful metamorphic behavior finally replacing the ancestral, more stereotyped, adult phase, even though in the case of apelike ancestors the adult phase was probably not very stereotyped to begin with. Nevertheless, the retardation of youthful; behavior into adulthood could be adjusted as to degree by heterochronic processes, i.e., by the evolutionary process of neoteny.

Once again, the direction of evolution we hypothesize as having occurred in many species of mammals—heterochronic selection replacing ancestral adult stereotyped behavior with a more juvenilized adult—is another illustration of ontogeny not recapitulating phylogeny. In reptiles and earlier forms there was no variational bonanza of play/learning behavior, such as that introduced by the metamorphic phase of mammals. We believe this process has been the chief agent in the phylogeny of mammalian learning in many species of mammals.

3. THE YOUTHFUL/ADULT AND ITS IMPLICATIONS

The phylogenetic history of mammals, from a closed reptile-like adult behavior system to a more or less open system in various species, may be precisely what made it so difficult earlier in this chapter to imagine a model adult mammal, unlike many present day adult mammal species, that had a closed system of behavior. Learning now plays a significant part in the adult behavior of some species, particularly among carnivores, cetaceans, and primates. The swift and easy learning made possible by the metamorphic phase of ontogeny may, through neotenic selection, have become a major opportunity in mammalian phylogeny.

The characteristics of play/learning are, we postulated, a consequence of the necessary youthful metamorphosis. Play/learning, then, would have little or no phyletic connection between species or even allochronically within a species. Since evolution is an active process, we would expect a radiation of adult forms as new niches became available or old ones changed. As the adult form changes, however, the metamorphic form must also change, allowing new behavioral and morphological phenotypes to arise and provide further material for variation and potential for rapid re-adaptation. Thus mammalian phylogeny has the potential for endless behavioral variety among species.

The positing of neotenic selection for youthful metamorphic behavior into the adult phase of certain mammalian species may help not only to unravel some of the complexities of mammalian development but also to explain some of the intricacies in the evolution of mammalian behavior. In particular it may help to account for the great diversity of play phenomena in mammals and birds, as well as its absence in other vertebrates.
One of the most arresting implications of this account of mammalian behavioral evolution is that metamorphic phenotypes become the material of evolutionary adaptation yet have no phyletic history to be found in any ancestral adult form. Neotenic retardation of the metamorphic phase makes possible radical and swift behavioral as well as morphological change (Geist, 1978, Wayne, 1985) with a minimum of genetic change (King and Wilson, 1975; Gould, 1977). The initiation of the youthful metamorphic phase created the mammalian potential for punctuated (Eldredge and Gould, 1972) radiation of new behaviors and forms (Hardy, 1951; de Beer, 1958; Montagu, 1962; Gould, 1977; Geist, 1978; Clutton-Brock, 1981; Price, 1984] by means of neotenic retardation. For these reasons the trend in mammalian evolution has been toward attenuation or loss of stereotyped behavior and toward more play and more learning in the new adult forms.

The fixed-action patterns of adult stereotyped behavior in most classes of animals would normally tend to offer great resistance to modification by learning. However, adult behaviors in many mammalian species are no longer anything like reptilian stereotyped, fixed-action patterns. Discussing this evolutionary trend in many mammalian adults, Eibl-Eibesfeldt (1975, p. 213) describes the breakdown of stereotyped behavior and its increasingly learned character in these words: "In higher mammals we can generally observe that fixed action patterns consist of very short movement sequences, which are combined by learning into acquired coordinations." Bekoff (1972, p. 424) wrote: "As we ascend the phylogenetic tree, there appears to be a correspondingly longer period of infancy, and more time for social interaction and play." Leyhausen (1973, p. 247) suggests that in their phylogeny "mammals gain ever better voluntary control of ever smaller motor units." Burghardt (1988) remarks that 'play' was a disparate constellation of ad hoc mechanisms to maintain continuity of endothermal and behavioral systems bridging the periods of juvenile dependence and adult responsibilities. The deterioration of certain neonatal response systems through parental care, the lowering of thresholds and broadening of effective stimuli, and the increased aerobic metabolic capacities resulting from endothermy led to a reorganization of developmental processes so that play, as well as other experimental avenues, was not only available to homeotherms but may very well have had to be exploited by them for continued survival, by replacing lost, suppressed, or maturationally delayed 'instincts,' p. 130,

Our present discussion has sought to relate and to extend such generalizations by emphasizing the study of the full developmental process of youthful behavior, including offsets as well as onsets and the concomitant fluctuations in motivations that occur almost daily, in contrast to the conventional study of play in isolation from the rest of behavioral ontogeny.

4. CONCLUSION: FROM ONTOGENY TO MAMMALIAN PHYLOGENY

In this explication of the evolution of mammalian behavior, we have proposed a hypothetical
model of the ontogeny of mammalian behavior from which we developed a theory of play and learning. Mammals all go through the specialized neonate stage. This neonatal phase provided a class-common behavior that connected species of mammals phylogenetically. Since mammals do not simply "develop" adult behavior but must metamorphose out of neonatal behaviors and into adult behaviors, the youthful metamorphic phase of ontogeny is characterized by fragments of both neonatal and adult motor patterns and motivations changing in character almost daily. The greater the number, the more independently motivated, and the smaller the motor fragments of behavior available to perform a variety of sequences, the greater the raw material potential for learning. Such behavioral variance produces vacillation between different motivations recombining motor units from diverse functional contexts giving rise to unpredictable behavior patterns that have been referred to as "play" and which lead to learning. Any fortuitous youthful behavior pattern that is reinforced can be remembered, used again, and can permanently modify behavior, i.e., play can result in learning. Like the lactation complex of the mammalian neonatal phase, youthful metamorphic play/learning seems to one degree or another class-common. Play/learning appears new in mammals and some birds and discontinuous with the behavior of reptiles and earlier forms.

We theorize that, at least initially, play/learning is the consequence of ontogenetic metamorphosis: a waning of neonate-stereotyped feeding and hazard-avoiding behaviors together with a waxing of adult-stereotyped feeding, hazard-avoiding, and reproductive behaviors. The wording "at least initially" is necessary because once metamorphosis had become a phase of ontogeny, specific developmental increments of this metamorphosis provided new behavioral as well as morphological phenotypes any one of which might have become selectively advantageous in different ecosystems. Because natural selection can act on neonatal or metamorphic behaviors as easily as it can on adult behaviors, selection has by now blurred the phylogenetic relationships with respect to behavior of many mammalian species.

We postulated that heterochronic processes, acting on the unique and rich behavioral characteristics of the youthful metamorphic phase, provided many mammalian species with new "adult" forms. Furthermore, we suggest that neotenic retardation of a species ontogeny implies that such major changes in genetic timing of development should affect the metamorphic as well as the adult phase and result in the display of unique patterns of youthful play relative to other species within the genera. Play arises, then, not from one intrinsic motivation but from many motivations and motor patterns, both neonatal and adult, which are all affected by ontogenetic changes. Since play is the consequence of a specific genetically governed metamorphic phase during the ontogeny of each mammalian species, its features will be more or less different from those of any other species. It follows that not only play but a certain range of likely learning will be idiosyncratic to each species.

If play/learning arises anew for each species or perhaps each genus or family, conventional play categories are not homologous between different species of mammals (to say nothing of birds). Yet play and metamorphic learning are not conventionally viewed as idiosyncratic to each species. It may be that as more accurate ontogenetic behavioral analyses are undertaken, the uniqueness of play and learning in each species will be revealed. We have emphasized the
usefulness of more subtle ontogenetic analyses, such as those either suggested or carried out by
Geist (1971), Count (1973), Chevalier-Skolnikoff (1974), Hall and Williams (1984), Pellis (1984, 1988), Bateson (1987), and Pellis and Pellis (1987, 1988) that include both neonatal offsets as well as adult onsets, and, in addition to these developmental dimensions, the almost daily fluctuations in motivations involved in both neonatal and adult behavior systems. We believe it is these conflicting motivations, acting on fragments of motor patterns from different functional contexts, that constitute play. It is unnecessary, perhaps confusing, to assume a separate unitary motivation or drive for play, to study play (categorizing it into object play, social play, investigative play, etc.) separately from other youthful metamorphic behaviors. Indeed, it is unlikely that conventional play categories are unitary drives even within a species when we consider, for example, the differences between object play in individual horses (Crowell-Davis et al., 1987).

From our model we should expect that the most morphologically and behaviorally neotenic species of mammals, e.g., those with the most retarded ontogenetic development and least morphological as well as behavioral changes between neonate and adult form and behavior (Gould, 1977), will be the species likely to exhibit the most play-like behavior both as juveniles and adults. Geist (1971) already provided evidence for this in mountain sheep, and we have found some evidence for the degree of neotenic form and behavior differentiating two breeds of sheep dogs (Coppinger et al., 1987). It may be possible to group other species taxonomically by careful investigation of their youthful metamorphic phase—i.e., their play behavior—in order to isolate subtle differences between species in ontogenetic timing of changes in motor patterns and their sequencing (Pellis, 1988).

The metamorphic phase of mammalian ontogeny, with its playful fertility of new behavioral repertoires, any of which can be swiftly selected for to adapt the adult, by learning, to changed or ever-changing environments, could hardly have been wrought by an evolution that worked according to the "biogenetic law." The evolution of mammalian behavior derived from a direct selection for a specialized neonatal phase so different from the adult phase that a profound metamorphosis was necessitated that has since served mammals as a kind of factory for shredding ancestral stereotyped patterns of behavior into smaller and smaller constituent micro-motor tools that can be played with and recombined into learned behavior patterns. The micro-motor units are still innate (Leyhausen, 1973) and can be selected for either individually or as a whole repertoire through systemic neoteny, retarding an entire stage of youthful metamorphic behavior into a new "adult" system of behavior in which some or most of the stereotyped macro-motor patterns are no longer expressed, or are expressed less frequently than in the ancestor. Radiations of new mammalian species often appear to have abandoned fixed macro-motor sequences for flexible micro-motor tools. These micro-units of behavior, which in the ancestor's ontogeny had been programmed to combine into stereotyped behavioral sequences at adulthood, in the new youthful/adult phase of the neotenic species remain free radicals that can combine and recombine into learned sequences. And it is the rich variety of possible motor and cognitive combinations in some species' youthful/adult phase that makes learning in these species not only easy in the laboratory (Kohler, 1926) but likely in the wild (Itani, 1958; Lawick-Goodall, 1968).
NOTES

Unfortunately, the term "neoteny" was used by de Beer (1958, pp. 64-66) in the same broad way that the word "paedomorphosis" (Garstang, 1922) is now used to refer to the result--retention of young characters of the ancestor--of two different evolutionary processes: first, the retardation of allometric development, and second, the acceleration of sexual maturation. Gould (1977, p. 27) refers to the latter process as "paedogenesis or progenesis which, like the former process of acceleration, results in a paedomorphic persistence into adulthood of young characters of the ancestor. In order to avoid confusion in terminology we wish to emphasize that we are not using the term "neoteny," as it was used by de Beer (1958) and by many writers since, to refer to both processes of acceleration and retardation. We restrict the meaning of neoteny to the process of retarded allometric development. Furthermore, we avoid the term paedomorphosis (aside from its being too broad in reference since it, too, includes processes of both developmental retardation and maturational acceleration) because its etymology suggests that only ancestrally juvenile morphological characters are retained, and we wish to investigate neotenic behavioral characters as well.

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