Settling Nature and Nurture into an Ontogenetic Niche

MEREDITH J. WEST Department of Psychology University of North Carolina Chapel Hill, North Carolina

ANDREW P. KING Department of Psychology Duke University Durham, North Carolina

All organisms inherit parents' genes, but many also inherit parents, peers, and the places they inhabit as well. We suggest the term *ontogenetic niche* to signify the ecological and social legacies that accompany genes. A formal name is needed to give the idea of the inherited environment equal status with its conceptual cognates; nature and nurture. We argue here that increased recognition of the inherited environment facilitates unification efforts within the developmental sciences by emphasizing the affinity, rather than opposability, of ontogenetic processes.

A Place for Nature and Nurture

In 1582, a teacher by the name of Richard Mulcaster delivered unto the educational world a set of terms he dubbed as "nature" and "nurture" (Mulcaster, 1582/1925; Teigen, 1984). He spoke of them in harmonious terms stressing their collaborative effects on the developing child. But history has changed the character of Mulcaster's creations, casting them more often in oppositional roles. The latter attribution would have been a deep disappointment to Mulcaster because to him they were allies: "whereto natur(e) makes him [the boy] toward, but that nurtur(e) sets him forward" (1582/1925, p. 39).

The aim here is to revive the relationship Mulcaster intended for his words. To do so, we provide his progeny with a setting, a niche designed to display nature and nurture as partners in the enterprise of development.

The Genius of Galton

It was the efforts of Sir Francis Galton that probably did the most to transform the relationship between this most memorable set of developmental terms

Reprint requests should be sent to Meredith J. West, Department of Psychology, University of North Carolina, Chapel Hill, NC 27514, U.S.A.

Received for publication 6 August 1986 Revised for publication 23 October 1986 Accepted for publication 27 April 1987 (Fancher, 1979). He used the terms as part of his analysis of the origins of scientific genius in English men of science. He wrote of the relations between nature and nurture as rivalrous ones. He used the words with an almost uncanny sense of their subliminal power, saying that:

The phrase "nature and nurture" is a convenient jingle of words, for it separates under two distinct heads the innumerable elements of which personality is composed . . . When nature and nurture compete for supremacy on equal terms in the sense to be explained, the former proves to be the stronger. (Galton, 1874/1970, p. 12).

The sense of an antagonistic relationship still lingers a century later. Even the syntactic change from nature or nurture to nature and nurture has done little to rule out the interpretation of competition between unlike forces.

But Galton also introduced an important caveat to his beliefs about competition between nature and nurture, a caveat signalled in the above excerpt by his assumption of "equal terms" for the competition between nature and nurture. Galton went on to explain the nature of these terms:

In the competition between nature and nurture, when the differences in either case do not exceed those which distinguish individuals of the same race living in the same country under no very exceptional circumstances, nature certainly proves the stronger (p. 16).

Galton thus restricted his predictions about nature and nurture to a special setting. In the case of English men of science, Galton recognized that such men inherit England along with their genes and that, without England, "English nature" could do little. Such words should not be taken as English chauvinism, but as Galton's most important point about the interdependence of developmental mechanisms.

We contrast Mulcaster's and Galton's words about nature and nurture to stress that the most serious problems with the concepts of nature and nurture today are in specifying the relationship between them. Some may feel such a goal is unnecessary because the concepts' proper setting is science's closet of skeletons. But others would argue that nature and nurture are very much alive and that efforts to revitalize their true spirit are warranted (e.g., Gottlieb, 1976; Johnston, in press).

The addition of a niche might seem only a semantic art. We argue later that it is not, but such an interpretation does not bother us because words matter greatly. If we are told nature and nurture compete, we assume divisibility, and we look for the strong and the weak. If we are told they are rivals, we go so far as to create numerical scores to determine which prevailed. But if we are told nature and nurture are allies, what different ontogenetic processes might be proposed and what metrics might evolve to measure their collaborative effects?

To alter the sense of the words, we first return to the theme Galton identified, the coinheritance and coexistence of species-typical genes and species-typical habitats, a proposition central to the ecological concept of the niche (Grinnell, 1924) and to theories of cultural evolution (Boyd & Richerson, 1985).

We propose the term *ontogenetic niche* to stand for the set of ecological and social circumstances inherited by organisms. We choose the term because it captures both the physical requirements necessary for the existence of a species and the particular role or occupation of that species within the broader ecological community. We are in effect combining the two meanings used by ecologists, the

physical and the functional (Hutchinson, 1978). Many ecologists also adhere to this joint meaning probably because of the natural affinities between the physical requirements of a species and the means by which they obtain them (Whitaker, Levin, & Root, 1973).

Hutchinson (1978) notes that the term "niche" originally was employed by ecologists as it is used by architects as a "place or position" adapted to an object's characteristics (p. 156). This meaning of "niche" as a recessed space to display something also has its place in our scheme because we hope to set nature and nurture in the best light.

Galton knew the importance of names—both for scientific phenomena as well as for English men of science. In our nomination of "ontogenetic niche," we recognize the dangers inherent in tampering with such nomenclature, that of oversimplification. This danger, however, is offset in our minds by the need for simple yet strong words to describe development. To say that nature and nurture "interact" is now a commonplace expression but advances our thinking very little because interactions can be of many kinds. The behaviors displayed by friends and foes can both be described as interactions but they rest on functionally different premises. Nor does the statistical meaning of "interaction" help because it implies that one can tally the segregated accomplishments of nature and nurture: adding numerical to nominal fallacies is not a step forward (Anastasi, 1958).

The relationship between nature and nurture has also been described as "bidirectional" as a way of specifying its operations. But what kind of bidirectionality? Is a symbiotic or parasitic or compensatory system? Interdependent systems vary greatly in form and have been applied in different ways to explaining relationships (Meier, 1984; Rosenblum & Moltz, 1983).

Before attempting to fit nature and nurture into a niche in any of its senses, any possible confusion among the terms "niche," "nurture," and "environment" must be addressed. Nurture is sometimes equated with the contribution of "the environment" to development. But to equate nurture with the environment is improper because the environment is equally a part of nature. Moreover, the term "the environment" itself has different meanings and should not be considered a synonym for "niche" (Schleidt, 1981).

To some, the term "environment" summons to mind the variable and unpredictable actions of "Nature" with a capital "N" as used in phrases such as "Mother Nature" or "Man against Nature." Here, the meaning is the broad set of controlling forces that define the biosphere. Ecologists would label this kind of environment as the "ecotope." But to others, the term "environment" defines the particular and unique surroundings of each species. Here, the term, "habitat" comes closest to the ecological meaning. The difference in meaning between ecotope and habitat is vital because we speak of organisms evolving defenses and buffers against the vagaries of the environment-as-ecotope, but speak of organisms evolving sensitivities and dependencies on the environment-as-habitat.

We see the ontogenetic niche as that part of the *environment-as-habitat* devoted to development and we leave analysis of the environment-as-ecotope to ecologists. Within this framework, nurture is *not* to be equated with "environment" in either sense, but with the business of living and developing within the niche.

We recognize that the triadic form "nature-nurture-niche" is more difficult to enunciate and perhaps to think about. But its very cumbersomeness might guard against the dangers of oversimplification. Managing three concepts may eliminate old habits, especially the tendency to depict development in two dimensions. What follows here are three perspectives derived from the triadic form. First, we look at niches as legacies that support and structure the development of their occupants. Second, we consider the niche as a link between parents and offspring, examining development as a transgenerational cycle. Finally, we look at some of the behaviors that occupy niche inhabitants particularly those that may provide for continuity and change in the life of a species.

The Niche as a Legacy

The Gibsonian approach to perception was once summed up as "Ask not what's inside your head, but what your head's inside of" (Mace, 1977). To understand the niche as a legacy, we amend that phrase to "ask not what's inside the genes you inherited, but what the genes you inherited are inside of." And we propose that genes inherit a rich and supportive environment, a fact few dispute but few discuss with any urgency. The dependence of genes on their immediate somatic environment is clear, but few have explicitly named the somatic environment as a unit of heredity (but see Medawar & Medawar, 1983; Montagu, 1959; Oyama, 1982; Schleidt, 1981). Montagu stated the relationship explicitly:

The potentialities of each individual are dependent on ontogenetic endowment, but these potentialities have a wider range than is generally observed, so that the environment which is part of the individual's inheritance is also the means by which heredity can be changed, modified, enlarged, and so on (1959, p. 109).

The concept of the ontogenetic niche derives from Montagu's idea. The niche is a legacy bequeathed to progeny and responsible for the diverse but dependable influences on the developing organism. Despite Montagu's words and many other's implicit recognition of the inherited environment, genes are still identified in most texts and dictionaries as the unit of heredity and the science of genetics has been dubbed the most basic of the biological sciences (Mayr, 1982). Because of the vast successes in understanding the nature of genetic material, it has become easy to overlook the seminal role of the gene's niche as an equally basic part of development.

An emphasis on genetic inheritance may also have been fostered by the aforementioned confusion about what is meant by the term "environment" and whether it is friend or foe. And, as technology has made genes and their components more visible and tangible, it has become easier to make their role seem more basic. And as long as the environment is viewed only in its ecotopic role as an uncontrollable agency capable of "infinite fortunities" to be thrust on the developing organism (Gesell, 1929, p. 318), its role will seem less measurable and less important (Boyd & Richerson, 1985). Gesell's thoughts about the nature of the environment might now be considered outmoded but for the fact that his description of the environment as unpredictable continues to appear in strong form, especially in the sociobiological arena where the idea of "the phenotype at the mercy of the environment" still flourishes (Stearns, 1982, p. 252; see also Gould, 1982; Marler, 1982).

It is the bounty of the environment-as-habitat, not the unmerciful nature of the environment-as-ecotope that concerns us. Ontogeny relies on *exposure* to such bounty—a point we shall continue to stress because it is still common in the 1980s to encounter the opposite point—that developing organisms need to be

protected or buffered from the vagaries of the environment. Leon Eisenberg (1971) offered the following explanation for why organisms are less often viewed as beneficiaries, and more often as victims, of their surroundings:

The challenge in understanding such [positive] interactions lies in overcoming the limitations of our own ingenuity in recognizing those aspects of the ubiquitous environment that we fail to see precisely because they are ever present (p. 523).

A developmental-ecological approach is required to see those aspects of the ubiquitous environment that underly niche-dependent development. By a developmental approach, we mean adopting paradigms that capture what animals do while developing and tell us the experience of ontogeny. By an ecological approach, we mean examining the nonarbitrary connections between species-typical surroundings and species-typical behavior (Johnston & Turvey, 1980).

G. E. Coghill is a model of a developmental approach. He and his colleagues studied the ontogeny of salamanders by walking around a laboratory table housing 30 specimens in 15-min rounds that were repeated without interruption for days on end to witness and record the ontogeny of behavior from embryonic motility to first swimming. Their efforts left a circular path in the floor at the University of Chicago, providing unusual physical evidence of the marks of good developmental science (Herrick, 1949). And Coghill's efforts allowed him to see growth as more than a preprogrammed unfolding. Of human development, he said a "Man is, indeed a mechanism, but he is a mechanism which, within his limitations of life, sensitivity, and growth, is operating himself" (1929, p. 110).

Gottlieb's two decades of work on perceptual development in ducklings exemplifies a developmental-ecological approach. Via a window he fashioned in the eggshell, he looked and listened to embryos within the prenatal niche. By observation and experiment, he identified the acoustic stimulation and appropriate prenatal behavior necessary to explain the duckling's postnatal identification of its mother, an instinctive response previously thought to rely only on genetic inheritance (1971, 1976). More recently, Gottlieb and his associates have shown that inheriting siblings plays a crucial role in when and under what circumstances imprinting occurs (Johnston & Gottlieb, 1985; Lickliter & Gottlieb 1985, 1986). Given the volumes of work on maternal, filial, and sexual imprinting, that so obvious a part of the hatchling's niche as its siblings are just now receiving due attention attests to Eisenberg's observation of the ease with which the obvious can be overlooked (see Kruijt, ten Cate, & Meeuwissen, 1983; Porter, Cernich, & Matochik, 1983) for other examples of sibling influences).

More recently, the embryonic environment of rats has become more visible (Smotherman, 1982; Smotherman, Richards, & Robinson, 1984) and the more we see, the more possible it becomes to see the embryo as a machine operating itself. Moreover, embryos and fetuses are active and aware in ways that affect present and later development. For example, Gandelman's mapping of the fetal mouse's neighborhood by sex of nearest neighbors has led to new discoveries about later sexual differentiation of males and females (Gandelman, vom Sall, & Reinisch, 1977).

Mapping of the ontogenetic niche can facilitate the description of not only ongoing, but also future developmental states. One means of knowing how cells in the adult cat's visual cortex will respond to particular patterns of light is to know that cat's history, or lack of it, with patterned light (Hubel & Wiesel, 1963). So too, a record of what sounds were available to young wrens during their first

summer can predict what songs they learn not only then, but also the next spring, revealing evidence of environmentally dependent sensitive periods (Kroodsma & Pickert, 1980). Both of these instances of development exploit the niche as a dependable form of inheritance. The odds that a kitten encounters patterned light and textured surfaces around its 4th or 5th week or that a songbird inherits conspecifics which sing in his presence are about even with those that predict the presence of whiskers and feathers, respectively.

The Niche as a Link

Niches are social and physical entities. And for the typically social animals for whom the topic of nature-nurture has been an issue, their niches rest on transgenerational social dynamics. The process of rearing young so that genes can be passed on brings us to the second perspective, the niche as a link between generations.

Genes are of course not passed on—the phrase itself is a vestige of the pregenetics era recalling the original meaning of inheritance as the transmission of names, homes, belongings, social status, or resources to offspring. Such social or exogenetic inheritance relies on different processes that those transmitting DNA (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981). Whereas genes are the permanent possessions of parents and their offspring, exogenetic forms of inheritance are highly vulnerable to rapid modification or extinction by the actions or lack of them by parent or offspring. Whether it be something so transitory as the value of a family name or so special as the family territory, parents and offspring are inextricably linked in the efforts to preserve the value of exogenetically transmitted properties.

In principle, legacies such as nest sites, breeding grounds, sources of preferred food, and migration routes exist independent of parents. But in practice, the links to these resources are often parents or peers (Galef, 1975, 1982; Mainardi, 1980; Rheingold, 1963). Galef and Wigmore (1983) describe the wild Norway rats' nest site as an "information centre" in which members learn about potential areas for foraging that exist beyond the nest. And they point out that for the young rats the link to such information is their mother and, in particular, the flavor of her milk. And, that link, the mother's milk, is available only by virtue of the joint behaviors of the dam in making her milk available and the pups in sucking and stimulating milk production.

That something so simple as mother's milk so easily indicates two kinds of transgenerational links, the nourishing and the educating of young, attests to the power of social processes. Diverse examples exist of the mechanisms that regulate the parent's ability to give, and the young's ability to receive the resources necessary for growth and survival (for overviews, see Gubernick & Klopfer, 1981; Rheingold, 1963; Rosenblum & Moltz, 1983). Adult-offspring regulatory mechanisms range from the physiological and hormonal to the behavioral. In rats, the nursing mother's loss of fluid and electrolytes is in part compensated for by the ingestion of pup urine. A behavior often thought of as an adaptation in response to the pup's needs is thus also an adaptation to the mother's needs (Alberts & Gubernick, 1983).

So too, in rats, maternal licking of the anogenital area of pups has other consequences beyond the mother's and pup's immediate needs. Chemical differences in the composition of male and female pup urine elicit different amounts of

maternal licking, a difference of direct consequence for later male sexual behavior (Moore, 1984). These examples are important because they again show the significance of the tangible contacts between parents and young. The "mother tongue" of the rat, as in many other mammals, represents a real and rich means by which to study ontogenetic linkages.

Exogenetic means of transmitting behavior takes many other equally real forms within the confines of the parent-young unit. Rat pups' postnatal recognition of nipples can be influenced by manipulating the odors experienced in the uterine environment, suggesting that the amniotic surroundings can familiarize the young with properties of their yet-to-be experienced postnatal environment—the link again is the mother who provides both intra- and extrauterine olfactory landmarks (Pedersen & Blass, 1982). Human infants also appear to exploit intraand extrauterine sensory analogs, in particular, the sound of their mother's voice. Prenatal "eavesdropping" makes possible postnatal discrimination and a preference for the human mother's voice soon after birth (Decasper & Fifer, 1980; Decasper & Spence, 1986). The capacity is fine-tuned enough such that newborns can discriminate the differences in the sounds of different Dr. Seuss stories on the basis of prenatal familiarity: they prefer the sounds their mothers read to them before they were born. Fathers' voices can also be discriminated after birth but are not preferred, revealing the significance of the physical link between mother and young (DeCasper & Prescott, 1984).

Parents, siblings, and other allies can thus serve not only to sustain ongoing development, but to promote the often rapid perceptual and social adaptations needed by the young to accommodate to changes affected by birth or hatching. Thus, when viewing the niche as a link, we can see the obvious ultimate dependence of the generations on one another, but more importantly, we can see and measure instances of proximate dependence.

The presence of adult and youthful adaptations to accomplish the "passing on" of genes stands as a broad comparative principle. Both generations display specialized behaviors when occupying the role of parent or offspring. That parents need to be "good" parents seems the more obvious case but "good" young, in terms of appropriate responsiveness, make "good" parents. And thus the broader principle to emerge is the interdependence of parent and offspring competence and the necessity to study them as linked processes. As Alberts and Gubernick caution, "the behavior of one is indecipherable when isolated from the other" (1983, p. 11).

Perhaps what is most exciting now about deciphering such linkages is the evidence that it can be done. The idea of the niche is not intended as a metaphor but as a descriptor of the context in which development takes place. The specific behaviors that constitute development in context bring up the issue of the "costs" of genetic and exogenetic means of transmission. It takes work and effort to turn genes into something. A growing challenge in psychobiology is to understand these costs (and benefits, see Galef, 1983) in physiological and psychological terms. The cost/benefit analyses popular among sociobiologists do not substitute for observation and measurement of the actual, as opposed to theoretical, economics of ontogeny.

A further challenge rests in understanding the processes by which mothers and fathers turn sons and daughters into the next generation of mothers and fathers. Although the human and primate literature suggests that parents also function as models and motivators of their offspring's subsequent parental

behavior, much more needs to be learned to understand the links within links (Hinde, 1974). The idea of a niche as a link within a link was best captured not by a scientist, but by a pianist who began a concert by thanking his parents for making his appearance possible and his children for making it necessary (Victor Borge). And his words advance us to the third perspective, the niche as a way of life.

The Niche as a Way of Life

Mother mason wasps have an architectural solution to parenting (Bonner, 1980). They lay their eggs in a series of brood chambers leaving each egg provisioned with enough food to last through pupation. When the young emerge, they travel through the partitioned and provisioned chambers toward ultimate independence. For most vertebrate parents, not only physical but also behavioral accommodations must be provided for the young to survive. And it is in this sense that the ontogenetic niche is a way of life because it specifies the behavioral adaptations of its occupants.

With respect to life in the ontogenetic niche, we select here only two broad categories of behavior, the play of the young and the prospective behavior of adults. These behaviors highlight the "forward reference" of ontogeny, i.e., the presence of structures and behaviors that appear to anticipate outcome (Coghill, 1929; Herrick, 1924). Play and prospective behaviors also permit a way of capturing the changing dynamics of the parent-offspring relationship. It is said of the climate in certain locales—if you don't like the weather, wait a minute. With respect to the nature of parent-offspring relations, the same advice holds. During the course of development, both parents and young change in ways that serve to advance both into new behavioral states.

The psychobiological concept that comes closest to specifying the behavioral accommodations of adults and young in the niche is that of *ontogenetic adaptations*, a concept derived from neuroembryology whose significance for behavioral development has best been explicated by Oppenheim (1981). Ontogenetic adaptations are transient neural, physiological, hormonal, or behavioral phenomena that have evolved to be used at specific points in development and then to disappear or develop into different behaviors. The egg tooth of a chick is needed to pierce the shell but not afterward—here is a morphological adaptation that literally disappears.

Many behavioral adaptations undergo less obvious but equally consequential transitions. Neonatal rats suck to obtain milk, but such sucking is not necessary in order for the development of later independent feeding (Hall, 1975). It is necessary for the pups to survive to be able to feed independently. Human infants show remarkable transitions in reaching abilities during the first year of life, marked at times by a decline in ability as reaching changes in form from an elicited to a guided behavior (Bushnell, 1985).

Oppenheim suggests that play may qualify as both an ontogenetic adaptation and as a developmental antecedent of later adult behavior. Ambiguity in the definition of play and the inability to manipulate the incidence or frequency of play have made it a troublesome category for establishing its role as a prerequisite for any later adult behavior. But there is one feature immediately recognizable to all who have watched young animals play arguing for its clear status as an ontogenetic adaptation—the young do it well. An ontogenetic adaptation in some

sense has to be done well—the egg tooth must be there and "work" when hatching commences; the rat pup has to suck vigorously when the dam is present.

Play has often been misunderstood with respect to its proximate functions because it appears to be designed out of bits and parts of later adult roles—hunting, socializing, fighting, and mating. But these bits and pieces often occur in such a random design that play can seem a Rorshach test for projecting later possible adult functions. But play is interpreted as immature and incomplete behavior only when the reference is later adult behavior. When the play of young is observed through less adultomorphically biased lenses, a different view emerges. Watching animals play is seeing them at their best. It is to view professionals in the game of growth. Woodworth (1942) said it best:

Nothing is more characteristic of the growing child than the eager use of all his powers . . . Excess movement is eliminated and different skills are combined. If the child does not learn to walk, at least he learns to walk well . . . (pp. 219-220).

Learning to do something well is a performatory metric not given enough emphasis. This is not to say that autogenous behavior (or so-called "practice") has not long been recognized as a functional part of development, but its role in "perfecting" a behavior the animal can already perform needs more study. Kaufman (1975) calls this the study of "learning what comes naturally," Anzai and Simon (1979) label the process "learning by doing", but, by any name, something that occupies so many of the waking hours of the young of so many species deserves more study.

First on the agenda should be to study what young animals are actually doing when we say they are playing (no matter what we call it). Given the theoretical importance attached to the concept of "early experience," it is time to study the experience of early experience. Play represents one of the most pervasive forms of such experience and so seems the place to begin. Surely studying animals when they are truly active should be as interesting as writing abstractions about the "active" organisms. Active, how? Active, when? Active, with whom?

Play is not the only youthful behavior of consequence but it is one of multiple consequences. Play is often nominated as a mechanism of cultural invention. Such youthful behaviors, in Piaget's words "supply evolution with its principal motor" (1978, p. 139). Play propels the young into the role of agents of cultural change, they become "niche-busters" to adopt a linguistic fad of the 1980s. It seems an especially apt term because the young often treat their physical and social surroundings with as much lack of delicacy as does the hatching chick when dispensing with its shell.

Prospective Behavior of Parents

We doubt if anyone knows if young mason wasps follow their mothers' architectural instructions without dawdling or tinkering or exploring along the way. Perhaps they just docilely eat their way toward independence. But for many species, the initial ontogenetic niche sets only a general course permitting the young to be players as they poke, prod, and provoke their surroundings. Presumably in other species, but acutely so in humans, it falls to parents and other adults to pick up after the efforts of the young. Niches remain stable across generations in part because of the prospective behavior of adults. Such behaviors

are most obvious in our own species where care-giving and culture-giving go hand-in-hand and where defining the line between liberty and obedience is a never-ending generational debate.

Prospective behaviors, so salient in human adults engaged in parenting, suggest that ontogenetic adaptations are not limited to youth. Lifespan approaches to development make abundantly clear that concepts first worked out with respect to early development such as that of developmental stages or sensitive periods apply to other points in development as well (Lerner & Busch-Rossnagel, 1981). Learning to be a parent may have its roots in sibling interactions or childhood care of other children. But the full force of the learning comes with one's own child and thus happens by definition in adulthood. The relevance of sensitive periods and stages of parental development to understanding effective parenting is now the topic of serious study that should soon yield examples of ontogenetic adaptations as concrete as those identified in the young (Flavell, 1974; Sigel, 1985).

If the behavior of the young provides evolution with a motor, then that of parents provides a map. Parents are responsible for the transmission of much information about the niche (Barnett, 1973; Galef, 1975; Mainardi, 1980). The social transmission of food preferences appears in many species to depend on the young being observant and quick to copy the actions of their elders. Wild Norway rats approach foods they have seen the dam approach (Galef, 1982) and in junglefowl, the mother vocalizes and inhibits her own eating as a means of orienting her young to food (Sherry, 1977). So too, mother cats and dogs bring prey and leave it for their young who often first lick the mouth and nose of the mother before turning to the object whose odor they have just experienced (Rheingold, 1963; Schneirla, Rosenblatt, & Tobach, 1963).

One need only watch the food-gathering efforts of passerine birds or attempt to hand-rear a young songbird to appreciate how dramatically parenthood changes the daily life of animals. But many of the accommodations adults make to be effective parents remain to be studied in detail because often everything seems to be running so smoothly that the behaviors responsible go unappreciated. Silver (1983) noted in ring doves that "Each transition in the development of the young is matched by an adjustment in the behavior of the parents. This orderliness emphasizes the function of behavior and obscures underlying mechanisms" (p. 148). Going behind the scenes to see how adults orchestrate care means looking for what at first seems hidden, making it a classic case for the developmentally-minded detective (Hofer, 1978).

The study of human parents is no less exciting and offers the additional perspective of how parents think about parenting—and think they do, day in and day out. They see in the refusal of their 6-month-old to drink from a propped bottle the specter of their son-the-soldier going off to war with weapon in one hand and parent in the other (Bettelheim, 1962). They see in each feature of their newborn genetic affinities with relatives and decide which "side" contributed what (Macfarlane, 1977). Such questions might seem absurd but emphasize the anticipatory thinking and actions of human parents. Talking to parents reveals that their antennae switch rapidly and often frantically to tune in the past, present, and future as they adjust to the signals of their young (Holden & West, 1983). Humans must be the broodiest beasts in the animal kingdom. They associate with their offspring for decades, allocate untold reserves of energy and resources to them, and all the while incubate endless anxieties about what lies ahead.

Summary: The Niche as a Nest

The ontogenetic niche has been considered as a legacy, a link, and a way of life for its occupants. We propose it as an objective way to represent the complex of genetic and experiential processes of development commonly subsumed under the names of nature and nurture. The value of the niche is, at one level, only nominal—it does not substitute for or even stand for the myriad of concepts that constitute the science of development (see Oppenheim, 1982; Oyama, 1982). But, at another level, even if the term's only contribution is to alter the familiar metric of the phrase "nature-nurture," then it has succeeded. The triadic form may trip us up and in our stumblings, new words will come forth.

But what is more important is if the triadic form causes us to ask questions about other familiar words. It should not be enough to say that a behavior is inherited—inherited how, by genetic or exogenetic means? It should not be sufficient to say that the environment altered a behavior—which environment and how? Nor should it be enough to say organisms learn about their environment—how do they do so? Ecological and social legacies are inherited, but, more to the point, they are earned. The law of effect must be matched by the law of effort. This second law is needed to emphasize that some of the behaviors that appear without the traditional trappings of learning, such as human language or upright locomotion, do not occur without intrinsically motivated effort. Walking and talking may not be taught but try to teach a toddler how to walk or how to talk or not to talk or not to walk.

We end with literal roots of the word "niche." It comes to us from the French, meaning "a nest." This literal sense is crucial. It is the best way to capture the social and functional framework the niche gives to nature and nurture. A nest is an actual site where parent and young can be seen settled into their natural relationship. As we have said repeatedly, we are attracted to the niche because it connects developmental processes. When we put nature and nurture into a nest, we see not their divisibilities but their affinities. And, as a nest unites and supports its occupants in their different ontogenetic endeavors, so too, the concept of the niche places the "distinct heads" of nature and nurture together again, portraying them not as rivals, but as kin.

Notes

Writing of this paper was facilitated by grants from the NSF BNS 84-01115 and NINCD&S (1 K01 NS00676-5). A similar version was read at the 1985 meeting of the Society for Research in Child Development in Toronto, Ontario. We thank J. R. Alberts for his encouragement and advice, M. Leon, R. W. Oppenheim, and E. Thelen for comments, and D. Fogelberg for writing "Leader of the Band."

References

Alberts, J. R., and Gubernick, D. J. (1983). Reciprocity and resource exchange: A symbiotic model of parent-offspring relations. In L. A. Rosenblum & H. Moltz (eds.), Symbiosis in Parent-Offspring Interactions. New York: Plenum. Pp. 7-44.

Anastasi, A. (1958). Heredity, environment, and the question "How"? Psychol. Rev., 65: 197-208. Anzai, Y., and Simon, H. A. The theory of learning by doing. Psychol. Rev., 86: 124-140.

Barnett, S. A. (1973). Homo docens. J. Biosoc. Sci., 5: 393-403.

Bettelheim, B. (1962). Dialogues with Mothers. New York: Avon.

Bonner, J. T. (1980). The Evolution of Culture in Animals. Princeton, NJ: Princeton University Press.

Boyd, R., and Richerson, P. J. (1985). Culture and the Evolutionary Process. Chicago: University of Chicago Press.

Bushnell, E. E. (1985). The decline of visually-guided reaching during infancy. Infant Behav. Dev., 8:

139-155.

Cavalli-Sforza, L. L., and Feldman, M. W. (1980). Cultural Transmission and Evolution: A Quantitative Approach. Monographs in Population Biology, 16. Princeton, NJ: Princeton University Press.

Coghill, G. E. (1929). Anatomy and the Problem of Behavior. New York: MacMillan.

DeCasper, A. J., and Fifer, W. P. (1980). Of human bonding: Newborns prefer their mothers' voices. Science, 208: 1174-1176.

DeCasper, A. J., and Prescott, P. A. (1984). Human newborns' perception of male voices: Preference, discrimination, and reinforcing value. *Dev. Psychobiol.*, 17: 481-492.

DeCasper, A. J., and Spence, M. J. (1986). Prenatal maternal speech influences newborns' perception of speech sounds. *Infant Behav. Devel.*, 9: 133-150.

Eisenberg, L. (1971). Persistent problems in the study of the biopsychology of development. In E. Tobach, L. A. Aronson, and E. Shaw (eds.), *The Biopsychology of Development*. New York: Academic Press. Pp. 515-532.

Fancher, R. E. (1979). A note of the origin of the term "nature and nurture." J. Hist. Behav. Sci., 15: 321-322.

Flavell, J. (1977). Cognitive Development. Englewood Cliffs, NJ: Prentice-Hall.

Galef, B. G. (1975). Social transmission of acquired behavior: A discussion of tradition and social learning in vertebrates. In E. Tobach, L. R. Aronson, and E. Shaw (eds.). Advances in the Study of Behavior, 6. New York: Academic Press. Pp. 77-97.

Galef, B. G. (1982). Studies of social learning in Norway rats: A brief review. Dev. Psychobiol., 15: 279-296.

Galef, B. G. (1983). Costs and benefits of mammalian reproduction. In L. A. Rosenblum and H. Moltz (eds.), Symbiosis in Parent-Offspring Relations. New York: Plenum. Pp. 249-278.

Galef, B. G., and Wigmore, S. W. (1983). Transfer of information concerning distant foods: a laboratory investigation of the 'information-centre' hypothesis. *Anim. Behav.*, 31: 748-758.

Galton, F. (1874/1970). English Men of Science: Their Nature and Nurture. 2nd ed. London: Frank Cass & Co.

Gandelman, R., vom Sall, F. S., and Reinisch, J. M. (1977). Contiguity to male fetuses affects morphology and behavior in female mice. *Nature*, 266: 722-723.

Gesell, A. (1929). Maturation and infant behavior patterns. Psychol. Rev., 36: 307-319.

Gottlieb, G. (1971). Development of Species Identification in Birds. Chicago: University of Chicago Press.

Gottlieb, G. (1976). Roles of early experience in the development of behavior and the nervous system. In G. Gottlieb (ed.), Studies in the Development of Behavior and the Nervous System. Vol. 3. New York: Academic Press. Pp. 25-54.

Gould, J. L. (1982). Ethology: The Mechanism and Evolution of Behavior. New York: W. W. Norton.

Grinnell, J. (1924). Geography and evolution. Ecology, 5: 225-229.

Gubernick, D. J., and Klopfer, P. H. (1981). Parental Care in Mammals. New York: Plenum.

Hall, W. G. (1975). Wearning and growth in artificially reared rats. Science, 190: 1313-1315.

Herrick, C. J. (1924). Neurological Foundations of Animal Behaviour. New York: Holt.

Herrick, C. J. (1949). George Elliot Coghill. Chicago: University of Chicago Press.

Hinde, R. A. (1974). Biological Basis of Human Social Behaviour. New York: McGraw-Hill.

Hofer, M. A. (1978). Hidden regulatory processes in early social relationships. In P. P. G. Bateson and P. H. Klopfer (eds.), *Perspectives in Ethology*, Vol. 3: Social Behavior. Pp. 135-166. New York: Plenum

Holden, G. W., and West, M. J. (1983). The parent as naive psychologist. Paper presented at the meeting of the Society for Research in Child Development, Detroit, MI.

Hubel, D. H., and Wiesel, T. N. (1963). Receptive fields of cells in striate cortex of very young, visually inexperienced kittens. J. Neurophysiol., 28: 1041-1059.

Hutchinson, G. E. (1978). An Introduction to Population Ecology. New Haven: Yale University Press. Johnston, T. D. (in press). The persistence of dichotomies in the study of behavioral development. Devel. Rev.

Johnston, T. D., and Gottlieb, G. (1985). Effects of social experience on visually imprinted maternal preferences in Peking ducklings. Dev. Psychobiol., 18: 261-271.

Johnston, T. D., and Turvey, M. T. (1980). A sketch of an ecological metatheory for theories of learning. In G. H. Bower (ed.), The Psychology of Learning and Memory, New York: Academic Press. Pp. 148-207.

- Kaufman, I. C. (1975). Learning what comes naturally: The role of life experience in the establishment of species-typical behavior. *Ethos*, 3: 129-142.
- Kroodsma, D. E., and Pickert, R. (1980). Environmentally dependent sensitive periods for avian vocal learning. *Nature*, 288: 477-479.
- Kruijt, J. P., ten Cate, C. J., and Meeuwissen, G. B. (1983). The influence of siblings on the development of sexual preferences of male zebra finches. *Dev. Psychobiol.*, 16: 233-240.
- Lerner, R. M., and Busch-Rossnagel, N. A. (1981). Individuals as Producers of Their Development: A Life Span Perspective. New York: Academic Press.
- Lickliter, R., and Gottlieb, G. (1985). Social interaction with siblings is necessary for visual imprinting of species-specific maternal preferences in ducklings. J. Comp. Psychol., 99: 371-379.
- Lickliter, R., and Gottlieb, G. (1986). Visually imprinted maternal preference in ducklings is redirected by social interaction with siblings. Dev. Psychobiol., 19: 265-277.
- Macfarlane, A. (1977). The Psychology of Childbirth. Cambridge, MA: Harvard University Press.
- Mace, W. M. (1977). James J. Gibson's strategy for perceiving: Ask not what's inside your head, but what your head's inside of. In R. Shaw and J. Bransford (eds.), Perceiving, Acting, and Knowing: Toward an Ecological Psychology. Hillsdale, NJ: Erlbaum. Pp. 43-67.
- Mainardi, D. (1980). Tradition and the social transmission of behavior in animals. In G. W. Barlow and J. Silverberg (eds.), Sociobiology: Beyond Nature/Nurture. AAAS Symposium 35: Pp. 227-256. Boulder, CO: Westuien.
- Marler, P. (1982). Some ethological implications for neuroethology: The ontogeny of birdsong. In J.-P. Ewert, R. R. Capranica, and D. J. Ingle (eds.), Advances in Vertebrate Neuroethology. New York: Plenum. Pp. 21-52.
- Mayr, E. (1982). The Growth of Biological Thought: Diversity, Evolution, and Inheritance. Cambridge, MA: The Belknap Press.
- Medawar, P. B., and Medawar, J. S. (1983). Aristotle to Zoos: A Philosophical Dictionary of Biology. Cambridge, MA: Harvard University Press.
- Meier, G. W. (1984). Behavioral development: A goal-directed dialogue. Dev. Psychobiol., 17: 573-586.
- Montagu, A. (1959). Human Heredity. Cleveland: World Publishing Co.
- Moore, C. L. (1984). Maternal contributions to the development of masculine sexual behavior in laboratory rats. Dev. Psychobiol., 17: 347-356.
- Mulcaster, R. (1582/1925). Mulcaster's Elementarie. London: Clarendon Press.
- Oppenheim, R. W. (1981). Ontogenetic adaptations and retrogressive processes in the development of the nervous system and behaviour: A neuroembryological perspective. In K. J. Connolly and H. F. R. Prechtl (eds.), Maturation and Development: Biological and Psychological Perspectives. Philadelphia: J. B. Lippincott Co.
- Oppenheim, R. W. (1982). Preformation and epigenesis in the origins of the nervous system and behavior: Issues, concepts, and their history. In P. P. G. Bateson and P. H. Klopfer (eds.), Perspectives in Ethology. Vol. 5. Ontogeny. New York: Plenum. Pp. 1-100.
- Oyama, S. (1982). A reformulation of the idea of maturation. In P. P. G. Bateson and P. H. Klopfer (eds.), Perspectives in Ethology. Vol. 5. Ontogeny. New York: Plenum. Pp. 101-131.
- Piaget, J. (1978). Behavior and Evolution (D. Nicholson-Smith, Trans.). New York: Pantheon.
- Pedersen, P. E., and Blass, E. M. (1982). Prenatal and postnatal determinants of the 1st suckling episode in albino rats. *Dev. Psychobiol.*, 15: 349-355.
- Porter, R. H., Cernich, and Matochik, J. A. (1983). Littermates influences on behavioral development in Acomys cahirinus and Mus musculus. Z. Tierpsychol., 62: 93-104.
- Rheingold, H. L. (ed.) (1963). Maternal Behavior in Mammals. New York: Wiley.
- Rheingold, H. L. (1963). Maternal behavior in the dog. In H. L. Rheingold (ed.), Maternal Behavior in Mammals. New York: Wiley. Pp. 169-202.
- Rosenblum, L. A., and Moltz, H. (1983). Symbiosis in Parent-Offspring Interactions. New York: Plenum.
- Schleidt, W. M. (1981). The behavior of organisms, as it is linked to genes and populations. In P. P. G. Batseon and P. H. Klopfer (eds.), Perspectives in Ethology, Vol. 4: Advantages of Diversity. New York: Plenum. Pp. 147-155.
- Schneirla, T. C., Rosenblatt, J. S., and Tobach, E. (1963). Maternal behavior in the cat. In H. L. Rheingold (ed.), *Maternal Behavior in Mammals*. New York: Wiley. Pp. 122-168.
- Sherry, D. (1977). Parental food-calling and the role of the young in the Burmese junglefowl (Gallus gallus spadiceus). Anim. Behav., 25: 594-601.
- Sigel, I. E. (1985). Parental Belief Systems: The Psychological Consequences for Children. Hillsdale, NJ: Erlbaum.
- Silver, R. (1983). Biparental care: Hormonal and nonhormonal control mechanisms. In L. A.

- Rosenblum and H. Moltz (eds.), Symbiosis in Parent-Offspring Interactions. New York: Plenum. Pp. 145-172.
- Smotherman, W. P. (1982). In-utero chemosensory experience alters taste preferences and corticosterone responsiveness. *Behav. Neur. Biol.*, 36: 61-68.
- Smotherman, W. P., Richards, L. S., and Robsinson, S. R. (1984). Techniques for observing fatal behavior in utero: A comparison of chemomyelotomy and spinal transection. *Dev. Psychobiol.*. 17: 661-674.
- Stearns, S. C. (1982). The role of development in the evolution of life histories. In J. T. Bonner (ed.), Evolution and Development. Dahlem Konferenzen. Berlin: Springer-Verlag. Pp. 237-258.
- Teigen, K. H. (1984). A note on the origin of the term "nature and nurture": Not Shakespeare and Galton, but Mulcaster. J. Hist. Behav. Sci., 30: 363-364.
- Whitaker, R. H., Levin, S. A., and Root, R. B. (1975). On the reasons for distinguishing "Niche, habitat, and ecotope." *Amer. Nat.*, 109: 479-481.
- Woodworth, R. S. (1942). Psychology. 4th Ed. New York: Holt.