

# The Inheritance of Niches

## The Role of Ecological Legacies in Ontogeny

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### EXOGENETICS: SEEING THE OBVIOUS

The study of genetics overshadows that of exogenetics for three reasons. First, no single unit of exogenetic inheritance exists. Even the most central feature of exogenetic inheritance, the concept of something “outside” the genes, lacks clarity. That something is the environment, but how do we define the environment? To some, the term stands for the complex of biotic elements that surrounds all organisms. To others, the term refers to a particular species’ or population’s habitat.

Lack of a name makes any concept easier to neglect. Dawkins’s “meme” (1976) or Lumsden and Wilson’s “cultorgen” (1981) do not qualify as appropriate constructs for our purposes because they represent attempts to parallel cultural and morphological evolution. The objective here is to consider exogenetic inheritance from an ontogenetic, not a phylogenetic, perspective.

The study of exogenetics is also made more difficult by its external diversity of form across cultures: What do nest sites, territories, dominance ranks, dialects, food preferences, money, furniture, names, and family businesses have in common beyond their fate as examples of legacies? The material of biological inheritance is known, and the means by which its information is decoded has been worked out for many organisms, revealing common rules. The lack of a common foundational material and/or common rules for exogenetic inheritance makes its study appear

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more complex. Consult the card catalog in any university library, and before you will be a bewildering array of entries to cover the historical and modern laws pertinent to the inheritance and rights to succession of property for countries, cultures, and religions. Whether or not something can be passed on, to whom, and under what conditions represent important questions for every society.

And recurrent among the questions is the issue of an individual's "right" to wealth or property in relation to behavior: Merely because of kinship, should land and/or money remain in the possession of those who did not labor for it? Humans have answered this question differently at different times in different places. It is a question much like that underlying debates about the degree to which "nature" or "nurture" plays a deterministic role in development—a debate also centuries old. Is it, then, surprising that the subset of humans designated as scientists have yet to formulate "the" principles governing exogenetic inheritance?

Finally, the heavy hand of human habit has also hindered the study of exogenetics. We of the twentieth century now feel comfortable equating heredity and genes. This sense of comfort is not easily disturbed. To say a behavior or a trait is inherited is now taken to mean something quite concrete; it is to say that exploration (and possibly engineering) of only the genetic substrate is in order.

An issue embedded within this third problem is the "value" of the behavior and the consequences to humans of decisions about a behavior's ontogenetic status. When the behavior in question is the phototactic response of an insect, only a handful of experts might quarrel about the role of genetics and exogenetics. But when the behavior in question is IQ, the quarrel cannot be contained in the laboratory, and the harm done by insufficient analyses is immense. Thus, explorations into any form of inheritance can be intimidating.

## THE SEMANTIC CONVERSION OF NATURE AND NURTURE

The phrase "nature and nurture" entered the language in 1582, the creation of a teacher named Richard Mulcaster (Teigen, 1984). He saw these entities as forces acting in harmony to advance a child's development: "Whereto natur(e) makes him [the boy] toward, but that nurtur(e) sets him foreward" (Mulcaster, 1582/1925, p. 39). Shakespeare and Carlyle used these words to put forth much the same view of ontogeny. It was Sir Francis Galton, as part of his analysis of English scientists, who cast the terms into different roles (Fancher, 1979):

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 the stronger. (Galton, 1874/1970, p. 12)

Mulcaster's friends became Galton's foes. In his transformation of the relationship between nature and nurture, Galton created a perception of the nature of the interaction between genes and experience that dominated science for many

years. Much has been written about Galton's words: less has been said about the visual image implied, that of the "distinct heads" of nature and nurture. The picture it brings to mind is that of the compelling, ambiguous picture often labeled the "wife-mother-in-law" picture (Boring, 1930). Boring brought this "puzzle picture" to the attention of psychologists because it displayed a more complex form of a figure-ground illusion (see Super, 1981, for the use of another illusion in relation to culture). Other illusions typically involve alternating figure and ground perceptions based on a shared external contour, but in the case of Figure 1, "the two alternating figures interpenetrate each other spatially and there is no definite division of the field by a contour" (Boring, 1930, p. 444).

Nature and nurture also have a complex figure-and-ground relationship, and they often compete for equal attention, leading easily to Galton's perception of them as rivals:

In the competition between nature and nurture, when differences in either case do not exceed those which distinguish individuals of the same race living in the same country under no very exceptional conditions, nature certainly proves the stronger of the two. (Galton, 1874/1970, p. 16)

Galton's use of the terms *competition* and the *stronger of the two* reveal his perceptual bias. But his words also explain why the concept of nature-nurture, like Boring's ambiguous picture, is so complex an illusion. Galton stated that he could



Figure 1. The wife-mother-in-law illusion. (From E. G. Boring, *American Journal of Psychology*, 1930, 42, 444-445).

not predict developmental outcomes except in the case where countrymen possessed not only their countrymen's genes, but also their countrymen's country. Thus, although Galton declared nature normally to dominate, he assumed that the contributions of nature automatically depended on those of a particular environment: The English inherit English nurture along with English nature.

It is the interpenetrability of nature and nurture that Galton perceived. At other points in his treatise, he noted the lack of clear boundaries between nature and nurture and presented a unified, as opposed to competitive, view of them. In this regard, he cited Carlyle's prior use of the term *nurture* (1838/1937) and his own subscription to Carlyle's view that "an infant of genius is quite the same as any other infant, only that certain surprisingly favourable influences accompany him through life, especially through childhood, and expand him, while others lie closefolded and remain dunces" (Carlyle, pp. 93–94). Thus, Galton could see both sides of the nature–nurture illusion: he could see companions, and he could see competitors. But in the end, he saw only the latter view.

Boring (1930) introduced his "puzzle picture" as a means of studying the phenomenon of perceptual set because "neither figure is favored over the other" (p. 445), so that the experimenter has an opportunity to explore how words change what subjects see. We consider it critical that, when Galton introduced the terms, he also introduced a perceptual set. If we are told that nature and nurture compete, we look for divisibility; we look for the strong and the weak. But if we are told that they are part of one another, that neither exists without the other, we come to apprehend their composite design. It is the composite view of nature and nurture that Galton had seen but chose not to stress: the interpenetrability of species-typical genes and species-typical habitats.

## A PLACE FOR NATURE AND NURTURE

We offer the term *ontogenetic niche* to capture the set of ecological and social circumstances that come with an organism's genes. The term *niche* is used by ecologists to specify both the physical habitat of a species and the role of the species in the ecological community. It gives the species' address and its occupation (J. Alberts, personal communication, 1987).

Given the disagreements that have been engendered by the terms *nature* and *nurture*, why risk additional unproductive debate by the addition of a niche? Three reasons motivate us. First, the major problem, as we see it, with the terms *nature* and *nurture* lies in specifying the relationship between them. To say nature and nurture "interact" is an agreeable but vague proposition that often does not lead to testable hypotheses. The time has come to find words, not diagrammatic arrows or numerical formulas, to capture the synergy of ontogeny. The ontogenetic niche is one means of stimulating the search for functional metrics of development, metrics that capture the translation of initial abilities into actual proficiencies.

A second source of motivation comes from observing the success of the niche

in the science of ecology. Ecology seeks to understand the relationships between organisms and the resources that they need to survive. It is not the study of nature with a capital *N* or of its conservation. The closest parallel we know is to a discipline, formerly labeled a science, now an archaic college major: home economics. Home economics has gone the way of husbandry. The study of house, hearth, offspring, land, or livestock smacks of the mundane in a modern world. But when the home under study is not yours, mine, or ours, but everyone's, it is the very stuff of current science—it is ecology. Thus, ecology is the study of homes with a capital *H*, and it has much to teach us about how the different social relationships and interactions of individuals serve as higher order regulatory mechanisms.

Ecology confronts the same issues as homemakers: What are the dynamics of organism–resource interrelationships? Clean clothes no more find their way into drawers or hot food onto the table than do crickets appear at the mouths of gaping nestlings or leaves appear on the trees just as nests become of interest to predators. The providential appearance of any ecology, animal or human, is misleading. It is the same providential quality of exogenetic inheritance that may have fostered its neglect. We take for granted that genes inherit an environment and that that environment supports ontogeny. But the time has come to recognize and analyze these implicit assumptions—assumptions we have found ourselves forced to reformulate in our own research because animals do not “interact” with one another in the same way that statistical variables do (King and West, 1987).

We define the niche as that part of an animal's environment constituting its species-typical habitat. We exclude from consideration those parts of an animal's environment common to all organisms, the universal environment or ecotope (Hutchinson, 1978). Within this framework, the word *environment* is neither a synonym for *nurture* nor an antonym to *nature* or *genes*. Despite the word's frequent occurrence in the vocabulary of psychologists, it often qualifies as no more than jargon. And thus, part of our fascination with ecology's niche is frustration with psychology's environment, a problem many others are now addressing (see Johnston and Turvey, 1980; Schleidt, 1981, 1985) and a problem boldly confronted by psychologists such as Barker (1960), Brunswick (1955), and Stone (1943).

The final incentive to adding a niche is that many others have recognized the role of the inherited environment in ontogeny, although few have formally labeled it as a unit of heredity. Montagu (1959) stated the idea explicitly:

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

Others have come to the same conclusion (see especially Boyd and Richerson, 1985; Medawar and Medawar, 1983; Oppenheim, 1982; Oyama, 1982; Super and Harkness, 1981). But genes still reign supreme in most texts, and most dictionaries define them as “the” units of heredity. By giving the concept of exogenetic inher-

itance a formal name, but one easy to say, we hope to make its trip beyond the tip of the tongue as painless as possible.

### THREE PERSPECTIVES ON NATURE–NURTURE–NICHE

The triadic form of nature–nurture–niche leads to at least three ways in which ontogenetic phenomena can be viewed (West and King, 1987). The niche represents a legacy, a link, and a way of life for its occupants.

It is the dependability of the niche in delivering certain resources to the young that makes it a legacy. Warburton (1955) once complained that genetic programs that explicitly excluded environmental feedback were “comparable to being sewn into one’s winter underwear” (p. 136). The concept of the ontogenetic niche demonstrates why the young of so many species need no such preprovisioning: they inherit the senses and the surroundings to find what they need. The Gibsons’ ecological approach to perception (J. Gibson, 1966, 1979; E. Gibson, 1969) offers, at present, the most powerful analogue for viewing the niche as a legacy because they developed their theories to deal with a similar problem, the nature of the mechanisms permitting accurate perception.

What the Gibsons proposed for theories of perception was a biologically and ecologically based taxonomy of the affordances of an animal’s habitat. They showed that an animal’s surroundings provide sure footing for perceiving. The need was not to search for the internal mechanisms to correct or protect the animal from the vagaries of an erratic environment, but to search for the behaviors used to explore and detect features of the niche and ways to measure and categorize the niches themselves. By so doing, they turned the study of perception inside out. Mace (1977) summed up the Gibsons’ approach as “ask not what’s inside your head, but what your head’s inside of” (p. 43). When viewing the niche as a legacy, we say the same: Ask not what is inherited by genes, but what genes inherit.

The basic task of describing the ontogenetic environment has often followed rather than preceded attempts to study ontogeny by depriving the young of or enriching them with certain external influences. Although such manipulative approaches address the historically relevant question of the degree of interdependence of genetic and environmental mechanisms, they often only indirectly illuminate the normal processes of development. Few of the studies on the effects of sensory or social enrichment or deprivation in young animals provide meaningful details of what happens *during* treatment. What do animals do when isolated that their socially housed peers do not? How do young behave when in the presence of increased or decreased levels of particular forms of stimulation? Measuring the experience of early experience must become a preeminent practice.

Such a practice is called for to deal with two facets of ontogeny. First, it is clear that many animals can and do undergo different kinds of early experience and yet show similar adult phenotypes—there are multiple pathways to the same goal. But animals can also undergo different experiences and manifest different

adult behaviors. Understanding which adult outcome occurs offers the opportunity to uncover the mechanisms underlying ontogenetic transitions (Meier, 1984).

The niche is also a link between generations. With this perspective, it is possible to see not only the ultimate dependence of the generations on one another, but their proximate dependence via mechanisms that promote orderly transitions in species-typical development for both adults and young. The niche is a link as well because many exogenetic legacies, such as nest sites, breeding grounds, food, and migration routes, require social interactions between parents and young in order for the resources to be used (Rheingold, 1963).

The study of the parent-offspring relationship in rodents offers diverse examples of the specificity and connectivity of the links. Galef and Wigmore (1983) revealed the wild Norway rat's nest site to be an "information center" in which members learn about potential sites for foraging that exist at some distance from the nest. Moore (1984) demonstrated that the mother rat's licking of her pups contributes to later sexual differentiation because the dams lick males more than females, discriminating chemical differences in the pups' urine. Alberts and Gubernick (1983) connected maternal licking and development even further by demonstrating that nursing dams replenish their loss of fluid and electrolytes by ingesting pup urine. And Pedersen and Blass (1982) demonstrated that odors experienced *in utero* and immediately after birth lead to nipple attachment by rat pups, thereby physically linking mother and young. And finally, Fillion and Blass showed that odors experienced while suckling facilitate the recognition of estrous females. Male rat pups denied experience with their dams' normal ventral odors show less reactivity to estrous females both in infancy (Fillion and Blass, 1986a) and in adulthood (Fillion and Blass, 1986b). Thus, there are links within links exposing the young to stimuli of future relevance when they initiate adult sexual behavior.

Links between parents and offspring or between offspring do not just happen. Members of both generations must act to realize their investments as parents or inheritances as offspring. The niche is thus a way of life and is the study of behavioral ecology. To illustrate the niche as a way of life, we consider the social and physical habitats inherited by the young of several different species. How do differences in their ontogenetic niches affect the offspring that inherit them? In particular, we are trying to begin to identify the overarching social mechanisms that affect an individual's development.

### THE ACORN WOODPECKER: THE ROLE OF THE FAMILY TREE

Finding the center of the acorn woodpecker's physical niche is easy: this species congregates in family groups guarding granary trees in which they have drilled and filled up to 30,000 holes with acorns or other nuts. For a young woodpecker, the characteristics of this tree dictate much of its future. But finding the center of the woodpecker's social niche is more complex and has even more relevance to the young woodpecker's ontogeny (Stacey, 1979; Stacey and Koenig, 1984).

In this species, in certain geographical locations, the demographics of the social environment vary with the availability of food: in areas in which granaries remain plentiful, the setting saturates with successful breeders bequeathing to the young the problem of finding a reproductive vacancy. Given that the young cannot affect resource saturation before hatching, they must accommodate to the circumstances they inherit.

If a young acorn woodpecker is hatched in an area such as coastal California, where the food supply is plentiful and available nesting territories are few, then it will probably spend at least one and perhaps up to four to five years as a helper in its natal group. In this group will be one or more mature breeders of each sex and juveniles from past breeding seasons. These juveniles will help to raise the new brood by gathering food, defending the nest and the granary, drilling holes in the granary, increasing the supply of stored food, and fighting off predators. All of these activities contribute to the survival of the young helper, to the survival of the family, and to the survival of the species. But this "good fortune" of the species may lead to problems for any given individual young woodpecker. If the survival rate is high, then juveniles abound, and as breeding age approaches, competition for nest sites is an event of uncertain outcome for the individual.

Some juveniles will not be able to contribute any offspring to the extended family unless all breeders of the opposite sex die or move on. If its parents are young and healthy, then the juvenile must strike out on its own in order to make its genetic mark in the woodpecker world. Finding an unoccupied nesting site or fighting to fill a reproductive vacancy in another group may then be its legacy. If unsuccessful, it may return home to assume the role of "protector" of the collective family resources, postponing, perhaps indefinitely, its own opportunity to be a parent.

The role of "protector" provides a more indirect pathway toward reproductive success. If ecological constraints on new colonization and new breeding opportunities exist, then the juvenile bird can maximize its contribution by preserving and protecting the "family genes" (Stacey and Koenig, 1984). It may also receive the bonus of acquiring better parenting skills, which will, at some later time, enhance its reproductive success.

If, however, a young acorn woodpecker is born in an area such as New Mexico, where the food supply is more limited, a different future unfolds. If the supply of food is not sufficient to last a group during the winter, then that group must leave its territory in search of food. Nesting sites are then available for the juveniles of other groups. Juveniles spend fewer years serving as helpers in their natal groups, and group size is much smaller than in California (Stacey, 1979). But smaller group size means fewer helpers, and fewer helpers mean less food, often leading to winter dispersal and decreased chances of surviving the winter.

Thus, for the acorn woodpecker, the composite nature of the family tree, in nutritional and generational dimensions, affects the duties that the young come to perform, the choice of mate, and whether they mate at all. And where the family tree is geographically situated has overarching effects on the nature and timing of these occupational transitions in the lives of individual woodpeckers.

The center of the scrub jay's niche is even easier to locate because the social and physical cores converge on the family nest. And as for some of the woodpecker groups, the state of the nest at the time of an individual's hatching has much to say about how the young will spend their youth and adulthood. Most remain apprentices or helpers for at least 1 year, some for much longer, before leaving to form a new breeding pair or taking over reproductive duties at the natal nest. Jays with large extended families appear to thrive, a fact suggesting that the occupation of helper or surrogate parent has benefits for both the group and the individual. There are not only immediate advantages in terms of nest and territory defense, but also the intangible advantages of learning what to do when assuming the role of actual breeder. Breeding pairs produce more independent young if there are helpers in the nest, and breeders that have been helpers produce more nestlings than novice breeders (Woolfenden, 1975; Woolfenden and Fitzpatrick, 1984).

But any individual's chances for actual parenthood vary greatly, depending on the initial and continuing state of its extended family. Within the family, there is a dominance hierarchy headed by a male breeder. Linear dominance also exists among male and female helpers, age being the primary factor. Thus, the oldest helper should be the first to leave and set up its own breeding pair. But the dynamics are more complex. A younger helper may be displaced by an adopted helper, usually low in the chain, which may appear after the death of the same-sex breeder. This immigrant may then mate with its adoptive mother, thereby displacing the previously dominant male helpers.

Because males dominate females, a male juvenile may inherit the family nest after the death of its father. Its mother may then be forced to leave and mate with a lone male in another group. The possibility of such a legacy may explain the degree of helping among juveniles because jays are philopatric, and thus, the young have a vested interest in the protection of the nest and the territory. Families with older male helpers (older than 2 years) frequently have larger territories than those with older female or younger male helpers. The territorial expansion may be due in part to a more active territorial defense by males. It may also result in direct benefits for the older male helper, which may then be able to establish an ancillary territory and thus increase its potential breeding possibilities.

In another jay species, the Mexican jay, several nests may exist within the same family territory. These nests belong to members of the same family that have mated with immigrant birds. Juveniles may help in the nest of their parents, their grandparents, or their siblings. Although maintaining separate nests, they forage and defend as a group and may also help feed all the young in the unit. These birds thus also have a special interest in the protection of their territory because it is passed down through successive generations (Brown and Brown, 1981).

The woodpeckers, and especially the jays, illustrate a crucial point about exogenetic legacies: the continuing behavioral efforts demanded of both young and old to maintain their value. Unlike genes, which are the permanent possessions of progenitor and progeny, granary trees and family nests are of changing value

depending greatly on the collective industry of their owners. The state of the granary tree is critical to opportunities for breeding and the survival of the young; so, too, the size of the jay's territory correlates with nestling success. Thus, in such species, behaviors must be transmitted as to how the legacies are to be maintained (e.g., how to drill holes, how to replace moldy nuts, how to drive off intruders, and how to attract mates). And it is the social obligation to shared family resources that makes the generationally intermediate role of helper seminal; it is a means to preserve exogenetic legacies. The young may be bequeathed a potentially supportive habitat, but its potential remains only that unless the young learn to exploit it. Exogenetic legacies are inherited, but they are also earned.

It is probably no phylogenetic coincidence that many human cultures also value and reward helping by the young by giving them precedence as legal heirs. A founder of the American jurisprudence system put it as follows:

It is in accordance with the sympathies and reason of all mankind, that the children of the owner of property, which he acquired and improved by his own skill and industry, and by their association and labor, should have better title to it than the passing stranger. (Chester, 1982), p. 41)

### THE COWBIRD: LIVING UP TO ITS GENETIC POTENTIAL

The most obvious exogenetic legacy of a mother cowbird to its offspring is also a nest, but in this case, it contains eggs of other species. Much effort precedes the choice of nest and the female lays many eggs. Ideally, female cowbirds get their offspring off to a good start by laying in a nest already containing an egg or two, ensuring that it will be actively attended, and with eggs slightly smaller than the egg containing the cowbird. The cowbird typically hatches first and, by virtue of being bigger than its foster siblings, can exploit its size and first-hatched status to thrive (King, 1978).

But beyond this inheritance, cowbirds would seem to inherit only an abundance of problems. Cowbirds can hatch into the nests of over 200 different subspecies, so that the natal niche is unpredictable and undependable as a means of acquiring species-typical behaviors. Cowbirds appear to possess no special adaptations and are no more or less successful nestlings than other "cross-fostered" young (Eastzer, Chu, and King, 1980). If anyone warranted Warburton's winter underwear, it would seem to be the cowbird. Given the differences in its natal niche compared to that of most vertebrate young, has the species evolved a comparatively reduced dependence on exogenetic heredity?

Cowbirds do not appear to be exceptions to many of the statements made here about exogenetic inheritance; the major difference is one of timing and type of inheritance. In this respect, the cowbird represents an excellent example of the need to consider transitions in the nature of niches, transitions common to many nonparasitic species that contribute to the realization of exogenetic and genetic inheritance (Alberts and Cramer, Chapter 1; Oppenheim, 1981).

That the cowbird begins life in a natal niche quite unlike the one that it inhabits as a juvenile is not really unusual for birds; it is the jay or the woodpecker that

is unusual in remaining for so long with its parents. Transitions in habitat and social groups occur in many species. The cowbird is perhaps only a more obvious case of the discontinuities that characterize many species' social and ecological circumstances.

But to leave the nest is to enter a new stage of development in which new capabilities are required and in which old ones are no longer applicable. After their foster rearing, young cowbirds form flocks with other young and adult cowbirds. How do they "know" to do so? Why not remain socially and/or physically attached to their foster species? Do special recognition mechanisms help them to meet other cowbirds?—probably none more complex than those proposed by Holmes and Sherman (1983) for many species. Cowbirds become attracted to other cowbirds because they have evolved a need of the same kind of food, food found in only certain locations: in the case of cowbirds, insects found at the feet of ungulates or on their grazing grounds.

Thus, initial juvenile flock formation in cowbirds is a case of association mediated by attraction to a common need: food. It is undoubtedly aided by innate social affinities as well. Young cowbirds reliably appear at our aviaries when under 30 days of age with nothing more to attract them than the sights and sounds of other cowbirds. But our aviaries border pastureland and cows, so that it could be the coexistence of preferred food and preferred stimulation that produces the result. Our experience suggests that cowbirds find cowbirds easily. What appears to be difficult is living up to the genetic gifts of their parents, gifts that begin to develop at about this time—in particular, the male's ability to develop courtship songs and the female's capacity to discriminate among songs.

Male cowbirds that have never heard other cowbirds sing can produce and discriminate potent songs (King and West, 1977, 1986). Female cowbirds that have never heard adults sing can respond appropriately and selectively to conspecific song (King and West, 1977). To some, these data are sufficient to suggest that cowbirds are the only songbirds that do not require species-typical experience in order to develop normal song (Rothstein, Yokel, and Fleischer, 1985). But such an interpretation is wrong because it ignores the fact that ontogeny involves both the natural origins and the natural modifications of behavior. It also ignores the fact that the natal niches producing origins may be quite different from the juvenile niches that facilitate modifications.

Burghardt (1977) termed the conceptual confusion in the interpretation of ontogenetic data the difference between the "O" question (for origins) and the "M" question (for modification). He cautioned that the "processes involved in the developmental shaping of a behavior may have little in common with those subsequently altering such behavior" (p. 79).

And it is just this kind of confusion that has led to confusion about whether the cowbird learns its song by genetic or exogenetic means. Males may inherit a potentially rich genetic legacy, but realizing its value depends greatly on the subsequent behavior of the legatees in relation to the social circumstances surrounding them. And here, cowbirds are like jays or woodpeckers because precisely what surroundings they live in have much to say about later reproductive success.

A series of studies sensitized us to "O" versus "M" confusions. The clearest

indication came from carrying the classic “deprivation” experiment to its functional conclusion. For many years, “Kaspar hausen” singers have been considered the genetic standard bearers for the study of birdsong, revealing to human listeners the “innate blueprint” provided by genes (Marler, 1982; Thorpe, 1961). Not only is the logic of such an experiment wrong; so is the typical methodology (West and King, 1985a). Isolation from song is usually confounded with isolation from social companions. Moreover, the experiment is often not carried out to its functional endpoint: How does the Kaspar hausen fare when faced with conspecifics?

We were empirically prodded to ask this question because our classic deprivation experiment yielded an odd result: the acoustically deprived males’ songs were not worse than those of normally reared males, nor were they the same—they were “better”! We had tested the songs’ potency by playing them back to receptive wild-caught females deprived of male company, and these females had responded twice as often to the songs of the acoustically naive males as to the songs of those with normal acoustic stimulation (King and West, 1977). Did the result mean that isolation from song was “good” for cowbirds? The finding seemed even odder given that song learning in the wild took place in a social setting containing singing adults. To understand this apparent anomaly, we took the next functional step: we asked if an acoustically naive male would be successful when actually courting females.

The songs of isolate males of many species have not been tested in a functional arena because of the often quite global pathogenic effects of social and acoustic isolation. But by being provided avian companions (sometimes other juveniles, sometimes females, and sometimes other species), cowbirds can be deprived of adult song and still be successfully tested for the functional end point of song development. In cowbirds, such individuals can settle into a captive colony under one important condition: that they do not sing their potent song to females in the presence of resident males. This is a condition that their previous isolate rearing has not prepared them for (preparing them perhaps in the opposite direction), thereby explaining the seemingly anomalous effect of naive song of “super normal” potency.

Thus, by observing captive colonies, we learned that, whereas males housed alone with females or heterospecifics can sing with impunity, new males in a social group cannot. A naive cowbird singing a potent song does not succeed in that context until it learns to behave effectively with the other males. Potency may be inherited, but the “right” to sing is not (West and King, 1980; West, King, and Eastzer, 1981). In cowbirds, the juvenile niche is a forum in which males learn the pragmatics of singing, which appears to be a performatory, if not sometimes martial, art. The juvenile niche also serves as an acoustic forum for modifying the exact acoustic content of song, making the male’s song more geographically specific and more attractive to local females. Without such opportunities for modification, the genetically well-endowed male is actually poorly equipped because the songs it produces may be representative of the species but not optimized to a particular population or individual.

These studies, however, do more than show the need to answer the two kinds

of ontogenetic questions. They emphasize the role of the particular ecological and social circumstances that surround maturing organisms. Our work has also shown that the presence of females is an especially important circumstance. In a series of studies, we documented the ways in which males modify what they sing as a function of the behavior of nonsinging female cowbird companions (King and West, 1983a; King, West, and Eastzer, 1980; West and King, 1985b; West, King, and Harrocks, 1983). What determines song modification is the dynamics not of one's auditory environment, but of one's audience. The cowbird's niche is a public arena.

Several studies revealed the potential power of the female as a silent partner in the process of song modification. First, we learned that adult eastern *Molothus ater ater* males would become bilingual only if housed with males and females from a geographically separate population of a second cowbird subspecies, *M.a. obscurus*, but not if housed with only *Molothus ater obscurus* males, a finding suggesting to us that the eastern adults required both the means (hearing *M.a. obscurus* song) and the motive (the female) to modify their singing.

Second, we studied naive eastern *M.a. ater* males housed for an entire year, with (1) other species; (2) adult eastern *M.a. ater* females; or (3) adult *M.a. obscurus* females. At the end of this period, the three groups of males (all obtained as eggs from the same colony and most likely full or half siblings) had developed structurally and functionally different vocal phenotypes, although none had ever heard another male sing (King and West, 1983a; West and King, 1985b).

The performance of the males with other species proved a convenient midpoint, as these males experienced abundant social and vocal stimulation from their starling or canary companions, but none of species-typical relevance. Their repertoires were diverse; they sang some prototypical *M.a. ater* and *M.a. obscurus* song and some highly atypical song, including imitations of starling and canary vocalizations. The nonspecific nature of their repertoires highlighted the biasing effects of the females in the other two groups. The females' presence apparently produced local song differentiation: the males with *M.a. ater* females sang all *M.a. ater* songs; the *M.a. ater* males with *M.a. obscurus* females sang predominantly *M.a. obscurus* song, but some *M.a. ater* song. In nature, such differentiation is undoubtedly further facilitated by feedback from males serving as fellow performers and sometimes censors of what is sung.

As a further test of the effect of female stimulation, we explored the impact of females when appropriate auditory input was present (King and West, 1983a). Here, *M.a. ater* males were tutored with a potent *M.a. ater* song and were individually housed with *M.a. obscurus* females or nonconspecifics. Again, the males developed significantly different repertoires. Males with other species sang significantly more of the tutor song than did males with *M.a. obscurus* females. The males housed with these females sang reliably more original song, but songs that were functionally unattractive to *M.a. ater* females. Thus, even when males were given the acoustic means of learning, the behavior of the heterosubspecific female modified the outcome (West and King, 1985b).

All of the effects reported took place before the females displayed any breeding behavior at all, and thus, the data are based on songs measured and tested

before the males had seen a female in a copulatory posture. The young males are apparently sensitive to stimulation from females from as early in development as they can sing (King and West, 1987). It is also important to say that however the females affected the differences in the structure and potency of the males' songs, they did *not* do it by singing. In the two experiments just reported, over 30,000 songs were recorded with an observer present; all were sung by males and none by females.

What was most visible about the vocal behavior of the males housed with the females in the aforementioned experiments was the number of songs and song attempts performed by males that were met with apparent indifference by the females. The seemingly indefatigable energy of the singing male stood in stark contrast to the passive posture of the "listening" female as, song after song, she stared straight ahead with not so much as a head turn toward her companion. Although we cannot yet specify how females communicate their likes and dislikes, their apparent inattention is quite likely a powerful social mechanism because it highlights the specific times when they do change their behavior by moving toward or away from the male, by moving their wing feathers, and by turning their heads. Because of the high incidence of no visible change in their behavior, when changes such as wing movements or approaches did occur, they had a high "signal-to-noise" ratio.

But why is it to the female's "advantage" to influence song development? Given that local females show a high level of intrasexual concordance in song perception, would not their individual efforts tend to homogenize song content among local males, thereby removing song content as a means of comparing males? Perhaps females "help" males learn to sing to enhance the female's ability to assess males. By stimulating males to sing the same song material, the females would then be able to make finer discriminations among males by judging how well the males sing a song the females know well. If males are to be "socially screened" in West-Eberhard's terms (1983), a screening based on the same material would appear to be most advantageous. Homogenization of song material might also have the effect of allowing females to assess males on other attributes, such as dominance status, that might be important indicators of a male's fitness.

The tutorial behavior of the female also brings us back to the original problem faced by the cowbird: How does it develop species-typical behavior, given it does not hatch into a nest with parents and peers of its own species? As our studies show, however, the cowbird inherits a juvenile niche containing other cowbirds, some of which may well be its own parents and/or siblings. Whether kin recognition occurs is not known; nor is it known whether related females or males associate with one another preferentially. But cowbirds may not have abdicated all parenting behaviors: care giving to the young may be carried out by a foster species, but culture giving may not be. The propensity of juvenile males to modify their song may then coincide in time with their contact with kin, an association that normally occurs earlier for other species.

These studies demonstrate the role of the inherited niche in quite a proximate sense. We now have evidence of the niche's impact at a more ultimate level. In all

of our work on eastern *M.a. ater* cowbirds, we conceived of the female as a guide, in part because its own behavior appeared inflexible, even after considerable attempts to manipulate its innate preference (King and West, 1983b, 1987). But studies of a different population of cowbirds suggests that such inflexibility may be a local response to the specific properties of the inherited environment.

Recently, we tested the perceptual responsiveness and modifiability of *M.a. ater* females from a different part of this subspecies' range: females living in Oklahoma near the morphologically described subspecies border with *M.a. obscurus*, the southern subspecies. We asked the same questions we had asked of North Carolina *M.a. ater* females: First, would Oklahoma *M.a. ater* prefer their own population's song in comparison to *M.a. obscurus* song, and second, would Oklahoma females show a lack of perceptual modifiability if housed with *M.a. obscurus* males?

The results revealed differences between the two populations of the same subspecies. Wild-caught adult Oklahoma females demonstrated as statistically strong a preference for Oklahoma *M.a. ater* song as did North Carolina females for North Carolina *M.a. ater* song, compared to *M.a. obscurus* song. But when young and adult Oklahoma females were housed for nine months with *M.a. obscurus* males, they showed no preference for either *M.a. ater* or *M.a. obscurus* song; they had developed an apparently equal tolerance for the two subspecies variants (King, West, and Eastzer, 1986).

The Oklahoma and North Carolina populations that we compared differ in four ways: (a) the Oklahoma females live in populations that are much denser than those in North Carolina, (b) the Oklahoma birds live much closer to the subspecies border (250 miles compared to 1,500), (c) they represent part of the ancestral population for the species, whereas cowbirds have colonized North Carolina only since the mid-1940s (Potter and Whitehurst, 1981), and (d), the Oklahoma females live in the central as opposed to the peripheral part of the species range. How these ecological differences relate to the potential differences in modifiability is now the topic of our inquiries.

At this point, our working hypothesis is that Oklahoma females are more sensitive to song differences because the acoustic and social environment surrounding them is different from that of the North Carolina females. The songs of Oklahoma males are more stereotyped in terms of their rhythms and musical qualities—subtle differences to humans, but not to the female cowbirds (King *et al.*, 1986). In order for the females to make the finer discriminations, especially when judging more males (given the greater population density), early exposure and learning may be beneficial. The degree of fine discrimination required has thus led to a more flexible developmental program to “tune” the female's perceptual system to the sounds of her local population.

Wild-caught females from Oklahoma show preferences not only for local songs as opposed to songs from 250 miles away, but for songs of their own subspecies from 1,500 miles away as well: when tested for their responsiveness to North Carolina as opposed to Oklahoma song, they show a strong native bias. In contrast, North Carolina females exposed to the same contrast show no discrimination, responding equally to *M.a. ater* songs from several locations along the east-

ern coast or from the Oklahoma site. Because cowbirds are more sparsely settled in the East, local differentiation of songs may not have evolved to the point where early exposure can have any measurable effect. The capacity for subtle song discrimination and modification of song preferences may be latent or absent in eastern populations, but in any case, it is different within the same subspecies.

Thus, the females from Oklahoma tell us that ontogenetic programs for song perception may vary even within the same subspecies because the "environment" of a subspecies varies in both a social and a physical sense. Determining which features of an animal's surroundings are stable or labile may help us to predict the ecological circumstances that will favor one ontogenetic pattern over another. Such an analysis may also elucidate how different geographic addresses demand different divisions of labor within the same species. Whereas in the East the female cowbird appears to take the lead in guiding song development, in the West the male's influence appears to be preemptive. But in both cases, synergistic links between the sexes and the settings obtain.

### HUMAN FAMILIES: CONFLUENT INHERITANCE

In much the same ways that woodpeckers, scrub jays, and cowbirds are shaped by the culture they inherit, humans also find themselves in quite different "nests." Much of what a human infant first experiences is determined by parental choice. Children are exposed to the foods their parents eat, hear the music that parents choose, meet the people that the family likes, wear the clothes that suit the parents' tastes, and live in rooms bearing the decorating biases of adults. In Rheingold and Cook's study (1975) of children's rooms in a university town in the 1970s, they found no weapons in the rooms of girls and no doll carriages or accessories in the rooms of boys. Given the supposedly "liberated" atmosphere of that decade, the data suggested a different atmosphere:

Clear in the findings of this study was the extent to which the boys were provided with objects that encouraged activities directed away from home—toward sports, cars, animals, and the military—the girls, objects that encouraged activities directed toward the home—keeping house and caring for children. (p. 463)

None of these early unidirectional influences are unchangeable, but for most children, parents have the upper hand in fashioning children's physical and social environment for many years. Of more lasting importance than the nature of their rooms or toys may be the social nature of the family configuration they live in. Much has been written about the implications of being the oldest, the middle, or the youngest child. Researchers have linked possible differences in such areas as personality, academic achievement, and language development to birth order and the age difference between siblings (Altus, 1966; Zajonc and Markus, 1975). Zajonc (1986) related the decline in scholastic aptitude scores that occurred from 1962 to 1980 to the birth order of the test takers. The reversal in the decline of test scores began in 1980, at the time when children from smaller families became

of test-taking age. The same trends toward higher scores were found for children in the elementary grades. If these data do point to important influences, then a child's college admission, career choice, and potential success in the "marketplace" may be affected by the number of siblings already in the family "nest" when he or she arrives.

Given the possibility of differences in such important skills, an important task becomes to find out how differences within the family structure proximately influence development. At present, a study is under way to examine families with one or two children, where the youngest child is under 12 months of age. The focus is on conversations between the mother and her child or children to give us a way of looking at both linguistic and social differences in the familial transmission of knowledge (Arberg and West, 1987).

Thus far, one-child families and two-child families seem quite different on even subtle measures of conversational style. In one-child families, mothers directed more speech to their babies, and infant vocalizations received more responses from the mothers. Vocal turn-taking, where mothers and babies participate in interactions thought to be important precursors to linguistic interactions, was frequent (Stern, 1977). The content of the speech involved the state of the infant or the state of the family, mothers routinely informing their infants that they "were really hungry," "were really sleepy," "liked eggs just like their daddy," or were "really excited about going on an outing."

In two-child families, both the type of speech and the dynamics of the interactions differed. If the infant and the sibling were close in age (a difference of less than 3 years), then conversation focused on and around the mother and the older sibling. Mothers spoke much less to the younger infant, and the older siblings rarely spoke to the infants at all. Compared to the one-child family, the younger infant overheard more speech but had much less speech directed to him or her. Moreover, when the infant vocalized, it was often not as a result of being addressed. The infant's vocalizations were also not acknowledged or answered, and turn taking seldom occurred. The most prevalent type of speech was information from the mother for the toddler—information about toys, family activities, names of objects, and instructions.

But when the older sibling was truly older, an age difference greater than 6 years, there was a different kind of family member present, a "helper" at the nest, if you will. The predominant interactional pair was the sibling and the infant. Moreover, the sibling talked to the young infant in much the same way that the mother did in the one-child families. The older sibling assumed what could almost be termed a surrogate-parent role toward the infant. The conversation was not only infant-directed, but also infant-focused. The older child used appropriate "baby talk," elicited vocalizations from the infant, and responded to vocalizations from the infant, thereby initiating a turn-taking role that seemed to maximize the infant's participation in the "conversation." The older child commiserated with the mother when the baby fussed, instructed the infant in "proper" behavior, and tried to convince the baby to eat its vegetables. Typical were comments like "Eat, little guy, so we can go bye-bye. No, don't chew with your mouth open."

What is the significance of these differences? In an immediate sense, the major

difference may be in the changes they make in the life of the mother, freeing the mother with more widely spaced children to expand her horizons in ways that the mother of two children under 4 cannot as yet even imagine. And for the older sibling, the opportunity to experiment with a parental role is provided, but on a voluntary basis, a liberty denied actual parents. In a less immediate sense, the teaching provided by not two, but three parents may influence intelligence and language, as Zajonc proposed. However, the two-child families with closely spaced siblings may find themselves with children that can be friends and playmates in ways not possible for more widely spaced siblings and may thereby provide the siblings valuable experience in gaining social competence.

Family dynamics also affect basic patterns of interactions with the physical world. Following on Rheingold and Eckerman's charting (1970) of the maturation of infants' willingness to leave their mothers and to explore a strange environment, Samuels (1980) found that this willingness was even greater if there was an older sibling present. Infants were tested both with and without their older sibling. When the sibling was present, the infants were more willing to explore, ranged farther afield, spent less time with their mothers, and fussed less. In this situation, the sibling served as a facilitator—a link between the novel and the familiar. Looking longitudinally at infants with closely spaced or widely spaced older siblings, Teti, Bond, and Gibbs (1986) reported that infants with much older siblings received more stimulating intellectual and social experience, especially with respect to language mastery and knowledge of objects.

We cannot as yet attach short- or long-term implications to these differences. All we seek is to emphasize that there are differences, and that a newborn inherits these differences with the family. A baby can no more banish an older sibling than can the sibling "send back" the baby. The family is a package of influences. It is as much a biological and social resource as the granary tree or the scrub jay's territory.

The challenge now is to explore the nature of the "packaging." Birth-order differences constitute naturally occurring instances of varied kinds of "early experience." They merit the kind of scientific attention thus far accorded to more contrived human or animal environments or to satellite configurations such as day care (Belsky and Steinberg, 1978). It is the "home" environment that implicitly represents the standard against which these other settings are evaluated. And it is perhaps because that standard appears to be a moving target that the study of human ecology is so complex.

#### SUMMARY: SEEING THE OBVIOUS

A Thai proverb has it that "The fish is the last to see the water." The ontogenetic niche is clearly as critical to development as its conceptual cognates: nature and nurture. Why, then, has the idea not undergone the energetic scrutiny accorded "nature" and "nurture"? We suggest that part of this reason is that we share the fish's problem. Eisenberg (1971) put it as follows:

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

As a start, we propose the need not only for new words, but for new images to help our eyes adjust to a finer level of observation. Let us begin by replacing illusion with reality. Instead of Boring's puzzle picture, we offer an actual picture depicting organisms engaged in the business of development (Figure 2). It should be a thousand pictures, all depicting interpenetrating alliances among individuals and surroundings. Enough puzzles exist in Figure 2 to suit scientists of diverse persuasions and to make the study of exogenetics as fundamental as that of genetics.

And with respect to words, we argue that the triadic form used here is only a start, soon to be replaced by better descriptors. Gone is the era when sketches of ontogeny relying on the security of black-and-white strokes will suffice. The expositions of ontogeny now available as a result of the efforts of several generations of psychobiologists constitute a gallery of art with myriad images, each in its own way as compelling as that of the double helix. It is now up to us to find the words to animate the science and art of development.

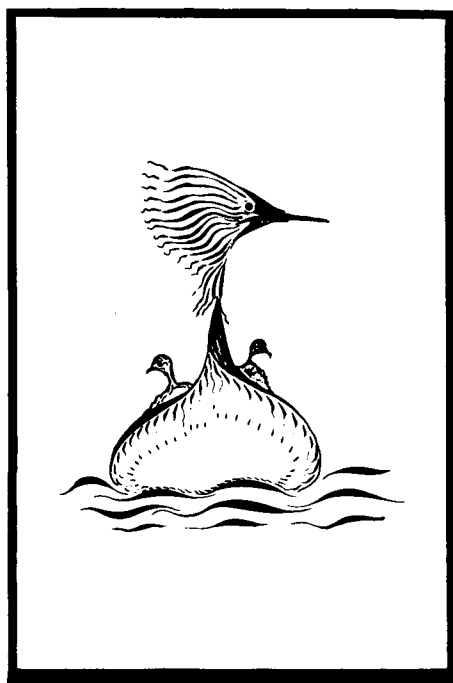


Figure 2. Untitled picture by Eddy Cobbiness.

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