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The Nature of Nurturant Niches in Ontogeny

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The concept of ontogenetic niche is used here to interpret how species-typical behaviors develop through active, context-dependent processes. Ontogenetic niches typically include social stimuli, such as those arising from parents, siblings, and others that provide 'nurturing' in the form of resources, stimulation, and affordances for development. This approach is a useful alternative to wrestling with artificial dichotomies such as nature-nurture.

Keywords: Cowbird; Huddling; Instinct; Ontogenetic Adaptation; Ontogenetic Niche; Rat Pup; Suckling

1. Ontogenetic Niches

The analysis and comprehension of complex problems usually finds only brief and limited value in simple dichotomies. Thus, the nature–nurture dichotomy is remarkably odd in its persistence. Rather than add to numerous expert and incisive critiques, including those in the present collection, I shall discuss the *ontogenetic niche* as an alternative construct in the analysis and comprehension of behavioral development, particularly the ontogeny of species-typical behavior. Ontogenetic niche is an especially satisfying framework in which to view organismal, especially behavioral, development. By necessity, this will be a brief presentation but the interested reader can find broader and more thorough discussions elsewhere (e.g., Alberts, 1987, 1994; Alberts & Cramer, 1988; Alberts & Ronca, 2005; Galef, 1981; West, King & Arberg, 1988; West, King & White, 2003).

Ontogenetic niche is a concept related, in part, to the traditional idea of an ecological niche, a definable locale that affords its inhabitants a peculiar set of

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environmental parameters within which they live. Some would refer to the physical environment itself as a *habitat*. With the organism living and adapting therein, a habitat becomes a *niche* (cf. Alberts & Cramer, 1988). By adding *ontogenetic* to the niche concept, we further specify a dynamic view, one that recognizes that niches change in ways that are sequential and orderly. This basic step is powerful because, for example, it can immediately alert us to the myriad ways in which a developing organism, even an immature and incomplete one, is finely specialized for adaptation to its environment. In addition, this same conceptual step also alerts us to ways in which the niche can change, shift, or be replaced during an organism's development. The view that is created, then, is one that frames development as a sequence of adaptations to a sequence of niches.

We have quickly arrived at a view of individual development as a journey through a sequence of niches. An example, Figure 1 illustrates a sequence of four ontogenetic niches in the life of the Norway rat (*Rattus norvegicus*). The fetal niche (A) is first. Depicted in Figure 1a are a few fetuses, each 'at work' in its amniotic sac within the mother's uterus. To earn a living in this uterine habitat, a fetus must express a slew of adaptive specializations. For instance, the working fetus obtains oxygen and discards CO_2 via the umbilical cord, the same conduit used for nutritive uptake. Indeed, on the levels of its cells, systems, and its overall behavior, fetal life is a story of adaptation to the uterine niche.

The next niche, located just on other side of the birth canal, is an entirely different world. Whereas the uterine habitat is aqueous, the postnatal environment is gaseous. It is also generally colder, replete with stronger light, a spectrum of acoustic vibrations, and more extreme gravity-related forces. In the postnatal niche(s), oxygen must be absorbed from the atmosphere. The newborn rat, like all vertebrates, accomplishes this via the surfaces of the lungs. It interacts with its new, gaseous environment with an uninterrupted rhythm of breathing cycles. Nutrition continues to come from the mother but the newborn must obtain it orally and digest and absorb it in new ways. Where the fetus' habitat was a chamber inside the mother, its

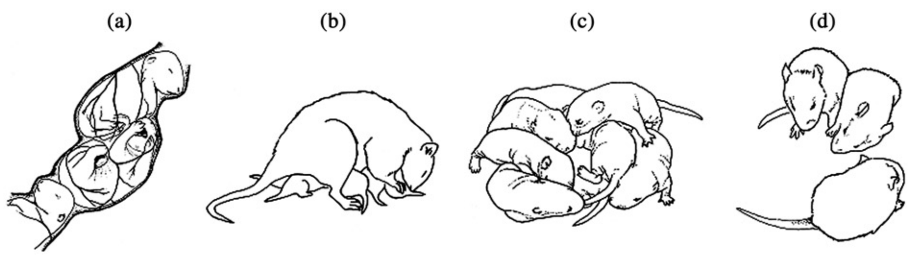

Figure 1. Four ontogenetic niches of rat ontogenesis. (a) The uterine niche, showing two adjacent fetuses and the anterior portion of a third fetus late in gestation; (b) The mother's body as niche, with a dam in nursing repose above some pups; (c) The huddle niche, as illustrated by some week-old pups; (d) The coterie as niche, depicted by pups converging on a piece of food.

early postnatal habitat is largely the exterior of the mother's body (Figure 1b). To survive and thrive in this niche, the newborn must behave in dramatic new ways, especially in relation to the mother and the littermates. The mother's body behaves, and each pup's behavior must adjust adaptively to her presence, her postures, her physiology and that of the littermate siblings (Alberts, 2007; Alberts & Cramer, 1988).

Continuing with this sequential view of development, the next niche in the pup's life is the pile of littermates in the natal nest (Figure 1c). After the first postnatal week, the rat dam's behavior includes longer and more frequent departures from the nest (Grota & Ader, 1969; Leon, Croskerry, & Smith, 1978; Thiels, Alberts, & Cramer, 1990). With her increasing excursions, the mother's body diminishes as the offspring's main habitat. In her absence, the remaining clump of pups, called the huddle, becomes a niche in which the pups function both individually, in coordination with others, and as a group (Alberts, 2007).

Figure 1(d) represents the social cohort as the next niche. The drawing depicts weanling pups interacting over a piece of solid food. In this developmental niche, the pups are exquisitely sensitive to cues of other rats, both age mates and adults. Together, they form habits of feeding, exploring, playing, and living a social life.

The niche concept embodies the purely physical habitat. The niche requires that individuals be seen in context, thus bringing into focus those aspects of the organism that are linked (fit) to the proximate environmental features—and there are always many such aspects. In this way, the niche concept also directs us to embrace the biological idea of *adaptation*, summoning its immediate, proximate meanings as well as the historical processes of natural selection (cf. Pittendrigh, 1958). Thus, ontogenetic niche and adaptation are closely-related concepts, for they *require* us to view the organism in relation to its environment and then to understand how the relations may (or may not) serve functional roles and contribute to biological fitness.

Ontogenetic adaptation, as a paradigm for analyzing and comprehending development, extends the themes of the niche concept, calling for recognition that selection operates *at each point* in development (Oppenheim, 1981), not simply on some idealized adult form or through the funnel of reproduction. Moore (2001) refers to the stream of 'event-moments' that constitute a life cycle, with each moment subject to testing by natural selection.

So, how does the framework of ontogenetic niche contribute to understanding the development of species-typical behavior? And, more specifically, how do we use the same concept to reframe the kinds of issues that have sustained the nature–nurture dichotomy?

The answers lie, I think, in 'the nature of niche.' Recall that we applied the term 'habitat' to refer to the physical parameters of the niche environment (the organism's 'address'). Each habitat in an ontogenetic sequence is a distinct context in which the developing organism must 'fit' or adapt (*in sensu.*, adaptation = *ad* [toward] + *aptus* [fit]).

If we return to ontogenetic niches as illustrated in Figure 1 and consider the life of the developing rat in each one, we can recognize some important commonalities, despite the dramatic contrasts across them. Common to each niche are channels of sustenance for the developing organism. For instance, in the uterine niche, the mother's body pumps nutrients into each fetus. The natal niche (b in Figure 1) provides mother's milk, some of her body heat, and various forms of behavioral stimuli such as licking and transport. The huddle, depicted in Figure 1c, provides insulation and conductive heat exchange at ages when body temperature and energy conservation are physiological priorities. Social stimulation and augmentation of feeding are among the numerous forms of sustenance present in the niche of the coterie (Alberts, 2007; Alberts & Cramer, 1988; Alberts & Ronca, 2005; Galef, 1981).

Research in the field of developmental psychobiology offers insight into the ontogeny of species-typical behavior of the Norway rat, particularly as displayed by a common domesticated strain (Sprague Dawley) in a laboratory setting. The developing rat provides a host of invariant, stereotyped, and adaptive species-typical behaviors. Many of these behaviors are controlled or directed by olfactory cues, and I will focus on a couple of these to pursue the theme of the present essay.

1.1. Suckling

Consider the suckling behavior of the newborn rat, keeping in mind that this is a behavior both universal among and unique to mammalian infants. Within minutes of abandoning the uterine niche in the mother's body and taking up residence in the natal niche under the mother's body, the newborn must locate a nipple and begin oral ingestion. At this early point in development, the rat pup is blind, deaf, spatially naïve, and has limited strength and motoric competence. Nasal chemoreception in air is also completely new. Nevertheless, the newborn actively locates one of the 12 nipples on the dam's ventrum, attaches to the teat and expresses milk from it. How does the newborn accomplish this remarkable and vital behavior in a new and alien world?

Olfactory stimuli are the key to the pup's suckling behavior. A pup's suckling capabilities can be seen by placing it against the ventrum of a lactating dam rendered motionless by anesthesia. The infant rat will autonomously orient to the dam's body, actively scan and probe along the surface, orally grasp a nipple and suck vigorously on it. Anosmic pups do not attach to nipples or suckle; they lie passively next to an anesthetized dam.

Olfactory cues on the dam's body stimulate the activities that culminate in the pup; findings and attaching to a nipple. These cues can be washed off and then replaced. The pup's suckling behavior vanishes when the cues are removed from the dam's body and is reinstated when a distillate of the wash is painted on the dam's body (Teicher & Blass, 1976, 1977).

Some would assert with confidence that the rat pups' suckling sequence is 'innate'. After all, suckling behavior is expressed stereotypically by naïve newborns and is controlled by a seemingly simple stimulus.

But, as we discover the developmental antecedents of suckling, it is no longer tenable to think of the newborn innately endowed with odor recognition for the nipple or with a behavioral module for suckling. Instead, the following picture has emerged: While in the uterine niche, fetal respiratory and swallowing movements bring amniotic fluid in contact with developing olfactory sensoria. The fetus can detect chemical cues in the amniotic fluid and the odors are learned. During the birth process, amniotic fluid is left on the dam's body; she grooms herself frequently during and after parturition and further spreads some of these fluids on her fur. The amniotic odors are a bridge of familiarity spanning the pre- and postnatal worlds. Newborns respond to the odors by becoming active and the configuration and texture of the mother's body shape their behavior into an organized form of scanning and probing.

That the amniotic odor is learned and used for suckling activation was shown by Pedersen and Blass (1982) when they added a nonbiological odor (citral) to the amniotic fluid of rat fetuses on gestational Day 17. About 5 days later, newly-delivered pups respond to citral odors on a washed dam and attach to her nipples. Saline-treated (control) fetuses do not respond to citral, and remarkably, the original citral-exposed pups do not respond to normal amniotic odors.

Mechanistically, there is reason to expect that large surges of the catecholamines norepinephrine and dopamine in the fetal brain during parturition may mediate the fetus' odor-learning. Compressions such as those experienced by the fetus during maternal labor and parturition induce these catecholamine surges (Ronca, Abel, Ronan, Renner & Alberts, 2006). There are indications that catecholamines mediate neural and behavioral activation, and contribute to learned associations (e.g., Rangel & Leon, 1995; Wise, 2004).

1.2. Social Huddling

Contact behavior, or huddling, is a species-typical behavior of *R. norvegicus*. Onset of the rat's social, or filial huddling, is developmentally 'fixed', with an onset on Postnatal Day (PD) 15. Prior to about PD 15, rat pups show no species preference: they huddle equally with a conspecific (member of the same species) *versus* a gerbil. Filial preference is demonstrated when a rat prefers to huddle with another rat, rather than a gerbil or a warm tube (Alberts & Brunjes, 1978). The basis of the filial huddling preference is the olfactory cues of rats. Deprived of the sense of smell, rats continue to huddle indiscriminantly with members of other species or with inanimate, warm objects.

The olfactory-guided species preference of rats is also learned. Annointing a mother rat with a novel odor induces a filial preference for that odor in her offspring (Brunjes & Alberts, 1979). Onset of the altered filial preference was on PD 15, the same as the 'normal' preference in rats. Alberts and May (1984) 'labeled' different experiences with different odors and then measured the preferences for the odors. Experiences labeled with odors that became preferred in tests of filial huddling were seen as 'inductors' of filial huddling. Surprisingly, suckling and receipt of milk proved uninvolved in the induction of filial preference, but thermotactile stimulation (conductive heat transfer from a warm body) was a potent inductor. Thus, scented nonlactating dams were as potent as scented dams that nursed and gave milk. Even more dramatically, a warm scented tube induced a strong filial preference, again implicating conductive heat transfer from a contact surface.

Again we find a stereotyped, species-typical, developmentally-fixed behavior is learned, with all of the key components–odors and thermotactile 'reinforcement' in the present case—existing as natural features of the ontogenetic niche. While in contact with mother (Figure 1b) and with littermates (Figure 1c), pups experience an inherent association of species-typical odors, tactile stimulation, and conductive heat transfer. These associations induce a filial preference.

Mechanistically, we now hypothesize that the neuropeptide oxytocin is released during contact behavior in the nest. Oxytocin is now recognized as a transmitter located in neural regions mediating a variety of social behaviors (Ferguson, Aldag, Insel & Young, 2001; Insel, 1992) as well as primary processes such as social memory (Ferguson et al., 2000; van Wimersma & Wintzen, 1980). And there is evidence that oxytocin plays a role in some forms of learning (Keverne & Curley, 2004; Lim & Young, 2006; Nelson & Panksepp, 1996). In support of the general hypothesis of oxytocin mediation of filial odor learning are the recent data from my lab that blockade of oxytocin binding in the brain interferes with the formation of filial preference during a controlled exposure to a scented foster dam (Kojima & Alberts, 2007).

1.3. Nurturant Niches

The association of mother and offspring plays a central role in both of our empirically-based examples of how species-typical behaviors develop. At different points in development, the mother-offspring association takes different forms (e.g., Figure 1a–c). Indeed, each form *is* an ontogenetic niche. Specific features of these niches elicit specific reactions and responses in the developing offspring. These reactions and responses constitute conditions sufficient for the formation of a learned association and, as a result, the differentiation of behavior.

The uterine niche nurtures with total physical support. During the transition from uterine niche to niche in the natal nest, the fetus is necessarily exposed to a mélange of stimuli. Many of these stimuli are effects of other primary processes. For instance, the primary function of parturition is to move the fetus from inside the mother to the outside. During the transition catecholamine levels soar. This is understood to be a primary adaptation serving the transition to pulmonary respiration. The catecholamine surge augments removal of liquid from the newborn lungs and protects the fetus from neural damage during possible episodes of hypoxia, as pulmonary respiration is established (Lagercrantz & Slotkin, 1986).

We think the catecholamine surge may be uniquely capable of creating a learned association between activated behavior and an odor cue. Set in the context of the natal niche, the consequence is a chain of behavioral reactions we call 'nipple search' and suckling. Milk transfer as a result of suckling may well reinforce and shape the behavior. Again, it is the sustaining, guiding, and facultative aspects of the niche that does the job. For this reason, it is appropriate to view niche as 'nurturant,' recognizing that the developing offspring may be actively involved in eliciting and extracting the nurturing. The utter reliability of the ontogenetic niches and the affordances that exist in each are inherited as surely as are genes. An offspring's behavioral interactions with the dam or with its siblings in the nest can be framed as active 'niche construction,' adding another dimension to ontogenetic adaptation (e.g., Alberts & Schank, 2006).

The process of inducing a huddling preference similarly involves an association co-opted from other, primary processes. Contact behavior results from the mother's presence in the nest, her nursing behavior, and the pups huddling for energetic benefits (Alberts, 1978; Alberts & Gubernick, 1983). These are primary adaptations to the natal niche and huddling niche. Within the mélange of stimuli involved in these nurturing activities, there exist natural associations and the developing pups' behavior is shaped by these. In both instances, we see that species-typical behaviors arise from development occurring in species-typical niches.

2. A Local Synthesis

The story of vocal learning in brown-headed cowbirds (*Molothrus ater*) as related by West and King (this volume) provides a view concordant with that offered herein. Historically, the cowbird's nest parasitism set the stage for generations of observers to conclude that *M. ater* was 'hard-wired' for its species-typical song. After all, the young are reared entirely by members of other species so that the entirety of the cowbird's early development is in the presence of other species.

The beauty and power of West and King's investigations, derives from their continuous focus on the ontogenetic niches, rather than on the temporal dimensions of development (or genetic dimensions, for that matter). Their adherence to the process of niche inheritance and especially the breadth of their perspective on the contents of the cowbirds' ontogenetic niches was a key to their marvelous discoveries.

Whereas the presentation of ontogenetic niches that I offered emphasized physical and chemical components, West and King emphasized *social* components in their analysis. In addition, West, King and their students exploited comparative dimensions and geographic variation in their analyses.

The similarities between West and King's (this volume) presentation and the present one include manipulations of experience during development. They suggest the term "experiential knock-out" (EKO) to refer to manipulations of flock composition so that the social structure lacked the presence of adult males. In contrast, most of the manipulations described in the studies of rodents, left intact the social and physical structures of the environment, but inserted novel olfactory stimuli as markers or 'labels.'

West and King's invocation of the term EKO is purposively ironic, with its clear reference to the 'knock-out' technologies of genomic studies, which are so often used with cavalier flair to assert the 'genetic control' of features with complex developmental origins. West and King's insightful 'deconstruction' of presumed innateness, coupled with a comprehensive view and treatment of ontogenetic niche, give support and hope to a future in which observers and analysts conceptualize the richness of development in ways that recognize the experience of context and environment at each point in the life cycle.

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