

## Adaptive Priorities in Brain Development: Theoretical Comment on Pravosudov et al. (2005)

Stephen Nowicki  
Duke University

William A. Searcy  
University of Miami, Coral Gables

V. V. Pravosudov, P. Lavenex, and A. Omanska (2005) reported that undernutrition in the first few weeks' posthatching leads to lower mean hippocampus volumes in adult Western scrub jays (*Aphelocoma californica*) and to poorer performance on spatial memory tasks. Together with prior work on the effects of poor nutrition on the development of the song system in songbirds, these results fit reasonably well with the view that natural selection determines priorities for investment in the development of neural structures. What seems somewhat anomalous under this view is that undernutrition did not affect the development of color association abilities in scrub jays. This work sets the stage for future comparative research on adaptive priorities in the development of brain and behavior.

*Keywords:* hippocampus, spatial memory, nutrition, birdsong, developmental trade-off

The postnatal period in many organisms is a time of extensive growth, during which a variety of anatomical and physiological systems, all requiring substantial investment, develop concurrently. If nutrition is good and other environmental conditions are favorable during this period, then the organism can invest optimally in each of its developing systems. If, to the contrary, nutrition is poor or the organism experiences other environmental stresses such as cold temperatures or exposure to parasites, then the organism may be forced to sacrifice investment in particular developing systems so that investment in others can be maintained. Evolutionary biologists have theorized that in such cases natural selection favors a set of investment priorities, such that systems essential to the individual's survival will be given first call on resources, whereas other less important systems are sacrificed (Schew & Ricklefs, 1998). Structures used exclusively in sexual display in particular may be given a low priority for investment (Andersson, 1986). The logic here is that an individual with poorly developed display structures that is able to survive has some chance of reproducing, whereas an individual with a well-developed display that is unable to survive has none.

Neural systems ought to be subject to investment priorities just as are other anatomical and physiological systems. Such priorities therefore provide a framework for interpreting the results of Pravosudov, Lavenex, and Omanska (2005) in this issue. These authors manipulated posthatching nutrition in Western scrub jays (*Aphelocoma californica*) and tested effects on hippocampal structure and spatial memory. The nutritional manipulation was fairly severe: Experimental birds were limited to 65% of the food intake

of controls from the time they were taken from the nest, at about 7 days' posthatching, until they were able to feed themselves, an ability that developed gradually between 30 and 75 days. Although severe, the restriction is certainly ecologically relevant, as undernutrition of all levels of intensity, up to and including starvation, does occur in nature. At 1 year of age, the nutritionally deprived birds were sacrificed and found to have hippocampal volumes about 8% lower than controls, with approximately 11% fewer neurons. Telencephalon volumes and overall brain masses did not differ between the two groups. Posthatching nutritional restriction in Western scrub jays thus had a lasting negative effect on brain structures that support spatial memory. Behavioral testing demonstrated that the anatomical difference observed between control and experimental birds correlated with a loss of function. At 6 months' posthatching, experimental birds performed substantially worse in a cache-recovery task than did controls, inspecting approximately twice as many locations in order to find their caches. At 8 months, the birds were tested in a spatial learning task that examined their ability to remember locations where the researchers (rather than the birds themselves) had hidden food. In unrewarded probe trials, the nutritionally deprived birds again performed substantially worse than the controls, inspecting approximately twice as many sites in order to find the food. By contrast, when tested for the ability to remember associations of colors with food rewards, the deprived birds performed equally as well as controls, providing evidence that the effect of nutritional stress on behavior was relatively specific to aspects of memory that are particularly associated with hippocampal function.

In mammals, including humans, it is well-established that both pre- and postnatal malnutrition results in a broad array of negative effects on brain growth and development, including not only reductions in the size of particular structures but also a variety of cellular and physiological effects (Bedi, 1984; Dobbing, 1981; Scrimshaw, 1998; Wauben & Wainwright, 1999). Some of these negative effects may be mitigated by compensatory growth at later stages of development if nutritional conditions improve, but other effects are permanent (Levitsky & Strupp, 1995). Not surprisingly,

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Stephen Nowicki, Department of Biology, Duke University; William A. Searcy, Department of Biology, University of Miami, Coral Gables.

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Correspondence concerning this article should be addressed to Stephen Nowicki, Department of Biology, Duke University, Box 90338, Durham, NC 27708-0338. E-mail: snowicki@duke.edu

brain structures that undergo significant postnatal growth are affected most profoundly by undernutrition experienced after birth. These structures, notably the hippocampus and cerebellum, also appear most likely to suffer irreversible effects of early malnutrition, at least on an anatomical level (Levitsky & Strupp, 1995). It is also clear from mammalian studies that the effects of undernutrition on neural development lead to corresponding functional deficits. Here, considerable work has documented the effects of early nutritional deficits on learning and memory (Smart, 1986). Much of this work has documented effects on spatial memory (e.g., Fukuda, Françolin-Silva, & Almeida, 2002; Goodlett, Valentino, Morgane, & Resnick, 1986; Huang et al., 2003; Jordan, Cane, & Howells, 1981), analogous to the findings of Pravosudov et al. (2005), but studies also reveal lasting effects on a variety of other memory and cognitive tasks (Smart, 1986; Strupp & Levitsky, 1995).

Songbirds such as the Western scrub jays studied by Pravosudov et al. (2005) are expected to be especially vulnerable to nutritional stress experienced early in life for at least two reasons. First, posthatching development is both extensive and astonishingly rapid in this group. The term *songbird* is used to describe members of the oscine suborder of the Passeriformes. Representing close to half of all living bird species, songbirds are noted for being exceptionally altricial, with young born in an almost embryonic state (Starck & Ricklefs, 1998). Following this modest start, however, a typical songbird will reach 90% of its adult weight less than 10 days after it emerges from the egg (Ricklefs, 1968) and be fully capable of flight when it fledges from its nest shortly thereafter (Düttmann, Bergmann, & Engländer, 1998). This steep trajectory means that even a brief period of poor nutrition may have a large impact on the outcome of development.

The second reason songbirds are vulnerable to posthatch nutritional stress is that their young depend entirely on food captured and delivered to them by their parents to fuel this growth. If parents have difficulty obtaining food, either because of poor conditions or because of limitations in their own foraging abilities, their young will go hungry. In mammals, the resources a lactating mother provides her young can be buffered, at least temporarily, by her own stored reserves. In songbirds, by contrast, every bit of resource provided by parents to their young must be obtained from the environment virtually immediately before it is delivered. Even after a young songbird leaves the nest, it typically continues to depend on food brought to it by one or both parents for days or even weeks while it learns how to forage efficiently on its own (Kopachena & Falls, 1992; O'Connor, 1984). Not surprisingly, the amount of food a young bird receives from its parents is a major determinant of both its growth rate and its probability of surviving long enough to leave the nest (Gebhardt-Henrich & Richner, 1998; O'Connor, 1984).

The effect of undernutrition and other stressors on brain development in songbirds has only recently begun to be studied, and here most work has focused on the "song system." The song system is a series of brain nuclei associated with the learning, production, and perception of song, organized in two pathways: a sensory-motor pathway that includes most notably the nuclei HVC and RA and the so-called anterior forebrain loop that receives input from HVC and projects back to RA (Mooney, 1999). The song system has long been of interest to neurobiologists as a model for studying the neural substrates associated with learning and

memory of complex motor patterns, and it is an especially interesting model because of intriguing parallels between the development of song in birds and the development of speech in humans (Doupe & Kuhl, 1999). The interest in effects of developmental stress on the song system and song learning abilities is an evolutionary one, however, stemming from the role a male bird's song plays in mate attraction and courtship. Song serves as a sexual display, analogous to the tail of a peacock (Searcy & Andersson, 1986). As such, theory predicts that structures involved in the production of the display (brain regions associated with song learning in this case) will have low priority in development and will be sacrificed to some extent if resources are limited (Andersson, 1986). In this way, the display is an "honest" indicator of male quality to prospective mates—lower quality males cannot afford to develop as much of a display as higher quality males (Andersson, 1994; Searcy & Nowicki, 2005).

Two recent studies have examined the effects of early nutritional stress on song system development. Nowicki, Searcy, and Peters (2002) nutritionally stressed hand-reared nestling swamp sparrows (*Melospiza georgiana*) by using an experimental paradigm much like that used by Pravosudov et al. (2005). The control group was given unlimited food, whereas the experimental group was provided only 70% the amount consumed by the controls. This nutritional restriction was imposed from several days after hatching, when the birds were first collected in the field, until they were about 28 days old, when individuals were capable of feeding themselves entirely on their own. When birds were sacrificed at 1 year of age, control birds had HVC volumes about 30% larger and RA volumes about 45% larger than experimental birds. The overall volume of the telencephalon was 15% larger in control birds than in experimental birds, but even with this difference factored out the RA volumes of the two groups remained significantly different, suggesting that RA at least is differentially impacted by undernutrition experienced early in life. Recently, Buchanan, Leitner, Spencer, Goldsmith, and Catchpole, (2004) found a similar effect of developmental stress on the song system in zebra finches (*Taenopygia guttata*); here, the volume of nucleus HVC was found to be differentially impacted by developmental stress experienced early in life. The anatomical effects found in these studies were paralleled by effects on song learning and production, with birds that were poorly fed when young copying model songs less well (Nowicki et al., 2002) or learning otherwise less complex songs by several measures (Buchanan et al., 2003; Spencer et al., 2003; Spencer, Buchanan, Goldsmith, and Catchpole, 2004). These results fit well with evolutionary predictions about developmental priorities (Schew & Ricklefs, 1998); because song is a sexually selected display, the brain structures necessary for its learning and production are given lower priority in the face of limited resources. As a consequence of this trade-off, song can serve as a good indicator to potential mates that an individual fared well overall during development because it was provided with abundant resources or because its favorable genetic makeup allowed it to develop well even in the face of resource restriction (Nowicki, Peters, & Podos, 1998; Nowicki & Searcy, 2005).

The results of Pravosudov et al. (2005) do not fit so easily with evolutionary predictions about developmental priorities. These authors found that Western scrub jays, when faced with limited nutrition during posthatching development, sacrifice spatial memory along with the brain structures that underlie this capacity.

Western scrub jays are caching birds and thus are among a group of birds in which spatial memory is thought to be particularly important to fitness. Individual scrub jays may store up to several thousand seeds or acorns during the fall and winter and then recover them later in the winter or early spring (Carmen, 1988; Curry, Peterson, & Langen, 2002). In a California population, cache recovery constituted over 40% of foraging activity at its peak in March (Carmen, 1988). Western scrub jays recover caches with accuracies greater than chance (Balda & Kamil, 1989) by using spatial memory (Gould-Beierle & Kamil, 1998). The importance of caching to overwinter survival has not been measured directly in this species, however, and Western scrub jays are considered to be less dependent on caching than certain closely related species such as pinyon jays (*Gymnorhinus cyanocephalus*) and Clark's nutcrackers (*Nucifraga columbiana*; Bednekoff, Balda, Kamil, & Hile, 1997). Western scrub jays produce fewer caches per individual than do the latter two species, use a greater variety of nonstored foods during winter, and lack any morphological specialization for caching such as the sublingual pouch used to transport seeds by Clark's nutcrackers (Bednekoff et al., 1997; Curry et al., 2002; Vander Wall & Balda, 1981). By some tests, scrub jays perform less well on spatial memory tasks than do more specialized cachers (Balda & Kamil, 1989; Bednekoff et al., 1997). Thus, spatial memory seems likely to be of intermediate importance to Western scrub jays: more important perhaps than in many noncaching species, but less important than in true caching specialists. It should be kept in mind, of course, that spatial memory has other functions in birds besides cache recovery, notably in migration and homing (Bingman & Able, 2002).

Given these facts, how can we make sense of the results of Pravosudov et al. (2005) on the effects of posthatching nutritional restriction? It should not be a surprise that the development of systems moderately important to fitness, such as those responsible for spatial learning in scrub jays, are sacrificed to some degree if an organism experiences a sufficiently severe nutritional stress. The nutritional stress imposed by Pravosudov et al. (2005) was fairly severe and long lasting and extended over a period in which the avian hippocampus is known to show substantial growth (Clayton, 1996). What seems more surprising is that although spatial memory systems were sacrificed, neural systems responsible for color association and memory apparently were spared. Caching species tend to have better spatial memory than do noncaching species but not better memory for color associations (Brodbeck, 1994; Shettleworth, 2003). Furthermore, Shettleworth (2003) has stated that "an enhanced tendency to use spatial as opposed to nonspatial cues in a short-term working memory task turns out to be perhaps the most robust difference between storing and nonstoring species described so far" (p. 112). The greater reliance of caching species on spatial cues would lead one to expect that scrub jays would sacrifice color association systems before spatial memory systems rather than vice versa.

One explanation for the Pravosudov et al. (2005) findings is that Western scrub jays are an exception to Shettleworth's (2003) generalization, a caching species that shows a relatively high reliance on color cues. In fact, Pravosudov et al. found that their control birds were nearly as likely to follow color cues as spatial cues when the two gave conflicting information. A second hypothesis is that color associations, or the neural substrates associated with this capacity, are of overriding importance to Western scrub

jays in some context other than cache recovery. A third, more prosaic hypothesis is based on timing rather than adaptive priorities: Perhaps the neural systems responsible for color associations develop outside the time in which nutrition was manipulated. Each of these hypotheses can be tested by further empirical work.

As organ systems go, the brain is obviously a particularly important one, but not all parts of the brain are equally important to an individual's survival and evolutionary fitness. The brain also is a particularly expensive organ to build and it is unlikely to be spared entirely if poor conditions prevail during development. If we accept these premises, then what is interesting is how the different parts of the brain are prioritized relative to each other and relative to structures outside the brain. This kind of question is inherently a comparative one. Even if our primary interest is the human brain, we can best understand how developmental history affects cognitive function in general by considering different species whose specific life histories and ecological circumstances lend themselves to predictions about how selection should affect the allocation of resources during development because of the fitness consequences of the different functions served by a complex brain. The work Pravosudov and his colleagues report in this issue is an important contribution, not only because it demonstrates that such trade-offs do occur when resources are limited but also because it does so in a system—food-caching birds—in which relevant evolutionary comparisons can be made for a cognitive function that is highly tractable to study. This work raises as many questions as it answers, but these will be fruitful questions to explore.

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