

Deconstructing Innate Illusions: Reflections on Nature-Nurture-Niche From an Unlikely Source

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Despite great advances in understanding genetic mechanisms, there still exists a bias toward equating genes with innate modules that determine important developmental events. But genes are equally relevant to understanding developmental plasticity shaped by ecological events. In other words, the term 'genetic inheritance' does not specify ontogenetic mechanisms. Here we present a case history of a species assumed to be under the control of prespecified genetic wiring to direct critical behavioral events such as communication and mating. We show, however, that exogenetic processes stemming from the species' ontogenetic niche provide an alternative view of the flexibility of development especially with respect to behavioral performance.

Keywords: Brown-Headed Cowbirds; Communication; Development; Learning; Nature-Nurture; Ontogenetic Niche

1. Goals and Background

The focus here is on exogenetic inheritance: the idea that organisms inherit parent's genes but also parents, peers, and places they inhabit (West & King, 1987). This is not a new idea—in fact, it is a very simple and old idea but it does not seem to be able to compete for relevance on a level ground with ideas about genetic inheritance. In this essay we will connect the nature–nurture concept to exogenetic inheritance, as it is relevant to present day research on the development of behavior. We will take a case history approach by discussing brown-headed cowbirds, a brood parasite with a long history of eliciting developmental questions about species and mate recognition

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(Lehrman, 1974; Mayr, 1974). We examine these same questions and show how the idea of an ontogenetic niche provides answers to the above questions while the concept of an assumed innate mate recognition system provides a widely popular but empty conceptual framework.

At a behavioral level, the ontogenetic niche is the set of ecological and social circumstances inherited by individuals. Exogenetic heredity can be highly reliable, probable and stable over generations, e.g., inheriting conspecifics is as dependable as inheriting genes. Sociality is an engine of exogenetic mechanisms such as niche creation and cultural transmission, which can adapt rapidly to changing ecological circumstances, a critical attribute of successful species. The best way to see these effects is to look at the life history of a species where development and origins of reproductive behavior are well understood. In fact, too often critical behaviors like reproduction are not studied developmentally and consequently the function and origins of behaviors are misunderstood which we believe contributes to all the common habit of relying on innate explanations (West, King, & Arberg, 1988; West, King, & White, 2003).

2. The Cowbird: A Wired Species?

The species we chose to study would seem to be a natural for innate explanations. Cowbirds (*Molothrus ater*) are brood parasites, which means that the young ones are raised by a foster species and have no reliable early contact with their parents (Friedmann, 1929). Thus, the young cowbird faces a chance of learning the “wrong” species typical behaviors leading to lower reproductive fitness. Evolutionary theorists have argued that cowbirds must be a hard-wired species immune to postnatal experience to avoid mis-mating. Even strong proponents of nurture have suggested that the cowbird would need an innate safety net to prevent mating errors (Lehrman, 1974; Mayr, 1974). The origin of these views followed the emotionally charged era post-WWII about innate and learned origins of behavior, e.g., Lehrman vs. Lorenz debate. But the argument was not just an esoteric science debate but was seen as having impact on public policy. The nature–nurture debate continued with the rise in the model of early experience and sensitive periods: an extreme example at the time was how to “inoculate” the young against effects of early social deprivation (e.g., ‘Head Start’). At the same time, the emerging study of bird song was then seen as an exemplar of an interactionist view between nature and nurture. The thinking was extended to many areas including a growing interest in language origins and the comparative role of innate modules vs. learning. Against this backdrop we started our investigation of the North American cowbird.

3. Assumptions and Methods

Our study of the development of song and mate recognition was rooted in the assumption that sociality was a basic mechanism for development. We viewed studies

that documented song development in nonsocial contexts as uninterpretable with respect to communicative development. Small cages or sound attenuating chambers were the typical laboratory environment but they structured, restricted, or eliminated social interactions. Such isolate housing and the reliance on isolate song supported the dominant view of complete social isolation as being capable of revealing the innate blueprint (Searcy & Marler, 1987). But, in all of our studies, housing conditions were a critical dimension, and while we housed birds in different social contexts from sound attenuation chambers to flight cages to large aviaries, we never housed birds alone. The first studies were done using a pair or triad of young cowbird males or females or with different companions including nonconspecifics. During the 9-month period a male takes to develop his song, we recorded vocal development as well as the social interactions with his companions who could be other males or females of different ages or nonconspecifics. In the spring, we would record the final vocal repertoire of the male and measure the female perception and reaction to song. For females, comparable developmental studies looked at the effects of vocal and social companions on the development of her preferences.

4. Species Identification

Our first study of the role of early experience in the development of reproductive behavior in cowbirds asked whether hand-raised males and females would develop typical songs and preferences without conspecific experience. Thus, during their first year we raised males and females from the egg with nonconspecifics. In the spring, we played back the males' song to the females. We discovered that while the males' songs were in many cases atypical for the species, these songs, when played back to the females, caused them to adopt a copulatory solicitation postures (King & West, 1977) (Figure 1). Thus, the naive females, when they were about



Figure 1. Female copulatory response to song.

1-year-old and the first time in their life they heard cowbird song, revealed the songs' functional properties. It seemed we had discovered the perfect innate safety net where mate recognition did not require conspecific experience. We called the playback procedure as the female bioassay and used it to measure male song quality. In addition, many developmental studies went beyond just measuring song quality by female preferences for song by playback, we also measured actual courtship and reproductive success in breeding aviaries and correlated performance across the two contexts (West, King, & Eastzer, 1981).

In light of the discovery of a lock and key reflex for species and mate recognition, we turned our attention to the role that experience might play in macrogeographic variation of song across the three subspecies of cowbirds (Friedmann, 1929). We were especially interested in the subspecies borders where we suspected song learning might play a role in incipient speciation (King & West, 1990). Because the cowbird's range extends throughout all of North America and is classified as three distinct subspecies, this permitted us to look for experiential differences against different genetic backgrounds. The female bioassay of male song took on great importance because it allowed us to do microphyletic comparative studies. It also allowed us to use our own experiential probes to examine behavioral plasticity. We found a range of phenotypes many of which could be culturally transmitted.

5. Investigations of Communicative Plasticity

We carried out studies to investigate the developmental origins of male vocal plasticity. We raised juvenile *Molothrus a. ater* males from North Carolina with adult *M. a. Obscurus* males and females from Texas. The *M. ater* males became bilingual adding lexical elements to their songs that were not produced by their natal population. We recorded the breeding season songs of the bilingual males and played them back to *M. ater* and *M. obscurus* females to measure their song preferences by the frequency of copulatory solicitation postures. We found that these males were functionally bilingual, as the playback females preferred the song variants from their natal population. We also found that in mating tests that females copulated more with males that were singing more of the females' local song variant. Thus, male vocal development was highly flexible at the macrogeographic level (West & King, 1985; West, King, & Harrocks, 1983).

After showing that juvenile males could become bilingual, we asked if adult females from the *M. ater* and *M. obscurus* populations could also modify their song preferences at the macrogeographic level. To do this, we housed adult males from NC with adult TX females and adult males from TX with adult NC females. We discovered that the nonsinging females did not change their preferences for their natal song but that the males they were housed with modified their song structures to try to appeal to the distant population females' song preference. Because the females did not sing, this finding was a complete surprise. At the time, current

theories of song learning were based on song copying and nonvocal social stimulation was not believed to play a role in vocal development (King & West, 1988; King, West, & Eastzer, 1980). We followed this study by raising juvenile males from NC with adult females from TX or local females from NC. We videotaped their social interactions during development to try to account for the females' influence on male song.

We discovered that the females used social cues in reaction to male song to shape the males' vocal behavior (West & King, 1988). While the female can use a variety of social cues, we were led to one particular female behavior by the males' excited reaction and approach to female movement during his singing. Specifically, we discovered that to some songs females would rapidly move a wing, a movement that appeared to be a precursor to a female copulatory solicitation posture. We called this behavior a 'wing stroke' and found that the songs that a female wing stroked to were likely to be repeated and retained in the males' repertoire. We also played back songs that elicited wing strokes, and those that did not, to a group of females and found that the songs that elicited wing strokes were the most effective elicitor of the copulatory posture. These data were important because they implicated nonimitative social stimulation in song learning for the first time (King, West, & Goldstein, 2005; Smith, King, & West, 2000).

We proposed that song learning was a matter of both copying songs from other males as well as of contingency learning based on social feedback from females. To begin the process, males produced a generic alphabet of sounds in their babbling or subsong. They elected to keep sounds based on the nature of social feedback from both males and females. Thus, during development young males produce original songs that are a consequence of vocal experimentation and their consequences as well as copies of songs they have heard. The choices of copied songs that will be retained are a consequence of the social feedback they elicit. Thus, the male song development system was open to both social and vocal stimulation at the macrogeographic level.

The next logical question with respect to male vocal plasticity was: what was the limit of this plasticity. Thus, we asked whether males housed with conspecific or nonconspecifics would be open to learning at the species level. To answer this question, we housed wild caught juvenile cowbird males with canaries, or as a control condition, with adult female cowbirds during the males' first year. We found that the males interacted with their companions by singing to them. In the case of the canary-housed cowbirds, they sang along with their companion. By spring of their first year, the males had incorporated elements of the canary trills into their crystallized songs. By contrast, the males housed with female cowbirds developed their songs faster and crystallized sooner (King, West, & Freeberg, 1996).

6. Investigations of Communicative Pragmatics

At the beginning of the breeding season, we carried out two tests of species recognition. First, we housed all of the canary-housed males in one large flight cage

and all of the female-housed males in another identical cage. After the birds had habituated to their surroundings, in a choice test, we introduced them, one at a time, into a neutral flight cage that contained both unfamiliar females and canaries. We measured approach, spatial proximity, and singing in the new surroundings. The female-housed birds did what we expected: they ignored the canaries and sang to the females who showed an interest in their overtures by allowing the males to approach and sing to them. By contrast, when the canary-housed males were introduced to the choice test, their response was a surprise as they ignored the female cowbirds and approached and sang to the canaries. These new canaries were not accustomed to being courted by cowbirds and so they uniformly retreated when males sang to them. This created a situation where the male cowbirds were constantly pursuing the canaries around the cage and trying to sing to them. While this was going on, the female cowbirds who were also present as part of the choice test were completely ignored by the males to the point where a female cowbird would occasionally adopt a copulatory solicitation posture to the song of a male but the male appeared not to notice. We found this to be an extraordinary finding because it seemed obvious that if there was any merit to the idea of innate mate recognition, the males' prior social experiences should have no influence on his ability to recognize and mate with a solicitous conspecific female (West, King, & Freeberg, 1996).

We carried out a second test of mate recognition in a socially more complex setting. For this test we used large outdoor aviaries that housed adult male and female cowbirds from local and distant populations along with canaries and with adult and juvenile starlings. We introduced the canary and female-housed males in small groups to these flocks and measured social interactions between the males and females. We found the female-housed males did not show the necessary social skills to consistently interest female cowbirds, preferring to sing to one another or undirected song. We had recorded the male's songs and played them back to an independent group of females and found that the female-housed males' songs were higher quality song than the canary-housed songs. This was not surprising in that the canary-housed males incorporated canary elements in their song. The high-quality song of the female-housed males explains why they did occasionally get a female to adopt a copulatory solicitation posture. However, as we had seen in the cage setting, the males generally ignored the female overtures. The males appeared to have failed to learn that courtship requires persistence and sustained attentional focus. After this test revealed male inexperience, we introduced experienced adult males as models to see if the young males could quickly learn to court by observing adults. The introduction of the adult males produced no change in the juvenile male behavior (Freeberg, King, & West, 1995; West, King & Freeberg, 1996).

We also introduced the canary-housed males to these flocks using the same procedures. As in the previous test, the canary-housed males continued to pursue and sing to the canaries. The canaries showed no reciprocal interest spending most of their time flying away from the males. Interestingly, the canary-housed males showed persistence in their pursuit of the canaries that the female-housed males did not show

in their actions toward female cowbirds. We believe this is explained by the fact that during development the canary-housed males had to work harder to sing at a close distance to their canary companions than did the female-housed males and so in the mating competence test were accustomed to having to chase and court. In that all of the cowbirds in this study were wild caught at around 50 days, we know that early experience with conspecifics did not guarantee the appropriate outcome. Taken as a whole it was clear that for male cowbirds, there was no hardwired system that insured mate recognition even at the species level. Thus, the earlier discovery that the males could produce a functionally effective song without conspecific experience was clearly not the end of the story as it was now apparent that the males needed social experience to know how to use their songs. Evolution had apparently selected a developmental system for the males that was heavily dependent on a socially rich ontogenetic niche. But, what about female cowbirds? Perhaps the innate safety net resides in the female, as they are the gatekeepers of reproductive outcome.

7. Female Song Perception

We had looked at female cowbird song preferences a decade before the aviary experiment described above. We had used triads of females housed together or with males from local and distant populations in sound chambers; we examined whether we could modify female preferences for male song. We used the female bioassay and actual mating tests to look for evidence of modifiability at both the micro- and macrogeographic levels. In all of these studies, we found that females preferred the songs of their natal population. In fact, the lack of evidence of female modifiability was striking (King & West, 1983). For example, even when females were housed with the same male for many months, in playback tests, they never showed any preference or aversion to the song of their companion when compared to unfamiliar males. Finally, we hybridized North Carolina *M. ater* females with Texas *M. obscurus* males. Many of the young ones died which seemed to suggest a genetic incompatibility, but one hybrid female survived and we raised her with other females in the absence of male contact. In the spring, we played back *M. ater* and *M. obscurus* song to her and she preferred *M. ater* song, her mother's natal preference, by a 3:1 margin. So, the evidence seemed overwhelming at the time that evolution had selected females to be the gatekeepers of reproduction and given them a genetic template to guide their perception (West, King, & Freeberg, 1997). This seemed to make evolutionary sense: if females retained their preferences, males interacting with them would be socially shaped toward effective song.

In sum, the ontogenetic niche for males and females is highly plastic with respect to mate recognition for the males while females appeared to be exemplars of the innate modules thought to be necessary for a brood parasite. The scale of the male incompetence was in two parts: song structure (e.g., learned canary song) and song use (e.g., what, when and to whom to sing). The incompetence seen in aviary-flock setting was not seen in the flight cage, so we were missing something by ignoring the

most social aspect of their niche, flock living. So the question becomes how do cowbirds learn when pragmatically challenged in more realistic ecologies?

8. Learning and the Ontogenetic Niche

Most work on social learning, however, occurs in labs where animals are individually housed and passively exposed to selected stimulation. By creating flocks that allow choices, the birds select stimulation and thereby opportunities to learn. As an example, a young male songbird may not have access to hearing adult song because adults do not sing when juveniles are close by and do not affiliate with juveniles. What do birds learn when the flock controls what is available to be learned? Said another way, what information is bio-available and how does an animal get access to it? Public information could be something so simple as degree of sex or age assortment, i.e., the presence of 'flock signatures.' Private information is embedded such that information must go through a social 'gateway', e.g., female wing strokes hinge on males singing to her first but that depends on his interest and ability to attend to her prior to singing. To give an example of a social gateway, male cowbirds in conventional restricted housing learn the songs they hear whether they are exposed through tape or live tutors. But what happens in flocks? We studied flocks of 20–25 birds in two adjacent aviaries separated only by a wire wall. In these aviaries, the birds could see and hear individuals in the other aviary as readily as in their own. To our surprise, we found no song sharing or social influences across aviaries in the 16 flocks we studied in this way (King, White, & West, 2003a; White, Gros-Louis, King, Papakhian, & West, 2007; White, King, Cole, & West, 2002). Thus, seeing and hearing did not define psychological borders, but social interaction did. This finding demonstrated the need to consider bioavailability as opposed to simple exposure to stimulation. The finding also showed that more is not always better as males copied less, and were more selective, in the flock setting than in restricted housing. The distinction is between what an animal has the capacity to do as opposed to how social/perceptual systems function to gate what is available to be learned. Restricted housing does not activate the systems responsible for ecologically relevant learning.

9. Experiential Knock Outs in Context

This finding led to a series of studies that applied principles of neo-phenogenesis to create 'experiential' knock outs (EKO's), a phenotype whose early social environment has been biased based on knowledge of natural ecological variation. We used EKO's to understand the role of social structure of a flock to guide learning. For example, we knocked out the presence of adult males in flocks composed of juvenile males and both classes (juvenile & adult) of females. We discovered atypical fall, winter, and spring behavior: few male–male song exchanges, no male affiliation with other males or females. The EKOs became self-imposed social isolates that sang frequently but in an undirected manner. The single largest effect in the first year is that they avoided

aggressive encounters apparently a consequence of their social isolation within the flock. During mating they showed little courtship or mate guarding, no fighting, no song exchanges with other males, and no genetic or social monogamy (Gros-Louis, White, King, & West, 2006; White, King, & West, 2002a). As we followed these birds beyond their first year, the lack of aggression proved to be a stable phenotype that persists for years which shows the robustness of ecologically relevant social learning. Thus, juvenile males are dependent on social interaction with adult males and females for social competence. The nature of flock structure becomes the safety net to guide male learning as it defines what is bioavailable (West, King & White, 2003).

We also looked at the role of flock structure with respect to female perception of song. We had found no evidence of female preference modifiability in our previous work. All of our studies on female perception had been done in restricted settings, a context we now saw asking a question about such a narrow dimension of behavior so as to limit inferences about basic developmental systems. Specifically, if bioavailability is shaping male development, the same might be true for females? To test this idea, we studied females in flocks where they could exercise more control over their exposure to male behavior. The first question we asked was whether female song preferences could be influenced by social context. We created *no male* EKO juvenile and adult females, who were housed together without males in a large aviary for 8 months prior to the breeding season. The females could see and hear wild males outside of their aviary. Wild males could land on the aviary and sing to individual females but the females could strictly regulate male access by moving away. In the spring, using the female bioassay we tested their preferences for local or distant song from two other subspecies of cowbirds. We discovered that we had erased the females' natal song preferences! This was completely contrary to what we had found in restricted housing. Erasing natal preferences in adult, wild caught females, may well be the first such demonstration of such malleability in song birds. This was an especially compelling finding in which some of the distant song variants were lexically very different from the natal song of their population. Thus, while males housed with canaries could incorporate elements of canary song the females obviously has a similar plasticity when studied in ecologically plausible settings (West, White, & King, 2003).

We then went on to ask the question whether we could build in a preference for certain song variants when females were in flocks, i.e., could we see constructive effects? To this end just prior to breeding, we both tape and live tutored flock females with specific natal songs and found that both types of exposure led to stable preferences for specific song types. Thus, females are able to re-set song preferences every year. The obvious difference between the flock setting and the restricted housing studies was that in the flocks many more females were in social contact with one another. In restricted housing, we frequently used pairs or triads of females with a single male or tape tutored. The evidence suggests that females observe other female reactions to song (e.g., wing strokes) and that the social dynamics among the females unlocks learning. Thus, as is the case with the males, it appears that the social structure is stimulating female learning for different song variants but also acting

as a safety net to constrain the underlying plasticity of potential preferences (King, West, & White, 2003; West, King, White, Gros-Louis, & Freed-Brown, 2006).

10. Pragmatic Learning in a Flock

Changing to a dynamic setting as in the flock manipulations revealed the importance of an animal's ability to engage a social context to obtain relevant information, information not available in restricted settings. Several examples illustrate this point. In restricted housing, when a male sings to a female she cannot leave, the best she can do is to move away a short distance but this still allows the male to sing to her. The male in this situation does not have to learn to be strategic in his approach or his attention to a female. In the flock setting, if the male simply runs up to a female to sing she is likely to leave before he ever has a chance to sing. In the flock, the approaching male must attend to subtle female social signals and modulate his approach in accordance with what she will permit without departing. This male is then learning social pragmatics of the how, when and where the song should be used. He is also learning to sustain his attentional focus to be able to pick up in the female signals. The same general principles apply when singing to other males who may react aggressively if their social skills are low. We know from examining the neural structures of males housed with interactive vs. noninteractive females during their first year that the males with socially interactive females develop a larger neural volume of nucleus rotundus in the visual thalamus than males with less interactive females. The nucleus rotundus is thought to mediate the perception of form and motion. Thus, during development the nature of the social environment is literally shaping the neural ability of the brain to process information. This is important because it shows that the neural development is also dependent of exogenetic influences (Freeberg, West, King, Duncan, & Sengelaub, 2002).

The story is the same for females. Restricted housing is generally justified as revealing basic innate capacity without distracting influences. For female cowbirds restricted housing reveals innate artifacts without illumination actual developmental pathways. Specifically, females need to be motivated by being part of a larger female social group and be sensitive to the social reactions of that group to modify their evaluation of male behavior. For example, in an all female flock composed of both juvenile and adults the presence of male song will trigger, in real time, rapid segregation of the flock by age (Gros-Louis, White, King, & West, 2003). The segregation will dissipate in minutes if no song is present. The effect can be produced with the presence of a singing male or by playback of song. By contrast, the presence of nonsinging males produces no segregation. During the period when a group of females are reacting to song in this way some females will wing stroke and the wing stroking elicits the attention of other females. Thus, it appears that the collective social context is the key to stimulating female preference learning. The collective social context necessary for this learning is not available in simpler housing in pairs or triads.

11. The Safety Net

For this parasitic species, it is clear that evolution has trusted an exogenetic system to transmit information vital to reproduction from one generation to the next. The 'safety net' is the social structure of the flock. The ontogenetic niche can be considered at several levels, but at the most basic level, an individual's niche is defined by his or her status or position within the flock. This position defines what is available to be culturally transmitted or learned throughout the lifespan. Consider the malleability of adult female song preferences at the macrogeographic level and the fact that the male's song is for the female. Female sociality/song preferences are the major determiners of flock organization and the goal of male behavior is to meet those preferences (Freed-Brown, King, Miller, & West, 2006; King, White West, 2003). This developmental system is designed to be open as ecologically possible and thus immediately sensitive to ecological change. This system is the antithesis of a closed developmental system. Is this system unique because of the parasitic habit? The answer is that we do not know because comparable experimental studies of non-parasitic songbirds have not been carried out.

Thus theoretically, to most people, this little brown bird occupies the status of the annoying gadfly. The cowbirds' rules of sociality are stinging rejections of accepted beliefs about songbird development by virtue of their use of nonauditory vocal learning and the ability of males and females to communicate about communicating. The cowbird findings also fly in the face of accepted rules about the role of early experience. We see it as a model for the dynamics of developmental growth where function alters function, within and across generations.

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