

The ontogeny of competence

Andrew P. King and Meredith J. West

Indiana University

Department of Psychology

Bloomington, IN 47408

APK, apking@indiana.edu

MIW: mewest@indiana.edu

Running Head: Competence

The ontogeny of competence

ABF Notes, Cornell. Morrill Hall. Aug 1968, new graduate students waiting for first teaching assignment. Practically first sentence of APK to MJW, "What is your theory of learning?" MJW thought it an odd opening; APK did not.

Prologue: Animal Behavior Farm: Mission and Lifestyle

At a recent national meeting, after a paper session on the development of mate choice, someone stopped MJW and asked about her "feminist political agenda." MJW asked for clarification, not aware of having so grand thing as an agenda. The questioner said, "Well, it's just you keep asking the speakers what the animals were doing, what they could see or hear... you know... little stuff, stuff not related to mate choice." The questioner had done a good job of characterizing the behavior she had seen, but perhaps did not have enough information to understand the underlying reason, the "agenda" as it were. Although we are interested in the big question of the process of development, we are also truly fascinated by the particulars of developmental systems. For us, development is in the details. As a result, we tend to ask concrete questions. Examples of such questions include the diet of study animals, the specifics of their housing, how often animals were observed, and most importantly, what

animals do when humans say the animals are “choosing” or “preferring” or “interacting”. In this chapter, we discuss our approach to the study of development. The specific domain for our work has been birdsong. The study of bird song is often touted as a model system for the study of learning, maturation, and experience. While we do not dispute this general view, we will argue that the study of song learning has much more to offer by considering developmental particulars, as well as developmental contexts. The editors asked the contributors to this book to frame their individual scientific journeys in terms of their own life history and development. We puzzled about how to capture our journey. The strategy we chose, as introduced above, was to include brief notes about life in our laboratory over the years as we chronicle the course of our research. These notes were chosen because they capture or caricature distinctive features of our approach. We hope these notes shed a more personal light on our scientific style. The accuracy of the memories is about $p < .10$.

The chapter contains four sections. First, we outline the theoretical context present when we began our work. Second, we show how our ideas evolved as we studied brown-headed cowbirds. Third, we describe the new approaches we are using to study of the pragmatics of song learning. Finally, we discuss some of the implications of this new knowledge for the general study of development and in particular, the need to shift from an individual to social perspective about developmental processes.

Cultivating behavior down on the farm

ABF notes, Liddell Farm, August, 1973. Students just returned from 72 hr vigil in barn, had been camping out for days to see what happens to baby cowbird when foster mom sees it is a cowbird... hot and humid in the barn amidst cows, pigs, chickens, mosquitoes, and so on. Finally, the object of interest appeared... baby cowbird emerged on rafter, fluttered, flapped, and floated right into the mouth of a pig... Students return hot, dirty, heart-broken; pig pretty chipper.

Our students call our lab "the farm". We are not sure who started this practice but we like it. In the Midwest, farmers grow corn, wheat, or beans. We grow behavior. We create circumstances allowing us to see young birds living in different social settings. For example, some birds may live with adult conspecifics, others only with other juveniles. These social arrangements produce what can loosely be called behavioral strains. We then evaluate the strains in different ways to assess the behavioral yield of the particular social conditions (West & King, 1994). As in all farming, we have had good years, not-so-good years, and never-in-a-million-years years.

We did not realize we were becoming farmers until it was probably ridiculously obvious to everyone else. There certainly were many clues. For the past 25 years, we had lived and worked in laboratories only steps away from where we lived. We began in a rental house, which we outfitted with large birdcages in the garage and sound attenuating chambers in the living room. Did we mention there were baby birds at our wedding? At the present, our laboratory is located on 90 a. of old field and forest edge. It consists of several lab buildings, nine outdoor-indoor aviaries, and two homes, one for us, and one for students, post docs and two parrots left scholarships by their now deceased Indiana University alumnus.

While we may not have hit on the analogy to farmers ourselves with respect to our research, we knew from the start that we wanted to study animals in social settings, that is, in settings containing fundamental parts of their natural environment. We also knew we wanted to watch the growth of behavior as it was occurring. We had entered psychology at a time when watching what animals did while developing was not a high priority. With some outstanding exceptions, coming primarily from the "Rutgers or Museum" group (Lehrman, 1970), description was not a high a priority. Inattention to descriptive work seems ironic in that research on early experience was thriving. But it was the outcome, not the process, of early experience that was valued; observing and documenting the "experience of early experience" was not so valued.

At the same time frame, the shadow of Harry Harlow and colleagues also eclipsed interest in normal development (Harlow & Harlow, 1962; Harlow, Harlow, & Hansen, 1963). The dark side of development, what happens to animals when raised in impoverished conditions, was the dominant paradigm. We were not interested, however, in what happened to animals living a life no member of their species had ever encountered. Perhaps such conditions were useful to create eye-catching models of psychopathology, but we wanted examples of normal ontogeny. We wanted to study animals as they developed the necessary skills for survival, a positive ontogenetic perspective, emphasizing "learning what comes naturally" (Kaufman, 1975).

We began our work in the pre- Gary Larsen cartoon era, a time when scientists perhaps found it easier to maintain the illusion that they were in charge of a lab animal's experiences. Few worried about how animals perceived the experimental task (Breland & Breland, 1961). We had had a memorable lesson on

the topic of animal-experimenter perceptual discrepancies early on. The lesson came during a brief stint observing ongoing studies of learned helplessness in dogs. The dogs lived in kennels a few rooms away from the testing room in which they were exposed to inescapable or escapable shock. The dogs, given no way to predict shock, appeared to give up. They did not attempt to escape to the safety of the other side of the apparatus. These studies, and many more to come, contributed to a heuristic model of human depression, focusing on the consequences for people of undergoing experiences they can not control (Seligman 1968; 1975).

But, when not inside the testing room, some of dogs seemed far from helpless or depressed: some resisted been taken out of their cage while the others walked towards the testing room with tails wagging. But once near the testing room, their behavior changed. Anyone who has observed dogs at the vet has seen examples of such transitions: Happy dogs frown and strong dogs whimper. Returning to the behavior of the dogs in the lab, our question was when did the experiment begin and end from the animal's point of view? We do not dispute that the different testing conditions had vastly different experimental outcomes, but we did wonder if enough appreciation was being given to comparing behavior inside and outside of the testing room.

The memories of these dogs have remained with us over the years as a lesson in evaluating tasks from the animal's and experimenter's perspective. More than once, we have found that the tables had been turned on us

Thus, to summarize, we wanted to study development in a system in which the animals' behavior was visible and amenable to thorough description; we wanted the object of development to be a skill with ecological relevance; and

we wanted to be able to follow development over time. The behavior we chose was the ontogeny of bird song. To set the stage, we first discuss the theoretical zeitgeist regarding birdsong circa 1970 and then how brown-headed cowbirds (Molothrus ater) became of the focus of our inquiries. In reality, the interests in song learning and cowbirds co-occurred but we will start with the theory.

Birdsong: The model behavior

ABF notes, 1972, Liddell Farm. Cowbird egg # 62 hatches, ... the nestling thrives, first one to do so in 62 tries! Turns out to be a female...APK/MJW perplexed... what to do with a female who cannot sing?

If bird song had not existed, Niko Tinbergen would have invented it. Birdsong is the perfect example of his definition of integrative study, requiring attention to cause, function, development, and evolution of behavior. With respect to one of these topics, development, Colin Beer (Beer, 1982) provided the best retrospective framework to categorize early approaches to the study of song ontogeny. He stated that "what developmental study [of song] looks for depends on what is thought to be there to find, which depends on how the social communication system is viewed in its syntactic, semantic, and pragmatic aspects" (p.300).

With respect to this study of birdsong, in the 1970's, the search for syntax ruled. Researchers such as Thorpe and Marler had established that song structure (a less anthropomorphic term than syntax) was learned in songbirds (Marler, 1970a; Marler, 1970b; Thorpe, 1958). Songbird species also showed remarkable continuity from generation to generation in the reliable transmission of song structure. Thus, the fact of learning or plasticity as part of " what was there to find " was not an issue. But, from our point of view, those studying

birdsong did not seem comfortable with the idea of plasticity in models of birdsong. The fact of learning was, in some sense, a problem to which a solution had to be found. Concern mounted about the dangerous side of learning: that is, what mechanisms keep birds from learning the wrong thing (Kroodsma, 1982)?

The ethologists' fears were, in part, an understandable reaction to behaviorism's quite grandiose claims that animals could learn all sorts of strange things by means of conditioning. But the concern also related to the foundations of ethology, i.e., the belief that behavioral traits of animals are reliable enough to be used in taxonomic decisions. Although most of us associate ethology with a "back to nature" philosophy, questions about phylogeny and the classification of species by ancestry represent its most important contribution (Lorenz, 1970). Until ethology, and even after, the classifying and reclassifying of species relied solely on the identification of morphological characters such as the shape of a bird's beak. For an ethological trait, i.e. a behavior, to be taken seriously, its reliable transmission from one generation to the other had to be established. Mechanisms were needed to explain how developmental programs fostered stable transmission by restricting learning to the "right" songs of the "right" species. Such a view favored innate explanations of transmission, that is, developmental programs closed to learning. How else to guarantee accurate transmission? Or, if song learning was not entirely closed, as appeared to be the case for song, what mechanisms were there to modulate exposure to social or vocal influences (Nelson & Marler, 1994)?

The question of limits on learning for song learning overlapped with interest in the concept of critical or sensitive periods. The idea of critical periods suggested fail-safe mechanisms or safety nets to protect young learners from the

vagaries of the environment by controlling the timing of vulnerability to environmental influence. The question of protected learning was of evolutionary consequence. The adaptive risk, for example, was that sparrows of one subspecies would copy and retain songs of a second subspecies. Such copying could then affect mate selection and thus potentially affect speciation (Marler, 1960).

The search for guided learning was also motivated by a different view of the construct of learning itself: was it a meta- or sub-category of behavior? In the hands of psychologists, learning was accepted as a superordinate category, a tool of very general use in many behavioral domains. Ethologists, on the other hand, preferred to think of learning as simply another type of adaptation such as nest building. In the words of James Gould (Gould, 1982):

Animals are perhaps in some sense molded and shaped by their environments and experiences, but within a set of complex, species-specific rules that do not at all fit the model that classical behaviorists maintained. Learning . . . is one of the standard, of-the-shelf programming tricks available to evolution and despite the usual dichotomy; this kind of learning is the epitome of instinct (p.275).

Thus, song learning was considered domain-specific plasticity. That view was also apparent when looking at how song learning was studied in the laboratory. If it can be said that life imitates art, methods must imitate theory. The general method involved housing young birds under conditions of controlled exposure to species typical stimulation. The kinds of experimental

conditions used to study songbirds in the 1970's emphasized physical compartmentalization, and the isolation of nature and nurture. The goal was to reveal the developmental "blueprint" for vocal ontogeny, the syntax or acoustic structure present in the absence of exposure to conspecifics. In general, these studies confirmed that songbirds housed with no exposure to conspecifics, i.e., isolate birds, did not develop typical song structure (matters of semantics and pragmatics were, as noted earlier, typically not addressed). The songs of isolates generally bore a resemblance to the species' songs(s), but lacked important features. Thus, the "innate song" upon which experience would build was assumed to be represented by song developed under conditions of complete of complete acoustic deprivation (Marler, Mundinger, Waser, & Lutjen, 1972; Thorpe, 1961).

Windows for development analyses

ABF notes, 1984, North Carolina home. Five-year-old son of APK/MJW is stunned to learn that he does not have 23-year-old brother.... try to explain to him that student he sees each in kitchen, bathroom, and outdoors is not sibling but academic offspring.....question of adoption raised.

We began studies of song learning against this developmentally conservative backdrop. As intriguing as we found song learning, we chose from the start to tinker with basic methods. We did not want to raise young birds alone, but instead, with social companions. Moreover, we wanted to study syntax, semantics, and pragmatics concurrently. These goals stemmed from a positive view of learning and an open or liberal view of developmental

processes. Harlow's research and much of the research on early experience seemed off center to us as they focused so much on negative outcomes. Our positive thinking came about in large part from immersion in ecological /Gibsonian psychology(Gibson, 1969; Gibson, 1966). We saw ourselves as part of a "performatory" school of thought about development, learning and perception. To understand how animals develop, we had to measure what James E. Gibson had called "performatory" feedback, that is, multimodal feedback obtained by acting or behaving in an environment rich in potential information. Thus, for us, to understand ontogenetic mechanisms of perception and learning required that we create constructive developmental contexts. We needed to see animals in action and animals with behavioral options in environments with something to offer.

In looking at our own thinking at the time, perhaps, the single most important difference in our view of development compared to others studying song was that we did not believe there was a neutral zone or holding pattern for developmental systems. Moreover, we did not accept that experience was passively delivered to young organisms, as emphasized in Gould's statement cited earlier. Thus, animals in isolation were still in environments and they could shape such environments and obtain feedback. These environments represented biased living conditions (*sensu* E. Gibson, 1969). Our job was to find out how the bias affected the process and outcome of development.

Our first attempts to design new contexts now seem awfully timid. First, we chose simply to use larger cages so those animals could be housed socially and enclosures with windows so that we could see them. Later, we used enclosures that eventually outgrew the size of most labs, culminating in the

construction of indoor-outdoor aviaries. These housing changes intersected with laboratory procedures, as we needed to find ways to measure what animals actually do with one another. If one were to look at the major change in the style of our research over the years, i.e. kinds of treatments, kind of questions, the trend would be toward more detailed social analyses carried out in socially more complex settings (West & King, 1994).

The cowbird: An unlikely but timely choice

ABF Notes, 1973, kitchen, Freeville, NY. APK/MJW eating dinner with bird cage on table housing 15 day old baby cowbird and 30 day old cardinal. We beg for a 15-minute break to eat, cowbird objects, cheeping at rate of 10 chips/sec. Finally, cardinal takes control... finds a stray piece of burlap and shoves it down cowbird's throat.

We have saved our inadvertently most brilliant move to the last, our choice of cowbirds. We did not know at the time that the species would thrive in the laboratory or be exceptionally tolerant of inquisitive humans. We also did not know how important female cowbirds, who do not sing, would be to our story. We had had the cowbird urged upon us, in some sense, by the writings and words of Lehrman. He pointed out that a brood parasite like the cowbird should have a very different developmental program to handle early experience than should a non parasitic species like its near relative, the red winged blackbird (*Agelaius phoenecius*) (Lehrman, 1974). Brown headed cowbirds do not raise their own young, the female lays her eggs in the nest of many other songbird species (Friedmann, 1929). How then do young cowbirds get to know other cowbirds and how do they avoid misdirected learning? Why doesn't a cowbird raised by a vireo sound like a vireo or try to mate with vireos?

In our exuberant state, we charted a course to study all 7 species of cowbirds from those in North America to those in South America. Not all cowbird species display brood parasitism, with the southernmost cowbird in Argentina, the bay winged cowbird, being completely non-parasitic. As of this writing, we are still engrossed with the North American species and still puzzling about developmental contexts applicable to it. We could never have anticipated the ontogenetic riches we were about to uncover. The beginnings of our interest in the species also seemed auspicious. Cowbirds were no further away than our front walk. We still use slides today that came from photographing our “first” cowbirds on our sidewalk in 1971.

When Lehrman drew attention to the cowbird, little was known about its development. In the next decade, we would learn that the cowbird's song ontogeny is exceptional, but not in ways that anyone had predicted (West, King, & Eastzer, 1981a). There is plasticity at individual and populational levels, there is sensitivity to social context, and there are really three inter-related stories, one for males, one for females, and one for the natural unit of the social group.

In our initial work, we used a modified version of acoustic deprivation to look at song development. We found that when acoustically naive male cowbirds are housed socially with non-singing females or members of other species but deprived of hearing adult song, they, like all passerines studied to date, produced atypical vocalizations. This finding was at the time somewhat surprising as cowbirds had been expected to manifest an entirely closed program for development to avoid learning the songs of their foster parents (Mayr, 1963, 1974). Acoustically naïve females, on the other hand, appeared to respond exclusively to conspecific song with no prior experience. But, even more

surprising than the male's plasticity, however, was the finding that naïve females responded more to playbacks of the songs of naïve, as opposed to wild, male cowbirds. To test the functional properties of songs, we played back songs to females living in sound chambers with other females but no males. Females responded with twice as many copulatory postures to the songs of isolates compared with those of normally reared males (King & West, 1977; King, West, & Eastzer, 1980; West & King, 1980).

We now have many new thoughts about the meaning of that first study (see West and King, in press). But, as a way to bootstrap a research program, there was no better way to start. First, we had discovered an important new assay, the testing of song function by playback to females. No longer did we have to rely only on pictures of song structure, pictures sometimes misleading, as human eyes could not discern what avian ears found most stimulating. We also had an anomaly, a Kuhnian gift to motivate our work. Why would the songs of isolated males be better than those of wild males? We reasoned that the naïve songs might have been more arousing because the males had been denied access to adult males whose influence might have diluted the song's copulatory function. Cowbird song is sung not only to females during mating, but also to males during mate competition, an experience that may change in song content.

The seemingly superior function of isolate song was also puzzling, as cowbirds are not acoustically deprived during song development but live in large flocks. What then did these data say about the effects of isolation from adult males on cowbirds? Briefly, the data told us although the young males lacked an adult model, they had been given a captive and noncompetitive audience in the form of females or nonconspecific companions. Isolation had

conferred on males by default the status of a dominant male. And like dominant males in a normal group, they could sing songs highly attractive to the female with less risk of attack by other males. When we allowed adult males to spend winter with only females: we found the same effect, the experience improved the perceptual potency of their songs of playback females.

Another set of studies clarified further the nature of the "experience" of isolation, namely, that its most obvious facet, lack of auditory exposure, was not responsible for the functional outcome obtained, songs attractive to females. We maintained males in a common auditory environment but exposed to different social experiences: Some males lived in a group of males and females; others lived with only females but could see the group; and others lived with females with only auditory access to the other birds. The results replicated those of the first study: The birds in visual isolation from other males but housed with females developed highly effective songs, whereas the males in a group or the males witnessing the group's interactions sang less effective songs (West & King, 1980). Cowbird song was thus highly dependent on a male's perception of the *social* consequences of singing. And that was indeed what isolation had biased, the performatory consequences of singing.

Expanding the developmental range

ABF Notes, Summer 1982, South Aviary. Have spent winter tutoring male cowbirds to sing local North Carolina song and foreign Texas cowbird song... males became bilingual, a first we think...now will test what NC and TX females think. Check aviary one day and find no birds but one very robust black snake ... only bilingual cowbirds in the world now in his gut. By next day, he digests our efforts and returns leg bands.

We next considered the idea that deprivation revealed the "innate" or "inherited" components of song production as discussed earlier. Examination of

the acoustic structure of isolate songs revealed that they contained "generic" structures for cowbird song, a cowbird-biased alphabet soup. The mix perhaps partly reflected the design of males' vocal morphology and syrinx and also sound preferences, perhaps acquired in flocks with adults and juveniles when they were quite young (King & West, 1988). Some isolates managed to string together effective combinations, others quite strange ones. To learn more about the building blocks and building process for cowbird song, we expanded our studies to new geographic populations. The ones of most interest here were birds from North Carolina (NC) and Texas (TX).

Comparisons of these populations revealed more male plasticity and little female plasticity. NC females responded most to NC songs, TX females to TX songs. But, we found that juvenile NC males became bilingual (singing clear renditions of both NC and TX variants) when exposed to adult TX males (West, King, & Harrocks, 1983). In contrast, adult AT males did not learn TX song when housed with TX males, but they did do so when housed with TX males *and* females. More-over, adult NC and TX males substantially altered their repertoires when housed only with non-singing females of the other population (West & King, 1985).

Maybe the handwriting had been on the wall since our first study in which we has used females as companions for males...maybe females affect song content? We tested this proposition directly by investigating the female's influence on naïve juvenile males. Thus, hand-reared, acoustically naive NC males were housed in acoustic isolation from other males but maintained in one of three conditions: individual housing with other species, with NC females, or with TX females for their first fall, winter, and spring. The three groups of males

developed significantly different vocal phenotypes from one another, although none had ever heard cowbird song and all presumably had the same template. Analysis of their first-year songs revealed that males housed with other species showed intermediate performance on acoustic and geographic measures of song content while NC males housed with NC females sang no TX song and NC males with TX females included TX specific song structures. Moreover, the two groups of males with females show non-overlapping distributions on critical acoustic measures (King & West, 1983). However the females effected this change, they did not do it by singing. And however the males learned, it was not accomplished by imitation, the only mechanism proposed to explain birdsong learning.

We were also led to consider the role of females from other studies using naive males whose social experiences were supplemented by hearing tutor tapes of normal male songs. When tutored with local songs, NC males housed with canaries copied significantly more of the tutor songs than did males individually housed with NC females (West & King, 1986). Thus, although all the males had access to the same "innate" program and the same tutoring regime, their repertoires differed reliably by group from very early in development. Furthermore, although the males with NC females learned the tutored copies, as did the males with canaries, they subsequently went on to improvise and change the material enough so that the original songs were no longer easily matched. The males with canaries did not deviate from the tutor songs. Thus again, female cowbirds appeared to provide a different learning environment than nonconspecifics.

Measuring the sounds of silence

ABF Notes, March 1984. APK/MJW reviewing videotapes of female cowbirds being sung to by young male cowbirds.... female has put on her psychoceramic make-up, no facial muscles moving. Then we see male hopping off perch and moving towards her.... we rewind tape to discover her moving her wing and covering it up with a wing stretch right before male had levitated off the perch...male delirious...he has found chink in her armor.... sings hundreds more songs.

We used several contexts to explore female influence. First, we studied a winter flocks. Did juvenile males have access to females during the time of year that their songs undergo the most rapid and extensive changes? The answer was yes -- juvenile males associated quite closely with females --much more closely in fact than with adult males (King and West, 1988). Juvenile males were captured with females in all eight banding sessions, yielding a higher ratio of juvenile to females than adult males to females. Thus, the access was there.

We also exploited a laboratory setting of males and females housed together in the same enclosure to videotape interactions between males and females during the time period when flocks begin to disperse and males and females return to prospective breeding grounds. We videotaped 22 pairs for 328 hours covering 82,080 songs. We found that most of the time, well over 90%, females appeared to do very little when a song occurred, it was often hard to tell from her behavior that she had heard a song. The clue to what was happening between the male-female pairs came from watching the males: every once in a while, when a male sang, he would suddenly change the pace of his singing, as well as sometimes abruptly move toward the female. With videotape, we retraced the males' movements (West & King, 1988). We found that such changes in the males' behavior were preceded by wing actions by females --

movements we called wing strokes --if a bird could point, a wing stroke would qualify. Wing strokes occurred infrequently. In general, males had to sing 100-200 songs between wing strokes. The data suggested to us that female cowbirds used a gestural signal system to communicate about an acoustic signal system: a visual system within a vocal system. Thus, the task confronting the young males was a multi modal one; they had to look as well as listen.

To find the functional value of wing strokes, we employed a playback test during the breeding season to see if females would adopt copulatory postures to songs that had elicited wing strokes as opposed to ones that had not. The answer was yes -- wing stroke song elicited significantly more copulatory postures from a different set of females, who knew no more about the singer than his song (West and King, 1988). And thus we concluded that wing stroking was a form of positive reinforcement, dispensed on a partial schedule, serving to shape the male's singing toward more female- preferred signals.

Before turning to the studies of the 1990's, let us bring together what we had found thus far. Early in our development, we had rejected the idea that species-typical deprivation provided a baseline or blueprint for song. In cowbirds, naïve males deprived of hearing adult males showed atypicalities in their song, but their origin of the difference could not be attributed solely to what was NOT there, but to social influences from companions or perhaps even themselves. Our data showed how important social effects were. Some have tried to dismiss or qualify our data as idiosyncratic because the data came from a species with a very different life history. To that charge, we counter-charged that other species had not been studied as our cowbirds had been studied. What

would happen in " traditional " species if the social context were richer but still uninformative about song structure? The results to date show that social context affects basic features of song ontogeny including the timing of sensitive periods and the kinds and quantity of songs copied from tutors(Baptista & Gaunt, 1994; Baptista & Patrinovich, 1984; Slater, 1989). Some of effects have been subsumed under the name of "action-based" learning, recognition of the role of social reinforcement in the selective attention to species typical and in the attrition of song material(Marler, 1991).

During the 1980's, we had also carried out parallel studies, not described here, asking about the function of song for mating and the consequences of learning neophenotypic variants such as NC males learning TX song [(West, King, & Eastzer, 1981b)West, 1983 #58]. These data helped us understand relationships among the three aspects of communication. The data showed that males in aviaries who were successful in courting and copulating with females produced songs that playback females (who heard only their song) responded to high levels. Mate choice experiments also showed that bilingual males' success depended on the perceptual preferences of the females. In general, females preferred natal song variants and thus mate success correlated with the amount of female preferred song in a male's repertoire. These data fit nicely with the data from studies of song development where we had shown that naïve males biased their emergent repertoire toward the songs matching their female companions' natal preferences. Thus, the story about structure fit well with the story about function (the analog to semantics). But, we still had not achieved our goal of incorporating the third part of a communicative system, pragmatics. That step consumed the 1990's.

Studying song use: what do males know and do they know they know it?

ABF notes, Summer 1983, South Aviary. Have new group of bilingual and monolingual males. One of monolingual birds, male 2G, put in aviary with females who like the other variant of song. His songs get him nowhere.... contrives new plan...sits in corner of aviary and waits for another male to induce female to mate; male 2G zooms in and knocks off the singer and copulates.... true avian finesse.

In the 1990's, we now wanted to see song and singing in a competitive social context. In retrospect, there were several reasons why we had not taken this step sooner. In the 1970's and 1980's, we had focused almost exclusively on the male cowbirds' song and the female's perception of it. Although we had looked at courtship in wild caught males, we had never considered looking at courtship in the neophenotypes we had created. Other labs had also not looked at the behavior of birds housed under such impoverished conditions. The simplest reason was that there did not seem to be much to study. Like Harlow's motherless monkeys, hand-reared, companion-poor songbirds exhibited fear, stereotypy, and stress when placed in open environments. What probably deterred researchers the most from such studies was that the birds' vocalizations were the true targets of inquiry, as it was assumed that the acoustic structure held the key to understanding song ontogeny. It was the state of the isolate bird's song, not the state of the bird, that was of theoretical concern. That little was known about the competence of the birds whose vocal histories were of such interest probably just seemed irrelevant.

The growing use of playback techniques to learn about song function also mitigated against further investment in looking at the behavior of socially and

acoustically naive birds. These techniques worked well to differentiate the functional properties of songs from males with different developmental histories (Searcy, 1992). If song structure could be connected to song function via playback, there seemed to be sufficient basis to conclude that the song functioned to affect female choice. The idea of connections between the production and perception of mating signals fit preconceptions of what one ought to see when studying the components of a communication system, i.e. intrinsic coupling of sender/receiver behavior. The ethologists' diagrams of stickleback courtship with a set of arrows connecting male behaviors to female behavior seemed applicable to many species (Morris, 1970). Lorenz too had speculating the primary, innate programming automatically allowed animals to summon species typical behaviors at just the right time and to the right receiver (Lorenz, 1965).

All of us know that naming a behavior does not explain its function, i.e., a nominalist fallacy. But could there also be a "connectionist" fallacy", that is, an automatically triggered assumption in humans that animals did not have to learn how actions become linked to consequences? All researchers implicitly adopt a connectionist mindset to link what they are seeing and what they think it means. But, in the case of cowbirds, were we projecting our intuitions about linkages between behaviors without sufficient testing of animals' abilities to link acts together?

Thus, we undertook the study of the translation of capacities into competencies. As we carried out the studies to look at song and singers in context, we discovered another reason why such work had not been done. It was hard! Figuring out ways to get cowbirds to assume social roles such as tutor or receiver and to perform these roles for young naïve males or females took

orchestration. At times, we felt more like the directors or producers of a summer play than researchers. We described one such study below in detail to demonstrate the complexity of arranging social circumstances in which to watch our subjects and the considerable payoff of such efforts.

The first study featured wild caught juvenile male cowbirds (*M. a. artemisiae*) from an ancestral part of the cowbird's range, South Dakota (Freeberg, King, & West, 1995). In the study, we combined controlled social housing, playback tests, and measures of courtship to obtain a yearlong look at social and vocal outcomes. To begin, we housed the South Dakota (SD) individually with canaries (*Serinus canaria*) or female cowbirds from the same SD site. Thus, we were using housing conditions we had used many times before. But, instead of stopping the study when the males' songs were fully mature, we initiated new means of assessment to see what the males would do if allowed to interact with female cowbirds, nonconspecific companions, or each other in new social contexts. We also used playback of the males' songs to SD females to relate male courtship success to the potency of the male's vocalizations. And we recorded the males' vocal production throughout the year to trace changes in the structure of their songs.

Briefly, the experimental design was as follows: first, the young males were housed with the pairs of female cowbirds or canaries with whom they lived for the next nine months, the time frame in which they develop song repertoires. In May, to initiate the new phases, we moved the males to flight cages by group, thus, the canary housed (CH) males were in one cage, and the female housed (FH) males in another. After several weeks, we moved the birds to large aviaries

containing many potential social companions including female cowbirds from South Dakota, Indiana, and North Carolina, as well as canaries and starlings. And, waiting backstage were adult male cowbirds from the same geographic locations. They would play a role in the final act. Our general question was what our naive males would do when given so many social options?

Observations of the FH and CH males after they emerged from the enclosures and were placed in their respective flight cages suggested that the aviary plans might be premature. The birds were in fragile, social states (even though they had had companions throughout the year, and thus were not true isolates). The day that the males were removed from their female or canary companions, even the most naive observer would have been able to tell that these cowbirds were different. Noise in the laboratory room, especially unexpected sounds such as a human sneeze, produced frantic flying and hovering as the birds attempted to locate a perch unoccupied by another male (there were many perches to choose from and burlap cloth to hide behind). Observers reported the birds to be frozen in place for long periods. Even so seemingly simple an act as flying to the floor of the cage to eat involved problem-solving--the males would make several tries before actually landing and eating or drinking if another male was already there. For the first five days, we did not see two males sharing a perch nor did we see two birds eat or drink at the same time. The canary-housed males appeared to be the more fragile group: they were even slower to show social interactions with each other.

But the cowbirds' singing resumed quickly, much sooner than other social behaviors. The first vocalizations occurred the day after emergence

and included typical cowbird sounds as well as some odd imitations and improvisations such as the sounds of female rattles and imitations of canary calls. The manner in which males delivered their song was, however, different from that of wild males. First, the songs were not accompanied by the typical song spread display. The display begins with the male raising the feathers on his head and chest, lifting and spreading the wings while bowing forward, sometimes to the point that his beak reaches the perch or ground (Lowther, 1993). The displaying male then wipes or rubs his beak against a perch. Song co-occurs with the display, although song can also occur without it. The CH and FH males sang but without the concurrent bowing actions. Most vocalizations were also not directed to other individuals. The birds often sat down on the perch while generating vocalizations with little sign of responsiveness to events around them. The singing looked more like reflexive hiccoughing than communicating.

During emergence, we saw social deficiencies, but some of these lessened considerably as the birds settled into their new surroundings. Within a week to ten days, the males had changed considerably. They were singing and displacing one another from perches, foraging as a group, and in the case of the canary-housed males, "guarding" the cage wall and singing through the wire to a new group of canaries in the next cage (not their former companions).

But the subsequent events of that summer greatly revised our thinking about learning to connect socially. First, in a large flight cage, then in a large aviary, we watched as the CH males chased and sang to new canaries. Had these males been displaying these behaviors to female conspecifics we would have labeled it "courtship." Even more striking was the inattention of the CH males to female cowbirds. The female cowbirds, in breeding condition, were generally ignored by the CH males. The CH males' persistence was striking and the canaries' patience admirable. Even when the canaries retreated, and even when the female cowbirds approached and solicited with copulatory postures, the males quickly resumed their canary pursuits. It was as if they were on a behavioral spring: the female cowbirds could pull the males towards them with active displays, but after awhile, the spring could be stretched no more, flinging the males back to their canary pursuits.

The FH males did vocalize to female conspecifics in the flight cage tests and ignored the canaries, behaviors that made sense to us. But what did not make sense was what happened when we placed them in large aviaries. They had little success courting female cowbirds in the more open and complex setting. The major failure was that they did not direct their vocalizations to female cowbirds. They devoted the majority of their time to interactions with other males, singing many more songs to each other than to females. At least the CH males showed the kind of energy and drive breeding male cowbirds usually display; they just chose inappropriate targets. But the FH males seemed lifeless by comparison, content to sing to one another or just to themselves.

After documenting the behavior of the young males with several sets of females, we brought on adult males. Would they court to the females effectively

and would young males learn something by watching them? The introduction of the adults had an immediate and salutary impact on the females. Until that time, they had showed little interest in the FH and CH males who, in turn, had paid little attention to them. The day the adults arrived we saw more females and more social activity than any time prior. The adults successfully courted and copulated with females. But their success did not change the behavior of the FH or CH males, except perhaps to suppress what little courtship we had seen. Thus, learning on the job did not appear to work.

By the end of the breeding season, we knew something about the playback females' opinions of the songs of the FH and the CH males. The females had responded significantly more often to the songs of the FH males compared to the CH males. In a second playback test, we found that the playback females responded as much to the songs of the FH males as they did to recordings of wild males from South Dakota. Thus, the lack of success of the FH males was not a result of having ineffective songs. The lack of concordance between the reactions of the playback females compared to the aviary females gave us more evidence that what was wrong with the FH males was not song related, but skill related.

Taken as a whole, these data challenged several long-held assumptions. In past studies, we had assumed that playback females could recognize effective songs, but we had also assumed that males could recognize when to sing such songs. Clearly, we were wrong. As we thought about it, the new findings suddenly cast song playback studies in a new light. When we carried out playback work, we did more than playback songs. We were borrowing skills naturally used by successful males. We were engineering links by our actions

and technology; links we assumed were second nature to the subjects themselves. We chose the song, its playback level, the time, and the distance of the recipient to the speaker. The new data suggested that if we left those actions to the FH males, the playback procedure would not have worked. It had never occurred to us that we had been supplying vocal skill for the male whose song we had recorded.

Throughout the entire aviary task, observers had also found themselves trying to instill some vocal skills by silently coaching the birds on what to do to court to successfully. When an FH male would sing to a female, an observer might say, " OK, now sing another song, wait... don't leave, look at her, look her in the eye, follow her, ignore that male, keep on her tail. "

In the following two years, we repeated the experiment with a new population of cowbirds, birds from Indiana(West, King, & Freeberg, 1996). We obtained essentially the same results: cowbirds from Indiana were not as persistent in "courting" canaries but they, and the female-housed males, showed little courtship skill with female cowbirds. We also carried out studies to rehabilitate the CH and FH males. We found they could be highly successful at courting if exposed to males one year older than themselves. Exposure to other same aged males did not improve courtship ability.

To summarize, these experiments revealed the multiple layers of learning needed to connect behaviors we had not known could be dissociated by social manipulation. Five lessons stood out. First, the CH males' orientation toward canaries made clear that species recognition is a sure thing in cowbirds, neither innate programming nor early learning guarantees mate recognition or courtship thereof. Had we stumbled on an imprinting-like process? The data from the FH

males argued against imprinting in that they should have shown strong mating affiliations towards female conspecifics and they had not. Second, the cage and aviary tests revealed the need to consider physical space as not simply an issue of animal well being, but as a social variable in and of itself. Differences in the social and physical setting lead to different levels of competence (or lack thereof). Had we stopped our studies after observing the CH and FH males in the confines of a flight cage, we would have concluded that F. H. males showed appropriate recognition and attention to potential mates and we would have been wrong. Only, in the aviaries setting, did we see that FH males did not seek out females. In the confines of a small cage, such seeking was not necessary.

The failure to find correlations between vocal function as tested by playback and vocal uses as tested by aviary performance was the fourth lesson, calling into question the continued acceptance of a sound-centered view of communication. While the data indicated a definite role for vocal behavior (we saw no consortships or copulations unaccompanied by singing), the data suggested that we had placed too much emphasis on the song. In the subsequent replicates, we also found that not only did song potency fail to correlate with performance within years, it also did not correlate across years, suggesting the social contexts exert effects after the first year. Thus, song structure, in and of itself, could not withstand the burden of explanation required to connect signal production and perception to successful reproduction. This was the assumption that had sustained us during the 1980's. We knew now that social influence must be considered as part of initial and subsequent conditions in which learning and assessment occur (Payne & Payne, 1993).

Finally, the studies showed that new tools were needed to confront the multi-dimensional nature of social influences. Songs can be recorded and analyzed and matched on objective acoustic criteria. In contrast, the quality and timing of song overtures, a male's ability to maintain proximity to a female, her willingness to be close to him, his persistence in following her, and his tendency to guard her from other males would require new social metrics.

Promoting culture in cowbirds

In these studies, we had focused on contexts that brought out incompetence, failures to court. It is always easier to break down a system than put one together. Our view of development as a constructive process demanded, however, that we find evidence that social contexts could facilitate the formation of functional behavioral connections. In Hubel and Wiesel's original work and much that followed, they showed the cells in the cortex of kittens could develop new receptive properties as a function of biased visual rearing. Could we show new communicative properties by biased social rearing?

Powerful testimony about the constructive properties of development came from studies of mate preferences carried out in our lab. In a two year long study, Freeberg studied the mate preferences of young male and female SD juveniles, exposed to one of two cultures (Freeberg, 1996; Freeberg, 1998). The first culture (natal) consisted of juvenile SD birds housed in aviaries with adult SD males and females. The second (novel) culture was composed of SD juvenile male and females housed with adults from an Indiana population. All of the juvenile SD birds had had experience with conspecifics before being captured and continued throughout the experiment to live with other juveniles from their

capture site. Moreover, as the study took place in spacious aviaries, the young birds were not forced by physical constraints to be near the adults or the other juveniles. Moreover, they could hear and see wild birds outside of the aviary.

Under these conditions, Freeberg found mate preferences were predicted by social or cultural experience, not by geographic background. Looking at the data from the female perspective was the more crucial test as females should have been more resistant to altering mate choice. Although the females all came from the same local population, social experience significantly biased courting and copulating. But the critical assay of the robustness of the cultural transmission followed. Freeberg tested whether the differences in preferences could be transmitted to a new generation of young males and females, also captured in South Dakota. Their models were the former pupils from the original study, the experiential F1's. The answer was yes, social experience again predicted mate assortment in the F2's.

Freeberg's work provided the evidence we needed to show that postnatal social experience could build new preferences. Second, the data again showed that the early experiences of cowbird with other cowbirds are not sufficient to prevent further learning. Moreover, the data showed a positive outcome: social experience during a young cowbird's first year influenced subsequent courtship. Given that cowbirds from South Dakota would not typically begin live or travel to breeding grounds containing cowbirds from Indiana, the guided learning would be beneficial.

The work also had special meaning to us because after many years of trying, these data were the first to show considerable plasticity in female

cowbirds. Up to this point, female preferences had proved hard to move around. We had tried to do so by housing females for almost an entire year with males from another cowbird population in sound attenuating chambers, thinking massive exposure would increase the chances of inducing malleability. We found little evidence of malleability in song preferences as tested by playback. And so, to have found malleability when females were faced with a seemingly more complex setting containing many options to avoid exposure was an important breakthrough. These data also make us wonder if failures in other species to find malleability reflect hitherto unrecognized inhibitory effects of standard isolate housing, such as higher levels of stress. Maybe males profit from one on one time with females, but maybe females do not.

As noted above, the malleability Freeberg found should not be taken as evidence of fragility of the connected system as a whole or evidence of misguided learning. Most theorists believe that one has to build a genetic safety net for each individual in a species. We are coming to believe the opposite: social learning affords a collective safety net and that net only emerges in a social setting. This view relates to our earlier statement that there were any least three stories to understand, the ones pertaining to the different needs of the two sexes, and the compound and synergistic story of their lives together. In that social environments typically provide stable and useful information, it becomes difficult to approach the study of vocal learning only as an individual adaptation.

Before turning to the summary, we should make clear that even in overly simplified environments, social learning is a systemic force, as we had seen in so many studies of male song ontogeny. Recently, we looked at interactions

throughout the year of young males individually housed with two adult females. Some males were housed with adult females from their local region to maximize synchrony between the two sexes with respect to local song preferences and timing of breeding. Some males were housed with adult females from a distant population, females with different song preferences and a different time course for breeding readiness. We predicted that different patterns of social and perceptual compatibility would lead to measurable differences in song development.

The results show that the actions of adult females were associated with different rates of progress throughout the stages of vocal development. Young males housed with local adult females developed stereotyped song earlier, reduced motor practice earlier, and produced more effective playback songs than did males with females from the distant population. The males with the "distant" females showed slower growth and more variable song well into the spring. Longitudinal observations of social interactions showed that the two groups of females reliably differed in social responses to males. The major difference in the nature of the social interactions was that the local females stayed when males sang instead of flying away, whereas distant females flew, sometimes even before the song was finished being sung. Female proximity gave males an opportunity to receive more social feedback to individual songs and conversely, gave females more chances to shape content by more subtle cues such as wing stroking or beak movements (Smith, King, & West, Submitted).

The importance of proximity even in such small enclosures (1 meter³) relates back to the observers coaching of the FH males in the aviary setting. Much of advice focused on maintaining proximity. We think that one of most

important pragmatic skills facing cowbirds is learning how to sing while close to a female while far from a male. He must have the social versatility necessary to deal with male competition and female attraction at the same time Proximity manipulation now seems one of the most basic lessons for young males and is the subject of our work in progress. In these studies, we are looking at how large groups of cowbirds aggregate when given lots of physical space and also comparing patterns of aggregation and interaction in social groups with different such compositions such as juveniles with only adult males or only adult females. From what we can tell, the matter of being able to get close and remain close is essential in learning among males and between males and females. Different patterns of proximity produce different opportunities for singing, listening and receiving feedback. Moreover, the amount of female proximity was correlated with playback song potency and the rate of progression to stereotyped song.

Developmental harvest

ABF Notes, Indiana University. Spring, 1996. Discussed authorship in ethics class: students suggested new publication format modeled after movies, with titles and credits for producer, director, actors and so on. Studies of summer 1992 fit the bill. Maybe the review would read:

“The play’s the thing” (ABF productions). A gripping story of the summer of 1992 for young males coming of age after sheltered childhoods. Red Green steals the show in his attempt at genetic suicide. Rated PG: Little sex or violence, some profanity especially from Southern females. Musical score uneven. Sequel in the works.

Years living and working with cowbirds have not changed many of the basic beliefs we held as we began our work. Social animals need a social context to show how they learn and develop. Development is not a passive unfolding or imprinting of information on a helpless young animal. It is easy to maintain the

scientific fiction that development is not dynamic, synergistic, flexible, and active if the settings in which one studies development are static, compartmentalized, rigid, and passive.

Our new beliefs rest the idea of a social gateway as the logical starting point in ontogenetic research. The 'social/cultural gateway' refers to the settings and sequence of events through which organisms obtain access to information relevant to learning. We begin with the rationale that many young animals do not have control over access to potentially important stimulation. Although young animals create that access by means of interaction with their natal social setting, the nature of the setting may impose constraints. In young rats, it is through the action of their mothers, stimulated in part by their own behavior and that of their siblings, that thermal, acoustic, visual, tactile, olfactory cues and their multi modal manifestations become available for learning.

Nor do many young organisms have direct control over proximate reinforcement systems that may consolidate and shape perceptual and attentional processes. In many species, it is only in the third social context we defined for cowbirds, the species typical group, that fundamental opportunities for developmental growth of knowledge take place. Such knowledge is inside the social gateway where older organisms or peers facilitate or limit sensory exposure and its timing and duration. The gateway may also "set " or "prime" learning and the opportunity to use newly acquired information in settings containing critical feedback mechanisms. For example, non dominant animals may not get to use what they have learned or may have to modify it further as a function of a social hierarchy; animals in the periphery of a group may not hear,

see, smell, or sense the same level o of sensory cues. Also, natural social aggregations create synergistic environments and kinds of stimulation not possible if done by individual animals. When we were kids, certain incompetencies between kids were explained by saying that " so and so must have been behind a tree when God gave out talent for hitting baseballs or [fill in the blank." The gateway is meant to capture the idea that not all animals, even if in the " same " environment, profit in the same way.

We would further argue that the social gateway has been bypassed in most laboratory research not only in development, but also in perception cognition, and neuroscience. Animals are brought through the laboratory door, stripped of any social gateway. Thus, how they naturally learn and how they are manipulated to learn may differ. Hamsters, for example, can be taught after many shaping trials to use a fishing technique to obtain food, their young can learn the same behavior in one trial if just allowed to watch mom and given access to the materials (Previde & Poli, 1996). Which kind of learning has been favored by natural selection and thus shaped cognitive and neural processes? We also wonder if some of the failures of animal models to predict human actions stem from the reality that humans come with gateways. Thus, whether the animal-to-human application is a new drug or a new theory of memory, its success or lack thereof, may be due to the differences in organisms living inside or outside the gateway.

The new fields of computational modeling propose distributed systems of intelligence. What we propose are distributed systems of information access. The idea of a distributed system opens up new ways to think about the delivery and potential use of information and forces us to recognize the inherent social

dependencies that probabilistically control the spread and dissemination to individual and groups in individuals (Bar-Yam, 1997). In cowbirds, a young male's opportunity to learn song from other males or to receive feedback from females depends on their actions as well as his behavior. In ongoing studies of social groupings, we have found that young males do not have automatic access to adults. Indeed, the willingness of adult males to interact with the young males appears to be a critical parameter. That willingness, however, is also a function of just how active and exploratory the young male is. In turn, a female's attention to a young male appears to depend on prior interactions by that male with adult males. We are far from being able to describe the structure of distributed opportunities, but we know the structure is there. The idea that gateways exist has many implications. First, it suggests that, for many animals, the idea of the world of an individual animal may not be a useful construct. Many have argued that the organism / environment bond one is a fundamental consideration in developmental theory. But the idea of a gateway goes a step further towards the idea that social contexts are logically the first mechanism to be understood in studying development or learning.

So too, we may have to re think whether behaviors represent individual or team efforts. For a male cowbird to be successful, many other actions by other organisms are required, including cooperation from females, a history of successful competition with other males, the presence (or absence) of other males with superior abilities, and a little luck. We would liken his success at courtship to a RBI in baseball. A hitter cannot get an RBI without the cooperation of the hitters ahead of him in the batting order, the skills of the pitcher and opposing fielders, and a manager smart enough to know which batting order will work.

Baseball is a distributed system for success, a fact often obscured by stunning individual performances such as hitting 73 home runs (and McGuire's team did not get to the playoffs).

Looked at from an evolutionary point of view, gateways also have relevance. Terkel has done fascinating studies of the black rat (*Rattus rattus*) in Israel (Terkel, 1996). The species has learned to strip pinecones to secure a new food source. The behavior is culturally transmitted from mother to offspring; the young do not seem to be able to learn it from simply handling partially opened pinecones or watching each other. The black rats' use of this food source is very new, and other species now live near the same Jerusalem pine trees. What is to prevent them from learning how to eat cones? The constraint may be that they cannot gain access to the social system unlocking the key to pinecone use. Researchers report they find no partially stripped cones laying about the forest floor: the only route to such learning tools is the adult, mother rat. Work on filial imprinting also has shown important differences in learning when exposure to an unfamiliar imprinting stimulus is filtered through the system of sibling interactions. There is seems that siblings have such an important role in defining social preferences such that their mother may have to compete with them. In sum, removing an animal from the socially distributed network of opportunities for learning may mean that we see only back up systems for modifying behavior, not the systems that define species/environment niches.

Final thoughts

ABF Notes, May 1991, Indiana Farm. Son's first grade class coming to visit...what to do

about facts of life...what if cowbirds show off mating skills? Son saves the day... when it happens, son turns to classmates and says, "see, that's how cowbirds populate."

We suppose the question we hear most often is. " How can you study the same species for so many years?" The answer is that it is not the same species year after year. As we learn new things, cowbirds continue to transform before our eyes into ever more interesting and ever more complex subjects. Perhaps, one of the most special experiences for us takes place in late winter, when Indiana is still gray and depressing. Migrating birds begin to return, among them, birds we have released but birds that still have their lab leg bands. A few are now five or six years old. Seeing a former subject induces the crazy feeling to tell Male RGR or Female GG what has happened in the lab or what we know about cowbirds that we did not know when they left. But, then we remember, they already know.... We are the ones who still have the learning to do.

Bibliography

Baptista, L. F., & Gaunt, S. L. L. (1994). Historical Perspectives: Advances in studies of avian sound communication. Condor, 96, 817-830.

Baptista, L. F., & Patrinovich, L. (1984). Social interaction, sensitive periods, and the song template hypothesis in the white-crowned sparrow. Animal Behaviour, 36, 1752-1764.

Bar-Yam, Y. (1997). Dynamics of complex systems. New York: Addison Wellsley.

Beer, C. G. (1982). Conceptual issues in the study of communication. In D. E. Kroodsma & E. H. Miller (Eds.), Acoustic communication in birds (pp. 279-310). New York: Academic Press.

Breland, K., & Breland, M. (1961). The misbehavior of organisms. American Psychologist, 16, 681-684.

Freeberg, T. M. (1996). Assortative mating in captive cowbirds is predicted by social experience. Animal Behaviour, 52, 1129-1142.

Freeberg, T. M. (1998). The cultural transmission of courtship patterns in cowbirds, *Molothrus ater*. Animal Behaviour, 56, 1063-1073.

Freeberg, T. M., King, A. P., & West, M. J. (1995). Social malleability in cowbirds (*Molothrus ater artemisiae*): Species and mate recognition in the first 2 years of life. Journal of Comparative Psychology, 109, 357-367.

Friedmann, H. (1929). The Cowbirds: A study in the Biology of Social Parasitism. Springfield, Ill: C. C. Thomas.

Gibson, E. J. (1969). Principles of perceptual learning and development. New York: Appleton-Century-Crofts.

Gibson, J. J. (1966). The senses considered as perceptual systems. Boston: Houghton-Mifflin.

Gould, J. L. (1982). Ethology: The mechanisms and evolution of behavior. New York: W. W. Norton.

Harlow, H. F., & Harlow, M. K. (1962). Social deprivation in monkeys. Scientific American, *207*, 136-146.

Harlow, H. F., Harlow, M. K., & Hansen, E. W. (1963). The maternal affectional system of rhesus monkeys. In H. L. Rheingold (Eds.), Maternal behavior in mammals (pp. 254-281.). New York: Wiley.

Kaufman, I. C. (1975). Learning what comes naturally: The role of life experience in the establishment of species-typical behavior. Ethos, *3*, 129-142.

King, A. P., & West, M. J. (1983). Female perception of cowbird song: A closed developmental program. Developmental Psychobiology, *16*, 335-342.

King, A. P., & West, M. J. (1988). Searching for the functional origins of cowbird song in eastern brown-headed cowbirds (Molothrus ater ater). Animal Behaviour, *36*, 1575-1588.

Kroodsma, D. E. (1982). Learning and the ontogeny of sound signals in birds. In D. E. Kroodsma & E. H. Miller (Eds.), Acoustic communication in birds (pp. 1-24). New York: Academic Press.

Lehrman, D. S. (1970). Semantic and conceptual issues in the nature-nature problem. In L. R. Aronson, E. Tobach, D. S. Lehrman, & J. S. Rosenblatt (Eds.), Development and evolution of behavior: Essays in memory of T. C. Schneirla (pp. 17-52). San Francisco: W. H. Freeman.

Lehrman, D. S. (1974). Can psychiatrists use ethology? In N. F. White (Eds.), Ethology and Psychiatry (pp. 187-196). Toronto: University of Toronto Press.

Lorenz, K. (1965). Evolution and modification of behavior. Chicago: University of Chicago Press.

Lorenz, K. (1970). Studies in animal and human behavior (Robert Martin, Trans.). Cambridge, Massachusetts: Harvard University Press.

Lowther, P. E. (1993). Brown-headed cowbird (*Molothrus ater*). In A. Poole & F. Gill (Eds.), The birds of North America, No. 47. (pp. 1-24.). Washington, D.C.: The Academy of Natural Sciences.

Marler, P. (1960). Bird songs and mate selection. In W. E. Lanyon & W. N. Tavolga (Eds.), Animal Sounds and Communication (pp. 348-367). American Institute of Biological Sciences.

Marler, P. (1970a). Birdsong and speech development: Could there be parallels? American Scientist, 58, 669-673.

Marler, P. (1970b). A comparative approach to vocal learning: Song development in the White-crowned sparrows. Journal of Comparative and Physiological Psychology Monographs, 71, 1-25.

Marler, P. (1991). Song-learning behavior: The interface with neuroethology. Trends in Neuroscience, 14, 199-206.

Marler, P., Mundinger, P., Waser, M. S., & Lutjen, A. (1972). Effects of acoustical deprivation on song development in redwing blackbirds (*Agelaius phoeniceus*). Animal Behaviour, 20, 586-606.

Morris, D. (1970). Patterns of reproductive behaviour. New York: McGraw-Hill Book Company.

Nelson, D. A., & Marler, P. (1994). Selection-based learning in bird song development. Proceedings of the National Academy of Science, 91, 10498-10501.

Payne, R. B., & Payne, L. L. (1993). Song copying and cultural transmission in indigo buntings. Animal Behaviour, 46, 1045-1065.

Previde, P., E., & Poli, M. D. (1996). Social learning in the golden hamster (*Mesocricetus auratus*). Journal of Comparative Psychology, 110, 203-208.

Searcy, W. A. (1992). Measuring responses of female birds to male song. In P. K. McGregor (Eds.), Playback and studies of animal communication (pp. 175-189). New York: Plenum Press.

Seligman, M. E. P. (1968). Chronic fear produced by unpredictable electric shock. Journal of Comparative and Physiological Psychology, 66, 402-411.

Seligman, M. E. P. (1975). Helplessness: On depression, development and death. San Francisco: Freeman.

Slater, P. J. B. (1989). Bird song learning: causes and consequences. Ethol. Ecol. & Evol., 1, 19-46.

Smith, V. I., King, A. P., & West, M. J. (Submitted). A role of her own: female cowbirds influence male song development. .

Terkel, J. (1996). Cultural transmission of feeding behaviors in the Black rat (*Rattus rattus*). In C. M. Heyes & B. G. Galef (Eds.), Social learning in animals: The roots of culture San Diego: Academic Press.

Thorpe, W. H. (1958). The learning of song patterns by birds, with especial reference to the song of the chaffinch, *fringilla coelebs*. Ibis, 100, 535-570.

Thorpe, W. H. (1961). Bird song. London: Cambridge University Press.

West, M. J., & King, A. P. (1980). Enriching cowbird song by social deprivation. Journal of Comparative and Physiological Psychology, 94, 263-270.

West, M. J., & King, A. P. (1985). Social guidance of vocal learning by female cowbirds: Validating its functional significance. Ethology, 70, 225-235.

West, M. J., & King, A. P. (1986). Song repertoire development in male cowbirds (Molothrus ater): Its relation to female assessment of song. Journal of Comparative Psychology, 100, 296-303.

West, M. J., & King, A. P. (1988). Female visual displays affect the development of male song in the cowbird. Nature, 334, 244-246.

West, M. J., & King, A. P. (1994). Research habits and research habitats: Better design through social chemistry. In E. F. Gibbons Jr., E. J. Wyers, E. Waters, & E. W. Menzel Jr. (Eds.), Naturalistic environments in captivity for animal behavior research (pp. 163-178). Albany, N. Y.: SUNY Press.

West, M. J., King, A. P., & Eastzer, D. H. (1981a). The cowbird: Reflections on development from an unlikely source. American Scientist, 69, 57-66.

West, M. J., King, A. P., & Eastzer, D. H. (1981b). Validating the female bioassay of cowbird song: Relating differences in song potency to mating success. Animal Behaviour, 29, 490-501.

West, M. J., King, A. P., & Freeberg, T. M. (1996). Social malleability in cowbirds: New measures reveal new evidence of plasticity in the Eastern subspecies (Molothrus ater ater). Journal of Comparative Psychology, 110, 15-26.