Birds, babies, and behaving

MEREDITH J. WEST
Department of Psychological; and Brain Sciences
Indiana University
Bloomington, Indiana 47405

Running Head: Birds, babies, and behaving

Birds, babies, and behaving

Childhood schooling

Perhaps because I study development for a living, I think I should be able to explain my own trajectory through developmental mechanisms. We all do so to some extent—harken back to our childhood for clues to the future. But my brand of developmental systems theory does not place as much weight on retrospective explanations—living is for the here and now and what is remembered from the past is often not very predictive unless we make it so through selective memory or, more to the point, selective forgetting. And so I begin my narrative with the caveat that my childhood is perhaps most important because it was happy—with regard to my future, I am not sure my parents or I gave it much thought (or more than likely did not share the thoughts we had)…life would happen but beyond being casually praised for being a good student in school, I don't remember much proscriptive developmental thinking such as whether I should be scientist or a secretary. It is also possible that future-oriented thinking had been blunted by the death of my older brother to cancer, thus good health and care occupied the top rank of concern. But most probably, given the times, thoughts for my future involved a house and family and a career in mothering. It was not until I was a full professor and gave a university-wide lecture that my parents happened to attend that the talking stopped about my settling down to "simply" take care of our sons. There was never tension about my decision (or the one to keep my name) simply loving anxiety that I was doing something untoward by pursuing a career.

I was one of six children and the group of us occupied much of my out of school time. We shared a love for animals and were always after our parents for more pets—chipmunks and snakes are two I remember the most vividly but there was also the stray cat or dog that just showed up to vie for attention with our tenured cats and dogs. My father even contributed to the dream for our zoo by bringing home two baby alligators, Shorty and Pete. They wore out their welcome by literally biting the mailman. We also had a chicken that laid eggs under sofa cushions. As I write this all down, I have to revise my childhood thinking that my parents were not pet-friendly but as a kid it seemed we were often at odds over just how big the extended pet family would be, but I now see it in a better perspective. It also never occurred to me that being surrounded by animals was a pathway to a career, as is the case with so many who enjoy careers in animal behavior and started as amateur naturalists.

My schooling undoubtedly led me closer of a position of scholar … I attended a private Catholic school for girls taught by the Sisters of Mercy, many of who would leave the order when the Vatican revolution took place in the 1970’s. In retrospect, they were great teachers and incipient revolutionaries in ways we students did not appreciate. I know we held them in deep respect. I placed out of several science courses when starting college, another gift from my teachers.

Perhaps one trait that has carried stably into adulthood is reading…I am always reading a book or two. As a child, one of my fears was that the world would run out of books before I died. I would purposely read slowly to make the treasure of books last longer. As another route to reading insurance, I took courses in Russian in high school and got to read some of the classics of that country when in college. I am happy to report my two sons are readers too. Later my years as editor of academic journals served an additional purpose of giving me more to read and extending my reading future.

Graduate School.

I graduated from Tufts University, at a time when there was a women's part called Jackson College although we had all of our classes with the Tufts men. Female-oriented things that I remember are the separate dorms, having to wear skirts to class and dinner, and check-in time in the evening. When I entered Tufts, I placed out of introductory chemistry and so I had a space in my freshman schedule that I filled with introductory psychology. One course was enough to determine it as a major and I spent several years in different labs as each psychology course had an experimental component in areas such as perception, personality, motivation, and learning. I did very little animal work and didn't know what I was missing in animal behavior for several more years. Moreover, I somehow missed Kenneth Roeder and his elegant insect work at Tufts…his lab was simply not open to undergraduates or majors in psychology. I liked having to write formal lab reports each week; a tradition now lost to most psychology departments.

The chairman of the psychology department was a woman named Dorothea Crook, who had studied perception at Cornell University. My family doctor, also a woman, had also gone to Cornell. Perhaps for these reasons Cornell was the only school I applied to for graduate training…. thinking I would study learning or perception. As I think back, I marvel at my naiveté in choosing only one school but I was lucky enough to have good mentors. I did not even visit Cornell before I attended, relying on the memories of the Cornell alumnae around me. Perhaps I was not desperate to go to school but as I had always gone to school, I guessed I figured I would just keep going.

My education at Cornell started with a series of lectures by the faculty in the summer before the school year started. We were given a stipend ranging in value with how early we came…the earlier the better. I had already been assigned an advisor , Martin E. P. Seligman, and gained experience in his lab at the same time. He worked on learned helplessness in dogs; a phenomenon that had grown out of designing the appropriate controls for studies of Pavlovian conditioning. In such conditioning, an arbitrary stimulus, say, a tone, is paired with an aversive stimulus, in this case, shock to dogs' feet. To show that it was the contingency causing the animal to learn to jump across a gate to avoid the shock, it was necessary to test the condition where the shocks and arbitrary stimulus came in random fashion (procedures stemming from the work of Allan Wagner and Robert Rescorla). Marty had found that such random conditions caused the dogs to give up, to simply take the shock and cease trying to avoid it by jumping, hence, the term learned helplessness. Marty thought it might be a good model for human depression and in fact went on to study with clinical psychologists at Penn on this idea which grew to be very popular as an animal model.

I was not interested in animal models of abnormal behavior, nor was I convinced that the dogs' behavior was due only to the random contingency…if so, it should work with positive or appetitive stimulation as well, but that did not seem to be the case. I also wondered about the effects of context. When we retrieved dogs from the small kennels to participate in the experiment, they did not seem helpless until they reached the experimental room. My memory is that some of the dogs were cooperative and easy going until they were in the apparatus. Why weren't they helpless all the time? If this was a model of depression, shouldn't we see the effects in all contexts, as depression, to my knowledge, was not context specific? I was not the only grad student to think this way and a number of us met frequently with Marty to discuss our concerns. He took them seriously but still maintained the dog model as a good analog of human conditions that led to depression such as poverty, uncontrollable noise, and the draft for the Viet Nam war. But Marty moved to Penn while we were still in our early years at Cornell and has gone on to study human behavior in striking and novel ways, focusing on "positive psychology."

But my interest in learned helplessness, which was never strong, was overshadowed by the summer lecture of William C. Dilger, a joint member of Psychology and Neurobiology and Behavior. He mesmerized me with his description of the field of ethology…. he said ethologists looked at animals as a set of answers, and it was our job to figure out the evolutionary questions. He illustrated his thinking by drawing (he was an excellent artist) the beaks of birds and engaging us in thinking up reasons for the different morphologies. He offered a combination of a respect for nature and animals with the instincts of a good experimentalist. He was one of the first to do playbacks in the field and had also done one of the most complete studies of behavioral genetics comparing the behaviors of hybridized members of the Agapornis parrot family. The contrast to the dog work was great: ethologists appreciated the whole nature of the animal they were studying, did not focus on arbitrary connections among behaviors but connections set up by natural history.

I did not come to question learning theory solely of my own accord…. a fellow graduate student, Andrew King, was also in the Seligman group. Unlike myself, he had a strong research history in animal learning and had come to Cornell to study classical conditioning with Marty. His first question to me in fact was “What’s your theory of learning?” I thought the question indicated perhaps too much of a dose of experimental psychology and that it was rather bold for a first year graduate student to have so grand a thing as a theory. Something clicked though as we eventually would marry and collaborate on theories of development and learning. We did not formally collaborate during graduate school, although we helped each other with our collective research. We both ended up with Dilger as our chairman and shared lab space. Drew’s background was similar to mine in that he had raised parakeets and bred fish, but he had more of a sense of direction about his future. His future, at that point, though was compromised by threat of the Vietnam draft, as was true of all the male American students. E.J. Gibson did her best to make sure they were assigned teaching assignments, which gave some relief. The war seemed to circle overhead during our whole stay at Cornell. The times also produced racial violence when a group of armed black students took over the student union. Cornell cancelled all classes that spring to allow for some chance at reconciliation and change, which slowly came about but probably not to the armed intruders' wishes. Finally, graduates who had received federal funding for post docs had the money impounded by President Nixon, a swipe at the seemingly left leaning NIH and widespread antiwar protests at major universities.

Our lab space became available at first through the graciousness of James and Eleanor Gibson, well known perception experts. We had been encouraged to hang out in their lab by older students from whom we learned a tremendous amount about science and politics. The Gibsons carried out independent and dependent lines of research ranging from theories of perceptual systems ("JJ" as he was called;(Gibson 1966)) and the development of perceptual learning ("EJ"; (Gibson 1969)). EJ was also referred to as Mrs. Gibson, which was not meant in any pejorative sense but for practical reasons (although I never heard any one address JJ as "Mr. Gibson"). At one point, I rebelled against what seemed like a sexist tradition and left a note in her box addressed to "Dr. Gibson." A few days, later I saw JJ who asked me questions about the message in the note, professing confusion as to what to do. Clearly Mrs. G had put the unopened note in Dr. G's box without a second thought. I decided if she could live with “Mrs.”, so would I. Although she had had to fight hard to get an independent academic position at Cornell, she never expressed anything but enthusiasm for science to us students. She was a keen mentor for female students and did much to help us find jobs or post docs.

Due to space constraints at the time, the Gibson’s laboratories were located off campus near the Ithaca airport and were known as the “airport labs” The labs had lots of space enough so that Drew and I could get offices there even thought Dilger was our major professor (he had limited space for his many students). EJ was on my research committee. The airport was, in the airport lab’s opinion, the best place to be in terms of intellectual stimulation and friendship. The lab was large and parking was just outside the door. The Navy funded JJ and some years he did not use up his entire budget and attempted to return the money to the Navy, something the Navy did not know how to do. One year we talked him into buying the first Xerox machine for the lab. JJ was writing a book when we were there and had a weekly seminar discussing his ideas about perceptual systems and things called “affordances”(Gibson 1966). The concept has now slipped into more common usage at least in psychology and generally refers to the functions that define an object such as a chair’s affordance in sit-ability and conversely anything with sit-ability, a log and overturned trash can, had something in common with chairs. Active perceivers explored the environment in search of affordability. For Drew and myself, the concept linked learning and perception and we will talk more about affordances later.

EJ was also finishing a book on perceptual development in animals and humans. The book is still useful today as a complete survey of theories and data on perceptual learning in animals through 1969. She had done work on goats' attachment as well as invented the visual cliff with Richard Walk. The cliff was a plank of wood in the middle of a glass tabletop with squares attached to the surface of the glass or the floor to simulate depth. Walk and Gibson studied many young animals on the cliff and showed the importance of whiskers in kittens and rats to judging depth, among other findings (E.J. Gibson, 1969). The amount of research they did goes beyond any autobiographical bounds but was an elegant example for me of how a young animal's own activities affected its development, a growing theme in my head for research. Dilger's work on parrot learning nest building also brought up the question of genetic and experiential factors, which was a broad banner for much of psychology and ethology in the 1960's and 1970's (Dilger 1964). Although Dilger taught us much about how to study animals and how to pose questions to animals, it was the Gibson's work on perception as a "performatory" activity-taking place in a stimulus rich world that formed the basis for our later work, even to this day. In both ethology and psychology, the sense was that experiences were imposed on passive perceivers with plastic parts of their nervous system to allow experience to do its trick. We now know that experience creates some of that plasticity and that the processes are interpenetrable. The Gibsons also stressed a different kind of environment than that of the learning theorists…to the Gibsons, the world abounded in information, the perceiver's job was to discriminate and act upon it.

Our later resistance or perhaps anxiety about templates for bird song development and schemas stemmed from the different worldview representing an environment of impoverished information.

I managed to package many of these ideas into my thesis on play and exploration in domestic kittens. My interests were sparked by watching a youngish cat attempt and finally succeed, over a matter of months, in getting an older cat to play. I could not get over the amount of motivation involved—what was so important about pouncing, facing off, and leaping toward one another? The topic included my ethological interest in naturally occurring forms of early experience and my psychological interests in perceptual learning, i.e., learning the function of things in the world. These topics also naturally drew me into developmental theories, which I found I loved to read and think about. In some sense the work on play was a Rorschach for portraying experiential effects. I studied a total of 42 kittens from 8 litters from 5 mothers. Three of the mothers were feral cats that lived outside and underneath our rental house. The cats knew well-hidden means of egress and ingress to our house and it took us quite awhile to learn how they were entering and why food was disappearing from our kitchen counter. I discovered the scheme one day when I and our dog came home at a time I usually was not in the house and found a huge tom cat sleeping on the bed…he was as surprised as I was but a lot faster and escaped though an opening where the pipes entered the house. I doubt I would have dared catch him as he was not at all friendly when we would encounter him outdoors…the other memorable meeting was when he discovered a litter of kittens in our garage and he gobbled down several of them. We steered clear of “Dad” as he was known.

The feral mothers were more tolerant of my presence as long as I did not try to touch them. Often I watched them through the window to the garage or while sitting in my VW beetle with which I could even follow them distances into the woods. The feral mothers were moms and sisters and they shared caretaking and nursing activities forcing me to rethink the idea of cats as not very social. The feral litters were very small due to poor nutrition, disease, and infanticide. Play seemed especially important in these litters because the mothers could not go off and hunt alone and had to tolerate playful advances that were much less frequent in the non-feral and larger litters where, during social play, mom could easily slip away. Several times I saw feral moms start to head for the fields and forests with a kitten that simply wouldn’t stay home, most often because it was singleton. The incipient dangers were realized once when a horse from next door got loose and ran into the same field…. mom scurried away but the kitten froze and was trampled. Marc Bekoff has talked about wild coyote pups and incidental function of play where staying together depended on playing together and I thought the same was true for cats. At some age mom did not protest but usually she brought prey to the kittens rather than the other way around. So although the mothers cooperated for kitten care, hunting appeared to remain a solitary fare.

At the time there was much debate over the definition of play as well as its function. I don’t think the same holds true today; I think play is more generally accepted as an important developmental category. But while I was working on it, I remember participating in a seminar on play organized by Bekoff for an ASZ Christmas meeting (West 1974). A comment from an audience member stayed with me...the speaker was Irwin Bernstein and the comment was that we should stop fussing about what we called play and focus on the activities that defined it such a jumping or running or manipulating. A graph of the amount of “play” meant little without good operational definitions devoid of the motivational confusions the term ‘play’ seemed to attract.

Thus, I began to think of my work as looking at the experience of early experience. What exactly is play doing? My observations of feral cats led to my beliefs about the function of play…I did not think the value was for the future, i.e., practice for hunting for example. I thought the value was for the present to provide the young a means to explore the properties of the emerging world as kittens obtained very different reactions when pouncing on a toy versus a real mouse. If anything, play seemed to be a misleading preparation because the object of the play did not respond in ways similar to that of potential prey or peers. For example, a common play move was to rear up on the hind legs with the arms outstretched in a sort of bear hug…. what better way to scare off even a non-vigilant mouse or bird? But, the experience delivered information for predicting behavioral properties of hunt-able objects. I can recall one of the feral kittens pouncing on Dad and getting swatted to kingdom come...I think the kitten learned rapidly that adults had different properties than other kittens. As they matured, sex differences also became apparent and females began to retreat from males’ initiatives because it seemed the males did not distinguish playful from sexual initiatives.

During this time, Drew and I wrote a paper for a course on comparative psychology—we complained that learning psychology did not necessarily emphasize the species typical skills of an animal but looked for abstract capacities to acquire stimulus response contingencies. Much of what was special about different species was deliberately ignored in order to find generalities, generalities we thought to exist probably throughout even simple animal species. To Drew and I, this approach was like using a dishwasher solely as a storage box but never turning on the electricity to see what the box could do. Thus the major affordances were missed. We sought learning paradigms with more electricity, paradigms focusing on motivated species typical learning. Such a move distanced us from those seeking laws of learning or perhaps focused us on different kind of laws. Laws of function/survival or development became more important. This view was shared by a small number of comparative psychologists such as TC Schneirla, Gilbert Gottlieb, Jay Rosenblatt, Daniel Lehrman and Don Dewsbury. Aside from Don, they represented the “Rutgers” group or the “Museum group” as many had appointments at the Museum of Natural History in New York City. They focused on actual problems animals faced such as the transition to filial, sexual, and parental behavior in rats, cats, or birds. They were among the first to look at multiple levels of analysis starting with behavior but often extending their thinking to underlying hormonal states.

Dewsbury represented another tradition, looking at a similar behavior, in his case sexual behavior in rodents, among other taxa. He compared closely related species and compared reproductive strategies in males and females. Drew and I were inspired by all such comparative work and began to plan a comparative program of our own—we would travel to the Galapagos Islands to study tool use in Darwin’s finches, species already studied for differences in beak morphology. We managed to secure fellowships to free up the time, but political events swept through South America that made travel risky with no guarantee of access to the birds (and thus a very risky means to complete dissertations) and so we shelved the idea always hoping to return to it once we had our degrees. The effort served as a model however for the kind of integrative work we wanted to do and the model would reassert itself when we began to think about the evolution of learning in cowbirds. We owe Cornell a great debt when it comes to stimulating integrative work. Cornell had a strong committee system fostering the creation of cross-disciplinary faculty representation for example between psychology and neurobiology and behavior. Comparative approaches were also fostered. As students, we had nothing to compare to Cornell and so it was not until I got a job at the University of North Carolina that I retrospectively began to appreciate what Cornell had to offer.

Like most graduate programs, Cornell had qualifying exams, which I took with W. Dilger, E.J. Gibson, and R. McLeod, an historian. He asked me the most challenging question: to trace the history of comparative psychology from Aristotle to the present. I also took it as an opportunity to include the growing role of ethology as an alternative way to approach learning and development. His question got me thinking about animals as models or surrogates for humans. At that time, this was the major role for animals in psychology. But I was skeptical that the desired simplicity of animal models would map onto the complexity of human behavior in a linear way. To borrow from computer vernacular of today, learning psychologists (or many of them) saw animals' minds as computer programming versions, with upgrades and updates in "higher" species that flowed linearly from one species to another, and so understanding a bird, rat, or primate bore direct relationships to understanding a human, the most advanced form of the same basic software program. The computer language was the common connection. But too much of the work focused on narrow fields of behavior, primarily conditioning, probably because it was only in such simple environments that rules emerged. While I could see similarities in some mental/neural capacities, one had to ignore too much of the animal to keep the comparative speculation clear. Psychologists such as Hull, Spence, Skinner or Tolman were articulate visionaries of this view. But what I thought about were all the capacities animals had that humans did not have, in particular, sensory apparatus such as echolocation. Does this ability simply get added into the program or subtracted from the human program, man minus the hard- and software of bat echo locating minus flying minus insectivory etc.

The Gibsons' views differed as animals were evolved to fit rich ecological niches. JJ looked carefully and comparatively at animals' eyes and their binocularity to develop his theories of depth perception and the role of motion parallax. Drew and I had a large fish tank in our office and JJ would spend time watching how the fish (cichlids) moved their eyes when swimming forward or backwards. His curiosity about animals encouraged us to think that psychologists could study behavior in “non-traditional” animals and was more in line with the thinking of those in neurobiology and behavior (whose lab was also located at the airport). JJ did not however think that studying the neuroanatomical correlates of vision was terribly helpful in creating theories of perception. He felt it was the ecology that held the answer. A review of Gibson’s work once noted his theme, as “It’s not what inside your head that matters but what your heads is inside of”(Mace 1977).

Living in Ithaca brought out the naturalist in everyone, as the environment was stunning: forests, streams, waterfalls, and gorges. Dilger’s lab was located at the Laboratory of Ornithology on Sapsuckers Woods Rd., a beautiful drive from campus. Most people we knew watched birds as a hobby. For graduate students, the physical features of Ithaca encouraged lots of outdoor recreation from boating to cross country skiing; there was an activity for every season. Drew and I lived in the country in a small house bordering acres and acres of New York State Forest. Fortunately, the animals of interest, kittens for me and cowbirds for Drew could be found in our front yard. We also had a dog, and bred parrots and tried to breed cichlids, a species known as Oscars, who grew to be quite large and were highly aggressive meaning that we could only keep two in a 75-gallon tank. They were visually quite alert, watching us as much as we watched them. I can remember that I used to read the newspaper at my desk next to the fish tank during the weekdays, but on Sunday, I read the Sunday times, which had color in the magazine section. The fish became quite excited at the color pictures on Sunday but paid little attention to the news in black and white. After a few years, we had assembled a small zoo; something we had both wanted as children but had no idea could become part of a formal education.

A final influence on us during graduate school came from the departmental chairman, Harry Levin, whom we got to know quite well because Drew was hired to assist Harry, whose spine had been injured, a consequence of unsuccessful back surgery. He was a psycholinguist but reached out to students in all fields. Harry treated students with the utmost respect, and in return, students tried hard to live up to that respect. Drew and I learned a lot from Harry about navigating the academic landscape from what turned into a close personal relationship, and he continued to mentor both of us after he became Dean of the Arts College and thereafter up until his death.

Harry, as chair, told all of the students that his vision was that we become skeptics in our respective fields and not follow the mainstream, but pursue overlooked tributaries that might be missed by those following major trends. We took his message to heart and credit our chronic lack of mainstream-ness to his influence. We have never done research that followed a popular trend, even though at times it would have helped us judge whether we were having any impact. Levin, as well as other senior professors, also did not stress publishing much as graduate students because they thought we did not yet know enough to make a substantive contribution (and because you could get a job without many publications). It was a quite different world from the present where students often begin to publish as undergraduates.

In 1970, Drew and I attended a symposium at McMaster University entitled “Can psychiatrists use ethology?” “Everyone” in the psychobiological world was there, headed by Robert Hinde. The Rutgers group was especially well represented and we heard talks by Ernest Hansen on play, Colin Beer on comparative methods, and an overview of developmental studies by Lehrman. Harry Harlow was also there, representing those trying to study affectional systems (the scientific term for mother love) in non-human primates. I had mixed feelings about Harlow. On the one hand, his writing about the comparative psychology of learning was outstanding—he argued that conditioning was probably one of the slowest ways possible to teach something to an animal and he demonstrated the role of cognitive reinforcement (curiosity) showing that rhesus monkeys would “work” for chance to look out a window at a faster rate than to obtain food (Harlow 1965). But his work on social development bothered me: he did several studies in which he housed primates alone in small-darkened cages (he called them “pits”) with no added sensory stimulation for a year (Harlow 1974; Harlow & Harlow 1962). The monkeys developed severe psychopathologies and Harlow’s work was cited as an animal model for autism. But I could not understand the parallel. Human infants were not subjected to “pits” in order to show abnormalities and I could think of no ecological parallel to solitary living without any stimulation except that that was self-generated. It is one of those cases where using a scientifically clean method (control of stimulation) was uninterpretable as it was completely bogus, at least in mammals. Young animals did not live alone for years in close confinement with without added stimulation.

To be completely truthful, I thought the work, although immensely popular, was inhumane and went from person to person explaining my discomfort. I don't think Harlow would have done the work today and I don't think an IACUC would approve it. But setting aside animal welfare concerns, I think Harlow's theoretical point of view would probably still be tolerated given the number of animal studies using isolation as a basic condition. Harlow also indulged in the sometimes tricky business of trying to find humor in some of his work—when he tried to breed motherless monkeys, he found they showed no interest in male sexual overtures and so he tied the limbs of a female to a metal frame and "allowed" the male to mate with her…he referred to the apparatus as the "rape rack". Such an approach reinforced in me the need for respectful animal conditions and the theoretical uselessness of such draconian methods. Although his work was very influential in showing the role of mothers and peers in development, I was convinced that more ecologically valid methods would have come to better conclusions but with more applicability to humans and monkeys.

Introduction to cowbirds.

While Harlow's talk at the conference did not inspire me, those of Hansen, Beer and Lehrman were exceptionally motivating. Hansen talked about the importance of play, Beer stressed the role of microphyletic comparisons, and Lehrman made intriguing arguments about how to choose animal models

(Lehrman 1974). He noted, for example, that scientists tended pick and choose animals to model whatever human behavior was of interest and so birds were often chosen as models of early experience because of the findings of those studying imprinting. But he posed the question which bird do we choose? He remarked that red winged blackbirds deprived of parental stimulation showed abnormal species identification and abnormal song learning but brood parasitic cowbirds, also members of the Icteridae family, did not appear to be influenced by their early experience with host species and lack of contact with “parental” cowbirds. The question then was which species do you choose as a model? Obviously the answer was that no one species would accommodate the role of “the” animal model. His words struck a chord with Drew and myself and we came back excited to look at questions of early experience in cowbirds. There are seven species of cowbirds, one of which is entirely non parasitic. Resurrecting some of our thinking about the aborted Galapagos project, we envisioned studying all the cowbird species while looking at the role of early experience as the species radiated north and became more and more parasitic. Drew took on the most parasitic species, Molothrus ater, the North American brown-headed cowbird, for his dissertation. Thirty or so years later we are still working on M. a. ater although we have studied eight different populations of the three subspecies but we have found enough to keep us busy still trying to figure out their learning and development. Ernst Mayr helped to frame the work with his 1974 paper on open and closed behavioral systems (Mayr 1974). He targeted the cowbird as a representative of a completely closed developmental impervious to postnatal experience a view based on speculation. This led Drew to test these ideas experimentally.

While I was learning about play, Drew was building his first aviary to study brood parasitism in cowbirds. His deeper interests included social processes such as how cowbirds managed species identification. North American cowbirds were raised by over 200 different species and subspecies until fledging, then fed by their hosts for a short time, and then were found in small flocks with other fledglings. To answer such questions meant having ready access to very young cowbirds. Thus, it came to be that Drew and I began to work as an informal team to try to raise young birds. It was simply more than one person could do. At first we thought we could convince other birds to raise cowbirds and developed a colony of canaries for that purpose. We found we could breed the canaries but that even though canaries would feed young cowbirds, sometimes twice the size as the canaries, something was not right, most likely the diet, leading to the early deaths of the young cowbirds. We also tried zebra finches but were not more successful. Before we knew it, we had colonies of adult cowbirds, canaries, and zebra finches requiring daily care. We sold canary and finch offspring to raise funds to pay for food and supplies. Eventually, we raised one cowbird, #62, that thrived, the last bird of the 1973 season. Unfortunately, or so it seemed at the time, she was a female and we were pretty convinced that vocal communication was key to socializing and females did not sing. We decided to try a playback experiment to her, following in Dilger’s footsteps and at the suggestion of Bob Johnston, a new faculty member in psychology. We were hoping that the female would approach the playback speaker but to everybody's astonishment, the female responded with a copulatory posture to cowbird song. Subsequent playbacks revealed the response to be selective to cowbird song and not nonconspecific song. We rightfully thought we might have the beginnings of a paradigm in which to test quantitatively the functional properties of different birds' songs. But we had to solve the husbandry problems first which would become the major focus of Drew's dissertation.

While this was ongoing, Drew would take data on kitten play bouts in the afternoon and I fed his birds in the morning, giving us both chances to get to campus and do other work. We were spoiled, we had inherited the Howard S. Liddell Animal Behavior Farm when the department moved into a new building and absorbed many off campus facilities including the airport lab. I had spacious rooms for litters of kittens and Drew had at least five rooms for aviaries. Our only neighbor was someone studying raccoons in one room; they occasionally escaped and trashed our offices but it was a small price to pay for almost unlimited space. Drew also had outdoor aviaries outfitted to study brood parasitism with perches on micro switches in front of potential host nests to count how often the nests were visited. We learned to make fake eggs (with the help of Joan Johnston) to place in the nests. They were made of frozen chicken yolk dipped in paraffin; the only problem was the heat—nothing smelled worse that overheated egg and wax. But we learned that we could breed cowbirds, and Drew's dissertation revealed a great deal about the egg laying behavior of females which along with the playback response, set the stage to study the developmental cycle: from egg to egg.

North Carolina.

But before we could pursue that goal, we had to finish theses and find a place to work where we could have facilities like those at Cornell. We were also hooked on the outdoors after living in Ithaca. Two people drew us toward North Carolina, Harriet L. Rheingold at UNC and Gilbert Gottlieb at the Dorothea Dix Hospital, an almost unique state funded basic research unit for which minimal clinical duties were expected. We chose to move there after I was offered a one-year visiting assistant professor position, with the expectation that I would work with Rheingold to learn how my thinking about play would fare with human infants.

Drew made arrangements to have contact with Gilbert’s lab although a post doc slot was not available. Instead, he accepted a lectureship at Duke with the support of J. E. R. Staddon. Gilbert also taught a proseminar in the developmental division at UNC where I was located. As a result we also got a good dose of the teachings of Kuo, as well as Gottlieb. Kuo had helped Gottlieb fashion a window in duckling egg shell to watch and manipulate the final stages of embryonic development. My duties involved teaching child development which was a challenge because I had never taken a course in child development and so I learned along with the students. As a visitor, I was not given any lab space but began to collaborate with Rheingold on studies of toddlers and social pragmatics of communication, which had some overlap with play. I saw enough infants to realize however that the much more slowly developing motor system of the human infant did not translate into anything that looked like social play in mammals. As I had no space to study kittens, my attention was changed considerably to look at how active infants socialized those around them. I was especially interested in their vocalizations, as their vocal play seemed closer to mammalian play in its paradoxical repetition and inventiveness. It was also clear that parents seized on infant sounds to carry out proto conversations and to divulge much information about the environment. I would eventually get an NIH career development award to study both birds and babies. During that time, I worked with a number of students interested in some aspect of parent-child relations. Jim Green and Gwen Gustafson looked longitudinally at mother –child interactiveness and Gena Emery and Anne Arberg looked at language. Finally, George Holden developed new techniques to look at parental reasoning. I also worked with Dr. Eleanor Leung, who had been a research associate in Rheingold’s lab and we collaborated to look at the properties of maternal speech.

I learned a great deal from Harriet about infants and also academics over the years. She read and commented on every paper I wrote and would discuss the craft of writing at length. Her writing was superb (her dissertation and almost every subsequent publication was published with no revisions). I still see or feel her looking over my shoulder as I write. She had been an undergraduate at Cornell and thus was another alum that helped focus my career. But my interests in cowbirds always overshadowed my interest in infants because the cowbird work seemed theoretically the most important contribution we could make to understanding broader principles of development. We also saw the bird work as well as a way to think up new methodology to use with human mothers and children, much of it modeled from the bird work.

We had started house hunting immediately as we needed a place for our animal collection which consisted of something like nine cats (I had given away 42 kittens in pairs as I did my work), one dog, and several dozen birds. We found a rental house with a basement and moved the birds into large flight cages and we housed the sound attenuation chambers we had had built at Cornell into what should have been the living room. The chambers were 1m3 with one-way windows in the front. We could watch bird TV, with the channel set to social development in cowbirds. After much searching we found a small farm with a great barn and a garage and we moved into more permanent quarters. Designing and building outdoor aviaries consumed much time in the first year but not so much that we could not follow up on cowbird #62's response to playback. We raised a new set of females and did playbacks to them of several cowbirds songs plus the songs of heterospecifics. They responded with copulatory postures and surprisingly responded more to the song of male cowbirds that sang atypical songs because they had been raised out of earshot of other cowbird males. Why would such song be more potent? We published the results of Science, our first collaborative paper and began to chart a five-year plan of research ((King & West 1977). Harriet was somewhat frustrated by the competition that birds gave to watching babies but was enough of a comparative psychologist to know that we had to pursue this anomaly as it might tell us something important about the development of song, and she was for any kind of developmental research. She would be pleased to know that in the last few years both Drew and I have begun doing as much infant as avian research and finding intriguing similarities on early stages of vocal development.

Animal Behavior Farm

Beginning in the late 1970's, Drew and I became a formal research team (co-PIs on grants) as it fit both of our interests and needs, i.e., the practicalities of doing the avian research pretty much single-handedly off campus with none of the traditional help a university might provide from animal care to technical assistance. We had decided that an independent lab/farm would keep us out of the space wars that occurred on campus and more importantly no one knew more about the care or housing of a wild species than we did and thus had no one on campus available to help in a meaningful way. We had also learned at Cornell the importance of easy access to one's lab and so living at a farm with the right facilities seemed the optimal course. I believe many of our earlier studies could not have been done any other way and the same is still true today. The best ideas still come from watching the birds. We generally feed and care for the birds ourselves because it keeps us closely tied to the animals' behavior. I think I remember a story about Konrad Lorenz and someone asking him, after he had won his Nobel, why he did not have a technician do the feeding and he quipped that he did not see why someone else should have all the fun.

Fortunately we were successful in grant writing from NIMH and NSF. The grant funds also intersected with the practical question of one vs. two tenure track jobs. We did not see how we could accomplish our research goals and have a family if both of us had the full measure of academic duties. We also saw how hard it was for friends who chose the two-job route to balance raising children with a research career. And so, when a tenure track job became available at Duke, Drew passed on it but remained an adjunct member. It was a risky move, especially given our unusual lab arrangement. But grant money not only facilitated the research but it also helped to legitimize the arrangement: PIs providing their own personal laboratory on private property. The off campus lab also had the advantage of allowing us to move quickly to construct new aviaries or modify existing structures without the “help” of a University architect or the physical plant.

Our approach might not seem odd to field workers and in many ways they represented a better model than lab workers. We firmly believed that the social ecology in which we kept the birds was playing a major role at a time when birdsong research focused almost entirely on vocal cues. Most birdsong researchers who studied development also used more stringent deprivation paradigms, often raising young males alone to reveal the “isolate” song of the species which was considered some kind of genetic blueprint for song ontogeny. We did not believe that solitary housing was developmentally legitimate because in nature although social conditions varied by species, young songbirds did not live in social isolation, thus it seemed evolutionarily suspect to use this as a baseline condition. But we still fell to some extent for the typical avian lingo and referred to our males who were raised with females (who did not sing) or other species as “isolate” males until it became abundantly clear that the term was a misnomer which we explored in a paper entitled “Enriching cowbird song by social deprivation” (West & King 1980).

During the late 1970’s and 1980’s we tackled the social question of why cowbirds with “abnormal” songs were preferred by females in playback studies. First, we built aviaries in which to watch flocks of birds as well as using indoor flight cages and more sound attenuating chambers. We also recorded cowbird song in the various housing contexts. We found the acoustic basis of greater song potency, with the help of J.E.R. Staddon at Duke University, who worked with Drew using a zero-crossings analyzer (ZCA), which allowed the user to see the song in real time without the frequency/time trade-off inherent in sonograms (West, King, Eastzer, & Staddon 1979). Real time analyzers are now commonplace and inexpensive but John’s invention was very new at the time. John’s main area was animal learning but was very open to ethological considerations and thus was an excellent collaborator.

During our tenure in NC, cowbirds were a common but not an abundant species; the population was a relatively new one from a phylogenetic point of view. We decided, with the help of a student, David Eastzer, to look at other populations of cowbirds and see if we saw the same pattern of vocal development and function e.g., (Eastzer, King, & West 1985). Each summer David would pack up his pick up truck with a portable cage in the bed and drive to Texas or Oklahoma to record more ancestral populations. All in all, he studied 8 populations and found variation in song to be the rule. He also looked at border populations between two cowbird subspecies and found an interesting mix of songs from both populations and when we brought females from that area back to the lab we found they had very broad preferences for the mix of songs present on their natal grounds. The comparative work on geographic variation fascinated us because we saw so much variation within subspecies, as well as across subspecies (King & West 1990). In retrospect, it is not as surprising given the ecological differences between populations from the nature of the habitat to the degree of migration. Cowbirds are found across North America thus there was much to differ in their life histories (Rothstein, Yokel, & Fleischer 1986).

Our home/lab became an even more treasured resource once we had children; it also reinforced our job decisions. At that time, babies at home and work on campus presented us with every parents' major dilemma, "How do I make time for both kids and work?" Even with our caretaking arrangements, I confess that the "kid/job" conundrum posed difficulties at least at a mental level. When in at the office I thought I should be home, and vice versa. But it was possible to divide the time between our two schedules and care for our sons at home. Raising human infants while raising birds also had much in common in that the adult/caregiver was not really in charge, the demanding youngsters took center stage. Having our lab at home also meant that our biological and academic children met and interacted. When our oldest son was about five, he asked whether David Eastzer was his older brother. A perfectly appropriate question given that David spent so much time at our home/lab. He received the real thing two years later and dove right into the role of sibling.

It was during the early child rearing years that two very fortunate things happened, albeit of very different natures. First, I received a five-year career development award from NINCDS, freeing me up from any teaching duties. Thus, we could focus full time on the latest interest in the lab, the role of nonsinging females in song development in young males. We had raised young males only with females who could not sing. Thus, they could provide social but not vocal stimulation. It took much exploring to discover the signal system of the females, which turned out to be visual gestures such as wing strokes and gapes to song onset. Thus, we discovered a remarkably open system based on social learning (King & West 1983a; West & King 1988). This was the second lucky event, a turn in the research that was unheard of in the field of birdsong. We were led to find a visual gestural system by videotaping the males when singing to females and saw that at times the males became very excited. When we traced back the males' footsteps, we found the female's very rapid gestures were hard to see with the naked eye as they lasted only 200-300msec (West & King 1988). What was groundbreaking was that the males were not learning by imitation, but through trial and error or operant shaping. The males had to read the female's behavior but not repeat it. Imitation, the thought-to-be core learning mechanism was not at work. Although the birdsong literature was beginning to find social effects to be important in species where male tutoring took place, this was the first evidence of female tutoring and a role for visual stimulation in vocal development. The nature of this finding was sufficiently surprising to some reviewers so as to cause them to propose that the females must be secretly singing. We pursued the effect in a series of papers and the social role of female behavior to structure male vocal and social behavior continues to be a theme in our work.

Indiana.

While our years in North Carolina were productive, we missed the integrative environment we had known at Cornell. UNC did not offer the transparency between programs that we had grown up in at Cornell. We did not have access to graduate students who came in through biology, and psychology had no program in animal behavior (although the developmental division supported animal work). There was no way to attract students interested in integrative work. Thus began a search for a school offering a more interdisciplinary program, as well as good access to cowbirds, and a nice place to live for our kids. I visited a number of schools in the Midwest, but after searching for a year Indiana University stood out because of the nature of its psychology and biology programs. The IU psychology department could not understand that we were not angling for two jobs and that Drew was perfectly content with a senior scientist position, a decision we have never regretted. We were invited to join Psychology in 1989, we were very welcome in the Biology Department, in fact, our first student at IU, Todd Freeberg, was in the ecology and evolution program, thanks to the efforts of Ellen Ketterson, Val Nolan, and Bill Rowland. I also became a member of the IU Biology Department in 1991.

Our move to Indiana was complex because we wanted to build a bigger lab and we wanted it to be within 10 minutes of campus to facilitate student participation. All moves for senior faculty are difficult because so much must be disassembled and re-created in both personal and professional lives. Many people went far out of their way to help find a property for our lab, with Lloyd Peterson, and his wife, Peggy, leading the list, which also included Bill Timberlake, Rod Suthers, and Esther Thelen. Having built a lab at Cornell and then on a bigger scale at UNC, we had in mind some basic principles that had guided us along the way. We had limited resources in both prior settings, first, as grad students, and then as faculty at UNC but with no funds for start-up. At Indiana, the Psychology department, the Dean’s office, and NSF through CISAB all contributed financially to our new laboratory named the Animal Behavior Farm as we had bought a small farm including a house for student offices and a kitchen to make food, a metal out-building to house equipment, flight cages, and our sound analysis equipment, and finally, large outdoor aviaries with shelters. It took a year to find an appropriate site: the land was too perfect to pass up and so we bought it with the commitment to build a home within a few years. Before that we lived in an IU dorm and then in the renovated old farmhouse at the lab.

We landed at IU at an especially crucial time as they were submitting a grant to NSF to develop interdisciplinary work in animal behavior, by gathering together faculty in biology, psychology, and medical sciences. The co-directors were Bill Timberlake and Ellen Ketterson. The Center for the Integrative Study of Behavior (CISAB) has grown to a faculty of over 40, an expanded mission in teaching and research, and hundreds of students have used CISAB’s resources and gone through its program. One the most distinctive features of the Center was its commitment to equipment such as computers, microphones, tape recorders, and finally a DNA and endocrinology lab run at first by Dr. Amy Poehlman. Dr. Shan Duncan ran the technological side of the center for many years and helped many students and faculty as well creating connections to the Animal Behavior Society. But the most distinctive mark of CISAB was the commitment to vertical and horizontal integrative training through courses, colloquia, and research plans. The nature of our lab and CISAB allowed us to attract graduate students seeking integrative training which we saw as critical to our long term goals to integrate communicative development in birds with converging studies of human communicative development.

Needless to say, the faculty in the developmental program in Psychology was the most compelling factor in our transition. Esther Thelen, Susan Jones, Linda Smith and Jeff Alberts formed the core of the developmental program, and we were soul mates with them in terms of approaches to developmental questions. The rest of the faculty contained many luminaries, making the new department even more inviting. Indiana was just beginning to support integrative research on a large scale. Our students had more resources to use and more faculty to choose for their committees. I must also add that the then Dean, Mort Lowengrub, never blinked an eye at our request to build an off campus lab that they would help fund and used the weight of his office to eliminate bureaucratic obstacles. The administrative web eventually included many people who were supportive but Mort’s enthusiasm and confidence stood out. Every subsequent Dean and system president has been helpful.

During my time at IU, I assumed new duties as Editor of Animal Behaviour from 1991-1994. Ellen Ketterson was the editor for Short Communications, and Kris Bruner, the managing editor, began her long productive association with the journal on our watch. This was before the journal had decided to go the multi-editor system, which began in a small way in my final year as editor. Now there are four or more American editors and an equal number on the other side of the Atlantic with our sister organization, ASAB. After the editorship, I was elected President of ABS and served during tumultuous times as we wrangled with ASAB and the publisher about profits and managed to strike a new deal giving the American executive editorial office more money which we dearly needed to keep up with the speed with which papers arrived at our door. We also established a central office for the journal at Indiana, ably staffed by Steve Ramey, Kris Bruner, and Lori Pierce. We could not have found a better or more dedicated manager than Steve who has spearheaded all of the features of the editorial process that now are handled electronically. Later, in 2000, I became editor of the Journal of Comparative Psychology, with Sue Linville as a wonderful managing editor. JCP attracted a somewhat different audience than Animal Behaviour, many more experiments on cognition, especially in non-human primates. I did try to represent other taxa as well, and other topics. So my childhood worry about sufficient reading material was somewhat assuaged. Journal work as Lee Drickamer, the previous editor, told me is “relentless” and follows you everywhere. But I truly enjoyed learning about the creative questions investigators thought up to ask and clever ways of answering them.

Aviary work.

On the research front, we were shifting our basic experimental designs to meet the affordances offered by flocks in the spacious aviaries. Thus, the major structures, outdoor-indoor aviaries at the Farm were the heart and mind of the lab. The experiment that set the tone for the next decade was done with Todd Freeberg (Freeberg, King, & West 1995). We used all our different facilities. First, we individually housed young wild caught SD male cowbirds with either SD females (FH) or canaries (CH). They lived together through the fall into the spring. The birds were housed in sound attenuating chambers (1m3 with a one way window). Then, in early May, we moved the males to flight cages (2.4m x 1.8m x 1.8m) with the 5 males in each group housed together. We had never done this before, systematically looking at how birds react to the greater freedom of the flight cage. At first, it seemed there would not be much to see as the birds sat quietly hardly moving—any sound sent then flying in a frenzied fashion with the males seemingly intent on not landing on a perch containing another male. And for some reason, the CH birds seemed to be more affected than the FH birds. But within a week, they were much calmer singing to themselves or to the canaries housed with the CH males. One of the reasons we had housed them in chambers was to control their experience with other cowbirds. So the CH group represented the closest we came to an isolated male. The FH males were also isolated from males but presumably were being socially tutored by female cowbirds. We saw this experiment as a definitive test of whether cowbirds had open or closed systems with respect to species identification. If the cowbird system was innate, as many presumed, all the males should end up courting local females.

We set up a test of social recognition by introducing the males individually into a neutral cage containing local female cowbirds and canaries. The FH males reacted in what appeared to be species-typical manner approaching and singing to females and ignoring the canaries. The CH males were different: the males courted the canaries singing and chasing them. Thus, socially isolated cowbirds do not have a template for species recognition; it is acquired through experience with adult females. We assumed adult males played a role as well, and our confidence in that statement grew when we placed all of the FH and CH birds in two large (18.3m x 9.1m x 3.7m) aviaries containing many potential mates. Included were female cowbirds from NC and SD and well as IN, canaries, and starlings, a novel species. Each day we recorded their singing, mating and social behavior. Much to our surprise, the CH males continued their canary pursuit ignoring other cowbirds most of the time. And so even seeing more normally raised males did not induce social learning. But the FH birds were not very good models, because here in the aviaries, they also did not court the solicitous females, nor did they sing much to other males. Typically male cowbirds exchange songs with one another in a behavior known as countersinging: we saw nothing like it.

As a last gasp effort to extract species typical behavior we introduced adult males who immediately began to court and countersing. But seeing adult models caused no change in the CH and FH males. Obviously for male experience to be effective they must interact much earlier in the year. This set of experiments represented a turning point in the lab…now that we saw the difference in behavior between conventional housing and the aviaries, we knew that work with aviary flocks would continue to be necessary. This work also clearly showed the limitation of assessing song quality by playback as males needed to learn to use their songs regardless of quality.

Todd Freeberg turned to aviary housing to do a daring dissertation of the cultural transmission of mate preferences, showing that mate preferences were influenced by postnatal experience with adults and that preferences could be passed on to the next generation (Freeberg 1996). The experiment was daring because the birds were outside and could see and hear wild cowbirds and yet appeared to be only influenced by the birds within their aviary. So social interactions appeared to matter greatly. We have since shown that song sharing, commonly seen in the field, can be limited by a transparent aviary wall separating two flocks: we saw no song sharing across flocks, but did see it within flocks. We have repeated this test with eight flocks with the same result each time. Thus, it became clear that social context predicted song learning, not simply exposure to song. This led us to start to investigate the role of larger flock dynamics to gate social stimulation.

Studying birds in flocks brought on many new methodological issues such as how to record flock dynamics. Anne Smith, a student in Biology, got us started with a study of a large flock of 74 birds, in which she used paper and pencil measures of near neighbor patterns (Smith, King, & West 2001). These patterns allowed us to see structure in the flock with birds assorting by age and by sex. But Anne also found that juvenile males whose second most frequent neighbor was an adult male fared better in the breeding season. And males for whom females were the second most frequent neighbors had males whose song development progressed faster than that of other juvenile males. This finding fit with earlier IU work on male and female influence using conventional housing and demonstrated the role of social structure to direct different developmental outcomes. Anne also analyzed DNA from the 74-bird flock and found no relationship between kin in terms of social assortment. We had long wondered what kin relations would look like since cowbirds can potentially have many siblings due to their brood parasitic habit.

But the problem with more birds was not space but methodology. We had reached the limits of paper and pencil: we needed a way to gather more data from many birds simultaneously. We began to look into alternative methods and with the help of Shan Duncan and a new postdoctoral fellow David J. White. We developed the use of voice recognition software so that observers could “speak” the data into a wireless lapel microphone without looking away from the birds and the information was transmitted from the aviaries to the lab building where computers received the codes and a database organized them into summary tables (White, King, & Duncan 2002). We found we could take many times more data and could for the first time record detailed reactions to songs in real time, not just the songs themselves. For example, in our first large flock study over an 8-month period four observers collected approximately 32,000 data points and entered the data manually into a database. By contrast using voice recognition and programmable databases, four observers can collect and analyze a comparable data set in about 20 days. With Dave as a collaborator, we went on to study social development of males housed since fledging in flocks ranging between 20 and 30 birds. Dave spearheaded an effort to look at juvenile male song and social development as a function of social context, i.e., the presence or absence of adult males (White, King, & West 2002). We found that males without adults differed on many dimensions from juveniles with males (all had females present). A behavior that emerged as important was counter-singing (CS), the behavior that we had found to be absent when males were housed with just females. CS consists of rapid exchanges of song between two or more males. We found that the males without adult males did not show CS but those housed with adult males did. Although females were not the targets of CS, they did appear to notice the behavior, as we found that CS correlated with the number of eggs laid (King, White, & West 2003). Further studies revealed the importance of social learning to CS and we found that CS could be transmitted from one generation to another. But we also found the absence of CS could be transmitted to a new generation of males (White, Gros-Louis, King, Papakhian, & West 2007). So, competence and incompetence were under cultural control.

The efforts are still ongoing but one enormous surprise was the finding that the males who seemed most dominant and generally singing the “best” songs did not sire the most eggs. This finding was particularly apparent when individuals were followed over several years interacting with different social companions from year to year. Thus, the ability to measure cumulative reproductive success over several years is beginning to present us with a very different picture. In particular, the role of singing performance and the ability to adjust behavior from year to year may well turn out to be critical to understanding reproductive success. Many ideas about the functional consequences of different male phenotypes can now be addressed. These findings have led to investigating the importance of communicative pragmatics. This work extended the Freeberg et. al. (1995) findings with CH males to show the role of exogenetic stimulation not only to alter development but to connect to cumulative reproductive success bringing our measures to the threshold of fitness.

We did not ignore the females in our expanding work with flocks. We had done a series of developmental studies using restricted housing in the early 80’s and had concluded that females, unlike the males, had a closed program of species recognition, a finding we replicated with several geographic populations (King & West 1983b). All of those studies housed females in small groups in sound attenuating chambers with or without a male and found no evidence that female preference for male song could be modified. Now in the flock setting we discovered a completely different picture of the development of female preferences. We raised one flock of only females. The females could of course hear male cowbirds outside the aviaries. We then tested the females’ playback preferences for local and distant South Dakota and Texas song (King, West, & White 2003). The results from the all female flock were surprising as adult females showed no preference for local song over those of other subspecies.

Neither did juvenile females. The finding was especially dramatic with respect to Texas song in that those songs were lexically very different from Indiana song. This was astounding because all females we had ever tested for local vs. distant population preferences preferred local songs. Thus housing females in a flock without males had erased preferences for the adult females at the macro-geographic level. We went on to show that contact with males mattered, even if it came from tape recordings of male song. Thus, by tape or live tutoring outdoors where wild cowbirds were present, we could induce specific preferences in the female cowbirds when they were housed in flocks (West, King, White, Gros-Louis, & Freed-Brown 2006). Thus, we could now see that the restricted housing work of the 80’s had the effect of freezing female preferences while the flock studies revealed that when females can observe groups of other females react to male behavior their song preferences were easily changed. This work dispelled the notion of a genetically predetermined safety net for reproductive behavior. Thus, the flock studies on the development of male singing performance as well as female preferences showed the presence of an exogenetic mechanism.

Largely through the work of Grace Freed-Brown we were also beginning to learn something about the development of female social dynamics in flocks and found important differences in the interaction patterns of juveniles versus adults, with the juvenile females being much more active and less discriminating in their choice of social partners (Freed-Brown, King, Miller, & West 2006). With Jennifer Miller, we also found that flock housed young females (reared from the egg) showed no evidence of same sex sociality as juveniles (Miller, Freed-

Brown, White, King, & West 2006). Thus, like males, females did have to engage in early learning, presumably from adults, in order to show species-typical behavior of strong assortment by sex. Taken as whole, these studies begin to show us the social mechanisms actually responsible for female preferences and we believe that these types of studies which will increasingly use social networking statistics to describe the developmental environment that is the safety net for the acquisition of appropriate reproductive behaviors in both males and females. Thus, we see network statistics replacing the ghosts of the innate safety net.

Flock studies are ongoing with an emphasis on vocal improvisation and its relation to pragmatic ability in young males as Jennifer Miller has found that males raised with adult females improvised more than juvenile males with juvenile females and the adult housed males showed superior courtship skills in their first breeding season. Thus, it appears that the adult females were socially shaping the song content as well as how to deliver the song. Improvisation has not been studied in anywhere near the detail of song copying but may well prove to be an engine of pragmatic skills. We believe that there is at present a ‘missing link’ in connecting birdsong capacity to birdsong competence, e.g., the use of song as an effective elicitor of reproductive behavior in females. The common assumption is that competence simply flows from some possibly innate by-product of birdsong development. Understanding the dimensions of competence, or what we call “communicative pragmatics” can be summed up as answering the “wh” questions, the “who,” “what,” “where,” “when,” and “why” of singing performance. We presently are investigation how young birds a) learn how to use their signals though social modeling and social operant learning and b) learn to lengthen their attention span so as to be able to acquire critical feedback from social companions. Indeed, we believe that acquisition of attention span, also critical for human communicative development, becomes the root mechanism for learning and using birdsong in myriad ways including territorial encounters, song sharing and mating.

During the years of cowbird work, two other lines of research were leading us to the same conclusion about the importance of social shaping. First, we worked for several years with starlings; many of who were hand reared and kept in human homes under different social circumstances. We found that starlings engaged in vocal sonar and their repertoires showed evidence of human shaping as they included human words if they had lived in interactive contact with a human (West, Stroud, & King 1983). Interactive contact simply meant that birds had much more social freedom than the control birds and routinely socialized with humans. Marianne Engle completed a dissertation of the social circumstances for mimicry and created a scale of interactivity. Starlings are an intimidating species to work with because their song is so much more complex than that of cowbirds, but they adapt marvelously to captivity and there is now a niche in the bird lover's world devoted to "pet" starlings, with terrific material on the web.

We also explored the life of one starling in depth, a starling that had been owned by Wolfgang Amadeus Mozart for three years. We were curious about the relationship, which we pictured as a comical, and affectionate based on reports from our 1980’s starlings. We also thought that Mozart left a requiem for his pet, the piece known as the Musical Joke K522, so-called because it has fragmented parts that do not quite come together and much repetition, including a nine trill note that sounded to us like the contact call of our 20th century starlings: they were idiosyncratic calls to say the least but their function seemed clear. Thus, we pictured Mozart’s incorporating starling phraseology into a simple folk song. We wrote a paper about the whole historical adventure and its relevance to social shaping for the American Scientist (West & King 1990). It is safe to say that it is the article most requested of anything we have ever written. I talked about the experience at an AAAS convention and the press got hold of it in 1991, the 200th anniversary of Mozart’s death. Our story became a popular part of Mozartiana and the report was in many science and popular magazines, newspapers, and radio…we still get requests for interviews 17 years later. I also get e-mails from starling owners wanting advice about health and food. Each story is a variation on the theme of “I found this ugly looking little bird cheeping near my home and I fed it for a few days (usually dog food which was not that bad of a choice) and before I knew it I was in love with the most imperious young bird I have ever met.” I still hear from owners with updates, as the birds can live into their teens in captivity.

But the starling work was also important because it showed another improvising species that was affected by social contact. We had had a second group of starlings in our first experiment that lived as caged pets in human homes and received good but not extra-ordinary care like playing in the kitchen sink. They were raised as most caged birds are raised. They mimicked household sounds but no human voices. Thus, the interactive contact, as in cowbirds, mattered. Merely hearing and seeing human voices was not enough. These findings served to deepen our interest in social shaping, especially what we saw as similarities to the development of human speech. This interest began with the work of Michael Goldstein. He decided to follow up on the wing stroking work in female cowbirds by looking at prelinguistic communication in human infants. Like the cowbird work, he set out to capture the nature of social maternal responding to the activities of their children. We first found that mothers perceived different infants' communicative signals in a consistent manner, ascribing the same function to the different sights and sounds (Goldstein & West 1999). This was important because it meant there was something in the prelinguistic sounds to hear, i.e., communicative meaning. But Mike's most important achievement occurred when looking directly at social shaping. He compared infants whose mothers delivered either contingent or non-contingent non-vocal feedback in an ABA design. He found that infants whose mothers were contingent responders had infants who showed advanced phonology in the second A trial, whereas infants whose mothers were non-contingent did not. Thus, we had strong evidence that social shaping of vocal structure also occurred in humans; at a point in development comparable to the time we saw it in birds (Goldstein, King, & West 2003). The PNAS paper garnered much media attention, second only to Mozart's starling. I think it was of interest because of the comparative theme and the fact that the effect did not depend on imitation. Imitation is the supposed mechanism in both species for vocal learning, but neither the babies or male cowbirds were copying their partner's behavior but extracting from it information about what sounds were effective in getting a response.

Julie Gros-Louis, a postdoctoral fellow, with a background in primatology and communication brought a fresh eye to both the bird and baby work. Julie analyzed the content of mother's behavior during free play and found the mothers responded differentially to infant behaviors and sounds, affording the infants contingent feedback that varied with the infant's vocal or behavioral action (Gros-Louis, West, Goldstein, & King 2006). Because the avian work points to a fundamental role for the development of attention to predict vocal and pragmatic skills we are beginning to study the development of attention in prelinguistic infants. Specifically we are investigating the role of caregiver contingent stimulation to lengthen or shorten infants' attention. Erin Ables and Jennifer Miller are just completing a series of studies that demonstrated that infants show differences in attention span depending on the nature of caregiver contingencies. We are doing similar studies in the cowbirds looking at directed or undirected song as proxies for attention or inattention. Juvenile males, housed with juvenile females, show shorter attention spans, for example, than juvenile males housed with adults. We should note that Jennifer Miller is the first student we have had that simultaneously has initiated research in both the bird and baby labs and used observation and theory from both preparations to guide a parallel research program. This has been a long term goal of our research to have both labs ask essentially similar questions of both birds and babies but to do so in the same time frame thus driving a comparative synergy.

Summary.

I have used the word “surprised” several times in the text to capture our emotions at experimental outcomes. We stand by this attribution and it is our fondest wish that there are more surprises to frame our future. But it is especially important to remember the first “flashbulb” surprise: the deprived female’s copulatory response to song. We knew we were being given a chance to ask very different questions about mate choice. Her greater response to the songs of deprived males suggested we had an adaptive “story”: cowbirds, with no experience with one another, appeared to have the ultimate safety net to insure mate selection. The male side of the story was just as exciting as in most species isolate songs were less effective than normal songs in eliciting copulatory responses, but in cowbirds, atypical songs seemed to be more potent than normal songs. Thus, without experience on either side, mating mechanisms seemed to be in place, suggesting that females, through sexual selection, mated with males with the “best” song. What a great story for a brood parasite who would seem to need especially closed programs to engage in species and mate recognition.

The “closed program” story began to unravel when we used more naturalistic settings and stimulation. First, we found that females living in flocks showed no song preferences. We surmised that competition among the females induced plasticity. Second, we discovered that we could manipulate preferences through social housing, something we had not seen in more conventional housing. We also had to come to grips with the finding that silent females affected song content and quality. These data suggested that sexual selection might not be focused on song quality, but song use. If so, females may be selecting on the basis of male learning and attentional processes, especially by males watching females. Thus, non-imitative song learning was as basic to song development as imitation. We think, but do not know for sure yet, that improvising males may be the product of more attention to female responsiveness. Thus, females are using song use (directed song, countersinging) when it available as a cue. The missing link was connecting male and female development. Ironically, we had always had access to female influence, as we never raised birds alone but thus used females as a control for housing with males. Even the males deprived of male company, say in the very first experiment with naïve males, had either other species or females with them. Gottlieb had frequently talked about non-obvious influences on development in his ducklings (such as prenatal vocalizations) and we considered the females' effect to be analogous.

Thus, the "adaptive story" of the lock and key female response to song turned out to be deceptive. Until we understood the sensitivity of the development of male song and social behavior to social context along with modifiable female preferences also responsive to context, we did not see that the actual safety net was an exogenetic mechanism afforded by a stable social ecology. In the early 70s when we started our research program we were profoundly influenced by the developmental work of Marler, Gottlieb, Lehrman, and Tinbergen, among others. At the time an understanding of development seemed to be central to the investigation of the evolution and function of behavior. We believe that the single most significant contribution of our work is to remind others of that fact. At the present time, it is our perception that many investigators do not consider it necessary to know the development of a behavior to understand its function or what has been selected by evolution as the mature behavior is assumed to be the endpoint (West, King, & White 2003). This convenient illusion is typically supported by a failure to understand individual and geographic variation of behavior that can be supposed to be genetic rather than ecologically driven. Even in research that focuses on the neural or hormonal basis of behavior the present reliance on the lock and key connection of male song production and female reaction to song in a restricted housing preparation is likely to be misleading about the systems responsible for reproductive behavior. Consider that female cowbird song preferences are “frozen” by the restricted housing setting.

Thus as we enter the late innings of our career, we are saddened by the present trend which seems to de-emphasize an appreciation of the essential importance of the development of behavior. Oddly enough the fact that we were so taken in by the power of innate behavior in the early innings to provide evolutionary answers both makes it easy for us to understand the attraction of this perspective but it also provides us with the motivation for our continued research efforts. We owe a lot to the illusion of an innate answer to provide opportunities for surprises which inform about the stability of exogenetic mechanisms that evolution has chosen to trust for the constructive transmission of critical reproductive behaviors.

Conclusion.

As I look to the future, I see more birds and babies but I do not see South American cowbirds or the Galapagos, goals that motivated us during the earliest years. We have found our wheel house looking at the myriad ways that social experience modifies developmental trajectories. To reduce the work to the simplest terms our research argues that nature and nurture exist in inherited niches—genes inherit environments, in other words, species-typical surroundings that shape the contribution of nurture (West & King 1987). To paraphrase Mace, what we believe is that it’s not “what’s inside your genes that matters but what your genes are inside of.” Elsewhere we have referred to our exogenetic theme as a message in a bottle hugging the shore of seas roiled by the Human Genome Project (West & King 2001). We are up against formidable theories and habits contained in the biological frame of “genes for x”. But, in the end, as been shown to be true for genetic explanations, one has to confront an environment and trace its direct and indirect effects. This gives us hope that our words and deeds will be seen for what they are: descriptions of developmental contingencies that require the “right” environment in order for ontogenetic principles to appear.

References

Dilger, W. C. (1964). The interaction between genetic and experiential factors in the development of species-typical behavior. *American Zoologist, 4*, 155-160.

Eastzer, D. H., King, A. P., & West, M. J. (1985). Patterns of courtship between cowbird subspecies: Evidence for positive assortment. *Animal Behaviour, 33*, 30-39.

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

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.

Freed-Brown, S. G., King, A. P., Miller, J. L., & West, M. J. (2006). Uncovering sources of variation in female sociality: Implications for the development of social preferences in female cowbirds (Molothrus ater) *Behaviour, 143*, 1293-1315.

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.

Goldstein, M. H., King, A. P., & West, M. J. (2003). Social interaction shapes babbling: Testing parallels between birdsong and speech. *Proceedings of the National Academy of Science, 100*, 8030-8035.

Goldstein, M. H., & West, M. J. (1999). Consistent responses of human mothers to prelinguistic infants: The effect of prelinguistic repertoire size. *Journal of Comparative Psychology, 113*(1), 52-58.

Gros-Louis, J., West, M. J., Goldstein, M. H., & King, A. P. (2006). Mothers provide differential feedback to infants' prelinguistic sounds. *International Journal of Behavioral Development, 30*(6), 509-516.

Harlow, H. F. (1965). Mice, monkeys, men, and motives. In H. Fowler (Ed.), *Curiosity and exploratory behavior* (pp. 91-103). New York: MacMillan.

Harlow, H. F. (1974). Induction and alleviation of depressive states in monkeys. In N. F. White (Ed.), *Ethology and psychiatry* (pp. 197-208). Toronto: University of Toronto Press.

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

King, A. P., & West, M. J. (1977). Species identification in the North American cowbird: Appropriate responses to abnormal song. *Science, 195*, 1002-1004.

King, A. P., & West, M. J. (1983a). Epigenesis of cowbird song - A joint endeavour of males and females. *Nature, 305*, 704-705.

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

King, A. P., & West, M. J. (1990). Variation in species-typical behavior: A contemporary theme for comparative psychology. In D. A. Dewsbury (Ed.), *Contemporary Issues in Comparative Psychology* (pp. 331-339). Sunderland, Massachusetts: Sinauer.

King, A. P., West, M. J., & White, D. J. (2003). Female cowbird song perception: evidence for plasticity of preference. *Ethology, 109*, 865-877.

King, A. P., White, D. J., & West, M. J. (2003). Female proximity stimulates development of male competition in juvenile brown-headed cowbirds, Molothrus ater. *Animal Behaviour, 66*, 817-828.

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

Mace, W. M. (1977). James J. Gibson's strategy for perceiving: Ask not what's inside your head, but what your head's inside of. In R. Shaw & J. Bransford (Eds.), *Perceiving, acting, and knowing* (pp. 43-66). Hillsdale, N.J.: Laurence Erlbaum Associates.

Mayr, E. (1974). Behavior programs and evolutionary strategies. *American Scientist, 62*, 650-659.

Miller, J. L., Freed-Brown, S. G., White, D. J., King, A. P., & West, M. J. (2006). Developmental origins of sociality in brown-headed cowbirds (Molothrus ater). *Journal of Comparative Psychology, 120*, 229-238.

Rothstein, S. I., Yokel, D. A., & Fleischer, R. C. (1986). Social dominance, mating, and spacing systems, female fecundity and vocal dialects in captive and free-ranging brown-headed cowbirds. *Current Ornithology, 3*, 127-185.

Smith, V. A., King, A. P., & West, M. J. (2001). The context of social learning: association patterns in a captive flock of brown-headed cowbirds (Molothrus ater). *Animal Behaviour, 62*, 23-35.

West, M. J. (1974). Social play in the domestic cat. *American Zoologist, 14*, 427-436.

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. (1987). Settling nature and nurture into an ontogenetic niche. *Developmental Psychobiology, 20*, 549-562.

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. (1990). Mozart's Starling. *American Scientist, 78*, 106-114.

West, M. J., & King, A. P. (2001). Science lies its way to the truth...really. In E. M. Blass (Ed.), *Developmental Psychobiology, Volume 13.* (Vol. 13, pp. 587-614). New York: Kluwer Academic/Plenum Publishers.

West, M. J., King, A. P., Eastzer, D. H., & Staddon, J. E. R. (1979). A bioassay of isolate cowbird song. *Journal of Comparative and Physiological Psychology, 93*, 124-133.

West, M. J., King, A. P., & White, D. J. (2003). The case for developmental ecology. *Animal Behaviour, 66*, 617-622.

West, M. J., King, A. P., White, D. J., Gros-Louis, J., & Freed-Brown, S. G. (2006). The development of local song preferences in female cowbirds (Molothrus ater): Flock living stimulates learning. *Ethology, 112*, 1095-1107.

West, M. J., Stroud, A. N., & King, A. P. (1983). Mimicry of the human voice by European starlings: The role of social interaction. *Wilson Bulletin, 95*, 635-640.

White, D. J., Gros-Louis, J., King, A. P., Papakhian, M., & West, M. J. (2007). Constructing culture in cowbirds (Molothrus ater). *Journal of Comparative Psychology, 121*(113-123).

White, D. J., King, A. P., & Duncan, S. D. (2002). Voice recognition technology as a tool for behavioral research. *Behavioral Research Methods, Instrumentation, and Computers, 34*(1), 1-5.

White, D. J., King, A. P., & West, M. J. (2002). Facultative development of courtship and communication in juvenile male cowbirds (Molothrus ater). *Behavioral Ecology, 13*, 487-496.