

# Developmental ecology

## Platform for designing a communication system

Meredith West, Andrew King & Gregory Kohn

Indiana University-Bloomington, USA

In this article we provide a case history of the development of a communicative system in songbirds. In particular, we explore how brown-headed cowbirds, male and female, cooperate in the development and use of species-typical song. The goal is to show how social interactions between and within sexes create a platform for the production and perception of song. We consider six perspectives. First, we discuss the nature of the acoustic signal. Second, we look at the process of song learning. Third, we describe a specific song mechanism, social shaping. Fourth, we look at the more general developmental process of neophenogenesis. Fifth, we consider the developmental ecology for social learning. Finally, we describe how social networks measures can be used to capture the nature of social interactions as the engines of song learning. Taken as a whole, we argue that culturally transmitted behaviors structure social interactions that predict the acquisition of species' typical behaviors necessary for successful reproduction.

### 1. Introduction

Many animals go through periods when they live gregariously, i.e. mixed age, sex, class, and/or species social groups. Clearly, group living has many advantages in finding food and defending against predators. Traditionally research on animal sociality has focused on classifying different social organizations, such as group composition and then exploring the group's underlying dynamics. However these underlying dynamics can be uncovered through examination of the communicative processes operating at several levels of sociality. The distinctiveness of group dynamics, at least as perceived by humans, is captured in our everyday language in rich form: there are exaltations of larks, gaggles of geese, parliaments of owls and so on (Lipton 1968). Growing up social affects opportunities for social interaction and learning species typical behaviors (Snowdon & Hausberger 1997). Therefore researchers must not only identify the physical composition of a group (how many males, females, offspring, etc.) but also explore the group's functional properties,

incorporating attributes like patterns of sociality, subgroup formation, and use of cooperative communicative signals.

Here, the objective is to identify the social ecologies that reveal species' typical behavior. Jeanne Altmann once said "One primate is not a primate." In other words, the behaviors displayed by single primates do not afford the social opportunities primates need in order to show their species-typical behavior. Therefore research on animal sociality should closely examine what animals do when we say they are interacting. Interacting how? With whom? For what reason? By examining the routine lives of animals we can also see how individual behaviors shape and are shaped by their developmental ecology (West, King, & White 2003). By developmental ecology, we mean the physical and social attributes that constitute the animal's habitat, including properties such as age, sex, population density and contexts such as courtship, maternal behavior or dominance that shape individual developmental trajectories. Developmental ecologies are created by and require self-motivated activity and effort for their affordances to be revealed (Gibson 1966). For example, male cowbirds inherit ecologies that contain female cowbirds, but males must approach and repeatedly sing to females to get a social reaction. Thus, the parameters of performance accompanying behavioral output are part of a discovery process that uniquely defines the developmental ecology at the level of the individual.

## 2. Six perspectives on the development of communicative competence

What information is available in groups that is not found in pairs or individuals? The phenomena of eavesdropping and mate copying are two behaviors that would seem to enjoy an advantage when more animals can be observed (McGregor & Peake 2000; Peake, Terry, McGregor, & Dabelsteen 2001). Both of these behaviors relate to two concepts: bioavailability and social gating. Bioavailability comes from the pharmaceutical world where it is one of the essential tools in pharmacokinetics, helping uncover how much of a pharmaceutical agent makes it into the body's systems and what metabolic processes affect passageway. We will ask how much of a given form of stimulation makes it into the organism's senses and is therefore usable and how the expression of behavior is affected by ecological factors. For example, in cowbirds, males living in adjacent aviaries separated only by aviary wire, do not copy each others' songs: all imitation is within aviary limits although the birds can be at times closer to adjacent aviary neighbors than same flock mates (White et al. 2007). Therefore, direct unhindered interactions with other flock members, and not just acoustic stimulation, is needed in order to imitate song. In the wild, males share about 50% of their repertoires (Dufty 1985). Thus, song is not

bio-available across contexts even if the acoustic and visual distance is the same. Clearly, it takes social interactions for information to be gated through the perceptual system. We hope to show the constructive role played by social interactions in making information available and influencing development outcomes.

Here we will explore six ways to look at social interaction and communicative development, approaches applicable to many taxa. The questions are interconnected but have at their core the role of the discovery process and the nature of the social interactions that comprise the developmental ecology (Catchpole & Slater 1995). The first perspective is the study of the communicative signal, in our case, song. What is the structure and function of song? Included here are receptive properties of song as well, i.e. female songbirds' reaction to singing. The second approach is developmental, searching for the origins of species-typical song and other social behaviors. This perspective is explored by manipulating the environment by social enrichment or deprivation, and by identifying how geographic variation in song patterns arise. The third method is behavioral manipulation at the individual level, e.g. social shaping of behavior. How does social interaction function as a reinforcer of behavioral output? The fourth perspective involves neophenogenesis, an attempt to look at overall plasticity by creating experiential 'knock-outs' where we excise part of the social ecology of the individual and record the effects (Flack, Girvan, de Waal, & Krakauer 2006). The fifth perspective investigates the role of group level organization to influence the nature of social interactions and developmental outcomes. Finally, in the sixth perspective, we describe the use of network statistics to supply a vocabulary to describe and compare group level activity that can be related to communicative outcomes (Sih, Hanser & McHugh 2009). We will argue that an understanding of mechanisms of communicative development require indentifying flock level sources of stimulation that determine what is available to be learned.

### **3. Product: The communicative signal**

Just as for other songbirds, cowbird song is critically involved in courtship and female choice. Cowbird song is sung at close distances, unlike territorial songbirds where greater distances are involved, reducing the role of vision. According to Crawford Greenewalt (1968, p. 119–120), the cowbird is the winner in the "decathlon" of avian vocalizations. Among the cowbird's achievements is the use of a wider frequency range, nearly four octaves, than in any other bird's song; a maximum frequency higher than that found for any other bird; a frequency spread between the two voices<sup>1</sup> of a full two octaves; a first introductory note with the most rapid glissando; and the highest modulating frequency in the high

voice. Greenewalt had no explanation for the convergence of all of the vocal accomplishments in cowbirds, “only madam cowbird will know,” he speculated.

*Song potency and the isolate song effect.* We asked “madam cowbird” about song via playback tests. Here females in breeding condition (they were laying eggs) were housed in same-sex pairs in sound attenuating chambers and songs were played to them six songs a day, one song every 90 minutes (King & West 1977; West, King, Eastzer, & Staddon 1979). The playback females (wild caught juvenile & adult) responded selectively to cowbird song with copulatory postures that began before the song was over. They did not respond to the songs of other species. We labeled songs as potent or not potent depending on how frequently they elicited a copulatory response. We played back songs recorded from typical adult and juvenile males socially housed in flocks (typical song) and from juvenile males housed in sound attenuating chambers with females or nonconspecifics (isolate song). Thus, the isolate males developed their song in a social environment but one that lacked species-typical male vocal and social stimulation. In doing playbacks of isolate and typical song, we came across a surprise: the isolate songs were different acoustically, but were more potent to females than typical song (King & West 1977). At the time, this discovery suggested a hardwired safety net to ensure that this parasitic species would be able to reproduce successfully.

We further pursued this “isolate song effect” through a series of experiments looking at males and females in more complex social settings. We housed adult and juvenile males in small groups with either males and/or females, or individually with only females (West & King 1985). We found that group-housed males regardless of whether they were adults or juveniles, had lower song potency than the male housed individually. We introduced the males from the group- or individual-housed conditions into large flocks of male and female cowbirds (West & King 1980). We found that individual-housed males behaved as dominant males when introduced to a new aviary: they approached and sang and attempted to displace males and females. Resident adult males reacted aggressively to both the song and behavior of the individually housed males. These individually housed males thereby received an education in aggression and quickly learned to reduce the potency of their song. When we introduced the group-housed males, who already had songs of lower potency, they integrated into the larger flock without attracting special attention from the resident birds. Social interaction with other males seemed to shape the developmental trajectory of song by reducing its potency. And so we found that males faced a social dilemma: songs that attract females provoke other males. However, from the female’s perspective, song potency may entail more than just the acoustic properties of a song, but also the context in which the song is used. We found in each aviary that there was at least one male who rarely sang, although independent playback data told us he had

a potent song. Females ignored these males the few times that they sang. Reproductive success may therefore depend upon male's pragmatic skills in performing the song. The discovery that a male could develop a functionally effective song (playback potency) but be unable to utilize it properly suggested a critical role for recurring social interactions to develop species-typical behaviors. Thus, we began the search for developmental correlates of song that relied on social interaction.

#### 4. Process: Plasticity pervades the developmental system

*Female plasticity.* Some have speculated that cowbirds have a safety net for song ontogeny because they are brood parasites. Since these assumptions were articulated in the 1970s (Lehrman 1974; Mayr 1974), we have completed dozens of developmental experiments manipulating the social and acoustic environment revealing plasticity in both male song development and female song perception. To do so, we have exploited the cowbird's vast range through North America and looked at the three subspecies of cowbirds, the eastern population, *M. a. ater*, the southern population, *M. a. obscurus*, and *M. a. artemisiae*, the northwestern population. If, as is often assumed, song can act as a reproductive isolating mechanism, songs should differ in the three subspecies to reinforce subspecies boundaries through mate choice (King & West 1990). We indeed found acoustic differences across the three populations and found that females responded most to playbacks of local, subspecies song in all populations (Eastzer 1988). This finding led to developmental studies manipulating intrasubspecies acoustic and social contexts (King & West 1988).

Space does not permit a full explication of the studies revealing male and female plasticity associated with the development of song. Suffice it to say that we saw plasticity in both sexes once we developed species-hospitable contexts for learning. For example, we found no evidence of modifiability in female song playback preferences when we housed pairs of females from populations in North Carolina (NC), Oklahoma (OK), Texas (TX), South Dakota (SD) or Indiana (IN) in sound attenuating chambers with males from a distant population (e.g. North Carolina with Texas). We obtained the same result across the species' range: naïve females preferred natal song over the songs of the males with whom they were housed. Moreover, all naïve females preferred local song even if they had not heard it developmentally (King & West 1990; King, West, & Eastzer 1980).

But when we housed juvenile and adult females in a same sex flock from fall to spring (20 females) in an indoor/outdoor aviary, we found that female song perception was malleable after all (King, West, & White 2003). In the spring we tested their playback preferences for IN song compared to TX, NC, or SD song.

Unlike females in all previous studies, these aviary-housed females showed no natal preference. Therefore living in groups afforded some mechanism by which females could modify their preferences (West, King, White, Gros-Louis, & Freed-Brown 2006). For instance, Freed-Brown et al. (2009) found that female preference for song could be modified by acoustic mate copying; females preferred songs that had elicited vocal reactions from other females. In addition, Gros-Louis et al. (2003) found that female flock level reactions, such as rapid age segregation within the flock in response to song, may provide a basis for female evaluation of differences in male song quality. Therefore group level reactions to song could be used by females to learn when to attend to song, which is a first step in acquiring discriminative behavior.

*Male plasticity.* We have of course also looked carefully at male song development to explore plasticity. There was much to find: male cowbirds showed vocal and social learning in almost every context we used (King, West, & White 2002). In a critical set of studies we tested four groups of naïve juvenile males. Over two years we tested two cowbird populations, Indiana in one year and South Dakota in the other, comparing juvenile males housed with female cowbirds or canaries from 50 days of age to the beginning of their first breeding season at day 300 (Freeberg, King, & West 1995; West, King, & Freeberg 1996).

We then investigated the basic properties of social learning, species identification and mate choice, by individually removing female-housed or canary-housed males from their housing conditions and placing them in an indoor flight cage with an unfamiliar female cowbird and canary. The female-housed males approached and sang to the new female and ignored the canary but the canary-housed males surprised us by showing active and vigorous courtship of the canary. We then placed all the experimental birds in a large outdoor aviary with a new set of canaries and female cowbirds. Again, the canary-housed males pursued canaries and ignored female cowbirds even when the latter were solicitous. Thus, the aviary setting revealed that under more natural conditions any speculations about the existence of a safety net linking males to females were wrong. Thus, species and mate identification in cowbirds is not predetermined but is a product of dynamic social interactions during development that potentially can have many different outcomes. Cowbirds avoid such errors in nature because of the rich species-typical context surrounding them after they fledge that provides a protective education.

The aviary results for the males housed with female cowbirds were just as surprising. Although these males had approached and sung to females when in a flight cage during the transition from chamber to aviary, they paid little attention to them in the aviary setting, singing mostly to other males. The females also showed little interest in the males. Perhaps their songs were not arousing to the females, although we found that they elicited as many copulatory postures in playback tests

as wild local males. Maybe the females were simply not reproductively stimulated? We ruled this out by introducing some wild-caught adult males with breeding experience. Within 24 hours of their introduction to the flock, the females were showing typical responses to song and the introduced adult males showed typical courtship. The females also laid eggs. The female-housed males did have potent songs when tested by playback and thus the problem was not an inadequate song but inadequate social behavior. Thus, we faced the fact that it is song use that determines whether males succeed at courtship: having a potent song does no good if it is not performed appropriately.

These data threw the standard playback procedure into a different light. In the standard playback test, the experimenter, not the male cowbird, decides on which song to play back, when to play it, to whom and how often. These are all decisions that males must learn to make for themselves, i.e. the domain of song usage. At the same time female song preferences are being modified by the social interactions surrounding male singing behavior and female-female reactions to male behavior. Thus, complex social skills, such as male song performance and female song preference, are shaped by social interactions throughout development (West & King 1980; West, King, & Freeberg 1997).

## 5. Mechanism: The shaping of behavior

The canary- and female-housed cowbirds showed us that malleability is extreme in males. "Cowbird courts canary" became a mantra in the lab as we re-evaluated the nature of song development in light of pragmatic variables. What kept male communicative behavior on course was that non-vocal female social feedback could influence male song development. The finding was groundbreaking because at the time it was believed that vocal development in birds and humans was purely an imitative process with no possibility for visual feedback to play a role. To understand how visual feedback from non-singing females influenced male song development, we videotaped interactions between juvenile males and adult females in the spring (West & King 1988). What we saw in the videotapes is that males seek out and receive social gestures from the non-singing females: male use these gestures as feedback that shapes their song repertoire, keeping song elements that receive positive feedback, deleting those that do not. The feedback is immediate within 200 msec. of a male song and it is subtle, the flick of a wing (wing stroke) or mouth opening (gape), being among the most frequent responses. During a morning a typical male sings hundreds of songs to his female and the most common response is for the female to ignore him, that is, to show no response. Thus, when a female does react to a particular male song, the female behavior

has a very high signal to noise ratio. We also found that songs that received wing strokes in the spring were most likely to elicit copulatory postures when songs were played back to different females in the breeding season, so receiving a wing stroke was good news for a male.

Social shaping appears to be systemic to vocal development in cowbirds (King, West & Goldstein 2005). First, social reinforcement occurs throughout the stages of song ontogeny. For example, from as early as song production can be measured in early fall, there is evidence of female social influence on vocal production of even the most primitive vocal precursors of song (King & West 1988). Thus, when the birds are producing only the variable and inarticulate sounds termed subsong and plastic song, they are affected by social interaction with females. The non-vocal stimulation from females represents a source of learning but does not involve imitation. Imitation is considered the most prevalent form of song learning in passerines and humans, along with improvisation and invention (Kroodsma 1996). But cowbird males do not copy the behavior they see females produce, rather they learn to alter their song from the contingencies between their own vocal behavior and the female's gestural behavior. The pinpointing of a role for social interaction in vocal development identified a new mechanism of song learning, as previously only vocal stimulation was considered to be relevant. To extend this finding we investigated the social composition of flocks, which revealed that near neighbor relations are constructed out of sex- and age-restricted populations: young with young, male with male, etc (Smith, King & West 2002). This suggested to us that we had to look at life in the flocks to see what effects the sexes had on one another. Our first efforts involved learning more about song usage: when, where, who, and why song occurred (Gros-Louis, West & King 2010).

We had observed that males elicit the most non-vocal feedback by singing directed songs to females. Cowbirds song can be undirected, i.e. oriented toward no specific individual, or directed, i.e. physically pointed toward a particular male or female from less than a foot (~30cm away). Male cowbirds perform a bowing/wingspread display when they direct their songs and the intensity of the visual display varies greatly. In a series of investigations, we have found that the degree of use of female-directed song during the breeding season increases reproductive (copulatory) success, and correlates with high song potency and neural changes in the brain, specifically in the anterior song pathway and the visual thalamic nucleus (Freeberg, West, King, Duncan & Sengelaub 2002; Hamilton, King, Sengelaub, & West 1998). Bioassay experiments looking at the bioacoustics of cowbird song show that the quality of note clusters (which could be seen as analogous to human phonemes) in the first phrase degrades rapidly in the atmosphere, making distances between signaler and responder critical (King, West, Eastzer, & Staddon 1981). Therefore, visual stimulation is an integral part of a directed song in cowbirds.

## 6. The creation of new behavior: Neophenogenesis

The combined practice of looking at the nature of cowbird's song, its developmental history, and the mechanism of song shaping comprises the fourth perspective, the use of neophenogenesis as a model for evolution and development of song. In our case, it supplies a way to integrate diverse findings into a theoretical framework. Used by Kuo (1967), and later by Johnston and Gottlieb (1990), neophenogenesis refers to the creation of novel behaviors that are within a species norm of reaction but rarely occur in the typical environment. Kuo carried out studies, for example, where he raised cats with rats who developed a strong affiliative bond for one another. Neophenotypes are now created all the time by genetic engineering to understand the function of genes. Genetic engineering can produce neophenotypes by turning on or off specific genes. Behavioral engineering can also create experiential knock-ins or knock-outs. An example is hormonal work in dark eyed juncos where males are given long term doses of testosterone and then are observed throughout a breeding season (Ketterson & Nolan 1994). These extraT males show increased offspring production but higher mortality. Thus, there are trade-offs in increasing T. In cowbirds, instead of injecting a resource like a hormone, we either add or subtract a resource, for example, removing all adult males from a flock (White, King, & West 2002).

The neophenotypes we in fact know the most about are juvenile males housed without adult males. Consider the example of the juvenile male cowbirds housed only with females. These juveniles, given conspecific experience in sound-attenuating chambers with adult females, developed poor social skills. In these and other longitudinal studies, we discovered a glaring disconnect between capacity and performance. The male cowbirds with potent songs, as measured by playback, apparently did not know how to use their songs when placed in the functional context of mate competition, even when the only competition was other young males like themselves. The males' incompetence was especially surprising because their interactions with females had initially appeared to have beneficial effects. The female-housed males' rate of vocalizing correlated with faster progress through the stages of song development and resulted in the production of crystallized song highly effective at eliciting copulatory responses when recorded and played back to new female cowbirds (Freeberg, King, & West 1995). However it seemed that exposure to males was necessary in order to learn the appropriate use of the song, such as maintaining a proper distance when singing to another individual. The idea that cowbirds had to learn so basic a skill as managing proximity and attending to a conspecific was surprising. On the face of our findings, it would seem that the parasitic cowbird is dependent on social learning for the acquisition of species critical skills. Thus, the neophenotypes revealed different aspects of learning that need to merge for development to follow an adaptive pathway.

All of our developmental studies led us to believe that we did not need any more testament to malleability in cowbirds; rather, we needed evidence of how cowbirds naturally put a system together, now we had to see how it became whole. This need was increasing, because the more we learned about cowbirds, the more fragmented the birds' knowledge seemed to be; that is, they seemed to have the capacity to learn both appropriate and inappropriate behaviors but were not endowed with any big picture. The most striking data came from the juvenile male cowbirds who learned to court canaries. How could mate recognition be so fragile? These birds had been wild-caught with other cowbirds; they "knew" their species. Furthermore, how could mate recognition be so unstable in a brood parasite? To begin to understand mate recognition, we needed to study the role of the social ecology to organize the diverse developmental pathways by looking at neophenotypes. The first important step in that direction was taken by Freeberg (1996), who studied the effects of social ecology on the ontogeny of mate choice. Freeberg's interest was cultural transmission of courtship skills in cowbirds: Could young birds be "taught" through exposure to an unfamiliar population of cowbirds to alter mating preferences? Furthermore, would these birds pass on any acquired preferences to a new generation (Freeberg 1998; West, King, & Freeberg 1997)?

Freeberg conducted a series of experiments that uncovered how social interactions shape the observed geographic variations in cowbird behavioral patterns. All of the birds lived in large aviaries where they could interact with other juvenile birds from the original population; adults in the aviaries were, however, from one of the two experimental populations. The first experimental adult population was composed of birds from the same geographic area as the juveniles; the other population was from 1,500 km away. The young birds, male and female novices, were randomly assigned to these conditions after having been wild caught with other cowbirds from their natal area. Thus, there was no targeted "tutor"; all of the adults were potential models, and from the young birds' point of view, their juvenile peers were also sources of instruction. The juvenile cowbirds in both experimental conditions acquired the songs and preferences of the adults with whom they were housed. Thus, the experimental adult cultures were transmitted, meaning the experiential neophenotypes "lost" their natal preference and preferred to mate with unfamiliar individuals who had been housed with adults from the same population. The cultural effects included mate preferences and the contents of songs. To obtain the outcome, the juvenile female cowbirds had to modify natal song preferences along with the young males' changes in song production. Thus, these data were also the earliest demonstration that female cowbirds could learn their mating preferences. Taken as a whole these findings show how easily new phenotypes can be created which can result in different reproductive outcomes. The phenotypes' influence could also be seen in the next generation when they served as models

for new groups of young birds who copied their behavior. Neophenogenesis thus affects mate recognition at the species, subspecies and population levels.

## 7. Group level effects create learning opportunities

Freeberg's cultural neo-phenotypes further revealed cowbirds' dependence on social and vocal learning (the young males copied the songs of the adult males even from the distant population). But they did not tell us what kinds of social experiences led to the development of neophenotypic preferences. What did birds do with one another in flocks to form and stabilize directional preferences? We began to answer this question by looking at what we called the "ad-lib" aviary, a collection of 74 cowbirds, adult males and females and juvenile males and females all from the same Indiana population (Smith, King, & West 2002). We quantified their affiliations by measuring near neighbor contacts, as well as approaches and departures from a social interaction. We also reasoned that spatial proximity afforded access to social information from conspecifics and promoted opportunities to engage in interaction (Coussi-Korbel & Frigaszy 1995; Frigaszy, Vitale & Ritchie 1994; Freeberg 1999). Near-neighbor measures have been used in this manner in birds, ungulates, and primates (Holekamp, Cooper, Katona, Berry, Frank & Smale 1997; Wynne-Edwards 1962). Although it does not necessarily follow that an individual interacts with all birds that are near neighbors, the nature of these associations provide a social overview of flock dynamics. The overarching question was could we use the ad-lib design to uncover distinct subgroups within the overall flock that could produce phenotypic variation? Could we demonstrate that the same general environment was composed of different proximate contexts for different individuals? By allowing free movement throughout a large outdoor aviary, we hoped to achieve a semi-natural approximation of self-organization.

The outdoor aviary was approximately the length of a football field and individuals could choose to aggregate in one area or move far enough away so as to be out of visual and acoustic contact from other birds. The physical dimensions of the aviary thus allowed self selected social groups to form. The difference between living in an aviary with many other individuals and living in a small enclosure with one or two birds had many consequences, but one of particular interest was the bioacoustic implication for the male cowbird's song, as it is critical to female assessment of mates. The female-salient elements of male cowbird song degrade rapidly at distances beyond a third of a meter (King, West, Eastzer, & Staddon 1981) Males living in a 1-m<sup>3</sup> chamber were unable to sing without having a clear rendition of their song available to their social companions, and their companions had no way to leave the area of singing. But even in such controlled

circumstances, proximity mattered: males with females that permitted males to sing at close distances developed more effective songs than males housed with females who moved away from song overtures (Smith, King, & West 2000). In the larger aviary, the females had even more social options, raising the question of whether females would associate closely enough with the juvenile males to hear the female-salient elements of the song. The bioacoustics of the ad-lib aviary had implications for interactions with other males as well. In a previous study during the breeding season, we found that adult males attacked socially naïve adults when placed with them for periods as short as 4 hours. The naïve males sang songs especially stimulating to females but had not also established dominance relations with other males (West & King 1980). Juvenile males may need to separate themselves from adult males while practising song to avoid stimulating aggressive responses.

All of these considerations converge on the role of social proximity. In addition to near-neighbor assessments, we also recorded singing behavior of adult and juvenile males over the year and measured their courtship success at the end of the experiment. We focused specifically on juvenile males, in light of our past work suggesting they had much to learn to become socially competent. Given a broad range of possible companions and given the ability to separate spatially, would juveniles select discrete social ecologies?

After daily observations in the outdoor aviary, we found non-random patterns of association emerging in the group of freely assorting birds. Cowbirds accumulated the most near-neighbor points per bird with others of their own age and sex, next most with birds of the same sex but different age, less with those of different sex but same age, and least with birds of the opposite age and sex class. This result was not surprising, but the rapidity with which the organization appeared and its general stability were noteworthy. Within six days of introduction to the aviary complex, we saw the pattern of birds differentially associating with one another at statistically significant levels (Smith, King, & West 2002). Regardless of how we divided the data, by season, by time of day, by number of days, or by observer, the result was the same.

But for all classes, there was cross-assortment, just at a lower frequency. It thus appeared the birds operated from the relatively secure similar base of age by sex groups, while making occasional excursions into groups of different age by sex classes. For example, with respect to the secondary groupings in the fall, adult males assorted less with juvenile males than did adult females with juvenile females. In winter, adult males associated more with juvenile males than they had earlier. Most striking, in fall and winter, adult females associated relatively often with juvenile males. Smith et al. (2002) also found that beyond the level of near neighbors, there were also different groups of singing neighbors. And it was in

these singing contexts that the most contact occurred between juvenile males and adult females.

Did these over-wintering patterns predict developmental outcome? We followed the flock into the spring to test the courtship success of juvenile males when they were competing against other juveniles. Courtship success of juvenile males was correlated with individual differences in association with adult males over the year. Juvenile males that associated more with adult males developed consortships with females faster than males with lower adult association scores. The singing rate of juvenile males was also affected by choice of social partners. Juvenile males that associated most with adult females sang less over the year, perhaps because the feedback they received also advanced the rate of transition through song stages. Juvenile males who associated with adult females also developed more original songs a finding we have since replicated (Miller, King, & West 2008). Thus, the data show that self-selected assortment during the winter affects communicative development, variation in phenotypic outcomes, and courtship success.

The results of the ad-lib aviary experiment revealed to us that the new housing paradigm of self-selection had potential to parse complex social interactions into functionally effective units of cultural transmission. In this ecologically relevant environment, we could investigate social behavior systematically and begin to understand the role of emergent properties of a group to shape phenotypes. Our approach to answering these questions is to consider the flock as a social network.

## **8. Relating social organization to developmental outcome: The role of the social network**

Recent interest in applying social network analysis to animal behavior studies has provided researchers with the tools for understanding the interaction between individual and group level effects. Social network analysis investigates how relations between individuals influence: (1) the construction of flock organization and (2) how flock organization channels the flow of information. Here individual behaviors may foster consistent responses from neighbors that lead to predictable patterns of social organization. Here we show how social network analysis provides a series of definitions and techniques for describing the relationship between social interaction, group structure, and developmental outcomes.

Miller et al. (2008) demonstrated that the non-singing female cowbird could shape male song development in large flocks, thus validating the previous wing stroke studies which were conducted in chambers or small cages. The cowbirds

were placed into four flocks: two with adult females and juvenile males (AJ) and two with juvenile females and juvenile males (JJ). Throughout the fall, the AJ males sang more variable song than the JJ males but at the same time, the juvenile females interacted apparently indiscriminately and at a higher rate than did adult females who were more selective in their interactions. To characterize these different patterns of sociality, network statistics were used. Both juvenile and adult females differed with respect to two social network measures of centrality, betweenness and closeness. These social network measures in turn corresponded to differences in developmental trajectory of song of the males with whom females interacted.

The centrality concept enlists a set of measures that seek to identify individual involvement within the network (Wasserman & Faust 1994). Betweenness centrality has been important in identifying potential information bottlenecks, or when information in a network is channeled through specific individuals. Individuals with high betweenness centrality are in-between interactions of many individuals and therefore serve as information "gatekeepers". In our study we demonstrated that adult females exhibited higher levels of betweenness centrality than juvenile females. This suggests that adult females positioned themselves in the network to be gatekeepers and selectively interacted with others. Closeness centrality focuses on how quickly an individual can interact with or influence all other individuals in the group. An individual is said to be close to another based on how quickly it can interact with all other individuals in the network. Individuals with high closeness centrality may therefore be less selective in their interactions and tend to interact with more individuals. Juvenile females exhibited higher levels of closeness centrality suggesting that they were more interactive, and less selective in their interactions with others in comparison to adult females.

Adult females are more selective with whom they interact in comparison to juvenile females. These different patterns of interactions may in turn shape the developmental trajectory of male song. Previous studies have demonstrated that adults selectively wing stroke in response to particular male vocalizations. Here juvenile females, who did not interact as selectively as adult females (low betweenness) and interacted with more individuals (high closeness), did not seem to be providing the type of social feedback necessary to foster vocal exploration. Therefore juvenile females may have simply overloaded the males with contingent response to song, and subsequently diminished the males' motivation to explore their own vocal capacity. Adult females probably responded selectively to certain songs and thus provided motivation for the juvenile males to explore their own vocal repertoires in order to garner responses from adults. This finding also supports the view that young females must learn how to interact with males in order to influence their song development.

Our current research investigates how social network metrics can be used to uncover the functional role of specific behaviors that influence social structure. Our analysis found a relationship between individual centrality measures and the occurrence of head-down displays (Kohn, unpublished data). Head-downs occur when one cowbird approaches another with the head angled down so that the beak is facing towards that individual's breast, if not touching it, while nape feathers are erect and the body is in a low crouched position. Despite its conspicuous nature, the function of the head-down behavior has eluded explanation. Head down displays have been documented in most other cowbird species (Ortega 1998) and among Icterine species, such as the Red-Wing Blackbird, where it is called nodding (Nero 1963; Rothstein 1980). Numerous studies report it to be linked to aggression (Rothstein 1980; Selander & LaRue 1961), preening, affiliation (Miller, King, & West 2008), dominance, or have no purpose (Scott & Grumstrup-Scott 1983). Our analysis showed that there is a significant correlation between closeness and the amount of head-downs that an individual initiates; however, there is no significant correlation between closeness and the number of head-downs received. The lack of correlation between individuals receiving head-downs and closeness suggests that the individuals who tend to initiate head-down displays may be less selective in their interactions with others. Also preliminary results suggest that these "high head downers", or individuals who initiated more head down displays, participate in more countersinging and enjoy a higher reproductive success rate as measured in the number of eggs laid. Taken together, these findings suggest that the function of the head down display might be to facilitate cohesiveness and affiliation within the flock with potential reproductive consequences. Head down displays may be a way with which individuals assess their relationship with others through drastically decreasing proximity (sometimes even touching the other individuals) and observing contingent responses. By decreasing proximity, individuals create more opportunities for receiving social stimulation and accessing social cues. Previous data has suggested that head-down displays are performed at a very early age, sometimes as soon as 40 days after hatching (Miller, Freed-Brown, White, King, & West 2006). Therefore head-downs may shape the development of social behavior by allowing individuals to garner more feedback from others in response to their advances.

Investigations of social activity aid our understanding of sociality because it increases the transparency of social dynamics. The social network perspectives are useful because they can operationally define what is meant by social interaction. Traditional statistics do not evaluate the intercalation of male and/or female behaviors during the everyday encounters that constitute the social nature of a group. In the broadest terms, analyses such as those shown here describe the "experience" of experience, a fundamental attribute of an animal's developmental ecology.

## 9. Conclusion: Culture and the discovery process

It seems counterintuitive that the cowbird, a brood parasite, is obliged to learn so much from others in order to navigate successfully the social relationships within a flock. Nonetheless, probabilistic recurrent social interactions provide the essential information that individual cowbirds utilize to develop functional behaviors. The dependency of cowbird development upon the social environment in many ways parallels how people conceptualize human culture. Our cowbird studies provide a rich example of a cultural phenomenon in birds from a developmental perspective. The semi-naturalistic aviary complex afforded us with the ability to investigate the direct social contribution to the development of behavior while letting the birds construct and maintain their interactions. Cowbirds exhibit population-level variability in social behavior (Freeberg & White 2006).

For many, a vital aspect of culture is that patterns of behavior are representative of the group. These population-level behavioral differences can be lost or recreated within individuals by controlling the composition of flocks during development. Therefore, both group and species typical behaviors in cowbirds are contingent upon social interactions for their proper development, and in a sense represent a rudimentary form of culture. Recurrent social interactions channel information to developing individuals, allowing them to reconstruct group specific behavioral patterns. The contingent social responses experienced during interactions provide the necessary information individuals can utilize to guide the development of their own behavior. Culture therefore, is the developmental process of becoming inculturated, or reconstructing specific behavioral patterns through social learning. Thus, behavior is not strictly inherited, or even transmitted, but reconstructed within each individual by utilizing information provided by interactions with conspecifics. The structure of the flock permits or restricts access to these social cues by altering the transfer of information. Social organization can thus act as a highly flexible learning-based developmental mechanism.

When scientists want to know how something works, they take it apart. But how does one break a social structure into smaller units while retaining the dynamic and magnetic characteristics of those units? How do we carve nature at its joints? One way to guide uncovering a natural taxonomy is to observe behavior at different levels of analysis and in varied ecological contexts. One has to accept a priori that behavior always occurs in a context: thus, it is dangerous to talk of enriched/deprived environments as the new conditions may make other environmental attributes more or less visible. Too often studies using developmental variations measure only outcome, not the discovery process of developing in neophenotypic surroundings. But culturally transmitted behaviors can alter the focus of the discovery process and so it seems necessary to us to understand

the development of a behavior in order to understand its function. Thus, the transmission of behaviors can be specific to a thing (a song) or influence the discovery process itself and result in creating variation in developmental trajectories (West, King, & White 2003; White et al. 2007). Such variation brings to mind the concept of developmental reaction norms as defined by Schlichting and Pigliucci (1998) as “the complete set of multivariate ontogenetic trajectories that can be produced by a single genotype exposed to all biologically relevant environments” (p. 22). The cowbird developmental story shows a reliance on culturally transmitted behavior for basic species-critical skills by allowing for a dynamic learning-based developmental system apparently operating through adulthood. The risks of mislearning are outweighed by the benefits of transgenerational accumulated knowledge to species survival... a system not unlike our own.

## Acknowledgements

We thank the National Science Foundation and Indiana University for many years of support. We also thank Irene Pepperberg and two reviewers who provided helpful comments.

## Note

1. Many birds have the capacity to use the two parts of their syrinx independently, one in each bronchus, to produce two different sounds at the same time: each is often called a voice.

## References

- Catchpole, C.K., & Slater, P.J.B. (1995). *Bird song: biological themes and variations*. Cambridge: Cambridge University Press.
- Coussi-Korbel, S., & Fragaszy, D.M. (1995). On the relations between social dynamics and social learning. *Animal Behavior*, 50, 1441–1453.
- de Waal, F.B.M., & Tyack, P.L. (2002). *Animal social complexity: Intelligence, culture and individualized societies*. Cambridge, MA: Harvard Press.
- Dufty, A.M., Jr. (1985). Song sharing in the brown-headed cowbird (*Molothrus ater*). *Ethology*, 69, 177–190.
- Eastzer, D.H., (1988). Geographic variation in cowbird song. University of North Carolina, Chaper Hill, NC.
- Flack, J.C., Girvan, M., de Waal, F.B.M., & Krakauer, D.C (2006). Policing stabilizes construction of social niches in primates. *Nature*, 439, 426–429.
- Fragaszy, D.M., & Perry, S., (2003). The biology of traditions. In D.M. Fragaszy & S. Perry (Eds.), *The biology of traditions: models and evidence* (pp. 1–23). London: Cambridge University Press.
- Fragaszy, D.M., Vitale, A.F., & Ritchie, B., (1994). Variation among juvenile capucins in social influences on exploration. *American Journal of Primatology*, 32, 249–260.

- Freeberg, T.M., (1996). Assortative mating in captive cowbirds is predicted by social experience. *Animal Behavior*, 52, 1129–1142.
- Freeberg, T.M., (1998). The cultural transmission of courtship patterns in cowbirds, *Molothrus ater*. *Animal Behavior*, 56, 1063–1073.
- Freeberg, T.M., (1999). Spatial associations provide a context for social learning of courtship pattern of brown-headed cowbirds, *Molothrus ater*. *Journal of Comparative Psychology*, 113, 327–332.
- 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.
- Freeberg, T.M., West, M.J., King, A.P., Duncan, S.D., & Sengelaub, D.R. (2002). Cultures, genes and neurons in the development of song and singing in brown-headed cowbirds (*Molothrus ater*). *Journal of Comparative Physiology A*, 188, 993–1002.
- Freeberg, T.M., & White, D.J. (2006). Social traditions and the maintenance and loss of geographic variation in mating patterns of brown-headed cowbirds. *International Journal of Comparative Psychology*, 19, 206–222.
- Freed-Brown, G., & White, D.J. (2009). Acoustic mate copying: female cowbirds attend to other females' vocalizations to modify their song preferences. *Proceedings of the Royal Society B*, 276, 3319–3325.
- Gibson, J.J. (1966). *The senses considered as perceptual systems*. Boston: Houghton-Mifflin.
- Greenewalt, C. (1968). *Bird song: acoustics and physiology*. Washington, D. C.: Smithsonian Institution Press.
- Gros-Louis, J., White, D.J., King, A.P., & West, M.J. (2003). Female brown-headed cowbirds' (*Molothrus ater*) social assortment changes in response to male song: A potential source of public information. *Behavioral Ecology and Sociobiology*, 56, 163–173.
- Gros-Louis, J.M., West, M.J., & King, A.P. (2010). Comparative perspectives on the missing link: communicative pragmatics. In M.S. Blumberg, J.H. Freeman & S. R. Robinson (Eds.), *The Oxford handbook of developmental and comparative neuroscience* (pp. 684–707). Oxford: Oxford University Press.
- Hamilton, K.S., King, A.P., Sengelaub, D.R., & West, M.J. (1998). Visual and song nuclei correlated with courtship skills in brown-headed cowbirds. *Animal Behavior*, 56, 973–982.
- Holekamp, K., Cooper, S.E., Katona, C.I., Berry, N.A., Frank, L.G., & Smale, L. (1997). Patterns of association among female spotted hyenas (*Crocuta crocuta*). *Journal of Mammalogy*, 78, 55–64.
- Holland, W., & Leinhardt, S. (1970). A method for detecting structure in sociometric data. *American Journal of Sociology*, 70, 492–513.
- Janik, V.M., & Laland, K.N. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, 21(10), 542–547.
- Johnston, T.D., & Gottlieb, G. (1990). Neophenogenesis: A developmental theory of phenotypic evolution. *Journal of Theoretical Biology*, 147, 471–495.
- Ketterson, E.D., & Nolan, V. (1994). Hormones and life histories: An integrative approach. In L.A. Real (Ed.), *Behavioral mechanisms on evolutionary ecology* (pp. 327–353.). Chicago: University of Chicago Press.
- 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. (1988). Searching for the functional origins of cowbird song in eastern brown-headed cowbirds (*Molothrus ater ater*). *Animal Behavior*, 36, 1575–1588.
- 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, MA: Sinauer.

- King, A.P., West, M.J., & Eastzer, D.H. (1980). Song structure and song development as potential contributors to reproductive isolation in cowbirds. *Journal of Comparative and Physiological Psychology*, *94*, 1028–1039.
- King, A.P., West, M.J., Eastzer, D.H., & Staddon, J.E.R. (1981). An experimental investigation of the bioacoustics of cowbird song. *Behavioral Ecology and Sociobiology*, *9*, 211–217.
- King, A.P., West, M.J., & Goldstein, M. (2005). Nonvocal shaping of avian song development: Parallels to human speech development. *Ethology*, *111*, 101–117.
- King, A.P., West, M.J., & White, D.J. (2002). The presumption of sociality: Social learning in diverse contexts in brown-headed cowbirds (*Molothrus ater*). *Journal of Comparative Psychology*, *116*, 173–188.
- King, A.P., West, M.J., & White, D.J. (2003). Female cowbird song perception: evidence for plasticity of preference. *Ethology*, *109*, 865–877.
- Kroodsma, D.E. (1996). Ecology of passerine song development. In D.E. Kroodsma & E. H. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 3–19). Ithaca, NY: Cornell University Press.
- Kuo, Z.Y. (1967). *The dynamics of behavioral development: An epigenetic view*. New York: Random House.
- Lehrman, D.S. (1974). Can psychiatrists use ethology? In N.F. White (Ed.), *Ethology and psychiatry* (pp. 187–196). Toronto: University of Toronto Press.
- Lipton, J. (1968). *An exaltation of larks*. New York: Viking.
- Mayr, E. (1974). Behavior programs and evolutionary strategies. *American Scientist*, *62*, 650–659.
- McGregor, P.K., & Peake, T.M. (2000). Communication networks: social environments for receiving and signaling behavior. *Acta Ethology*, *2*, 71–81.
- 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.
- Miller, J.L., King, A.P., & West, M.J. (2008). Female social networks influence male vocal development in brown-headed cowbirds (*Molothrus ater*). *Animal Behavior*, *76*, 931–941.
- Nero, R.W. (1963). Comparative behavior of the Yellow-Headed Blackbird, Red-Winged Blackbird, and Other Icterids. *The Wilson Bulletin*, *75*, 376–413.
- Ortega, C.P. (1998). Cowbirds and other brood parasites. Tucson: University of Arizona.
- Peake, T.M., Terry, A.M.R., McGregor, P.K., & Dabelsteen, T. (2001). Male great tits eavesdrop on simulated male-to-male vocal interactions. *Proceedings of the Royal Society of London, Series B*, *268*, 1183–1187.
- Rothstein, S.I. (1980). The preening invitation or head-down display of parasitic cowbirds. II. Experimental analysis and evidence for behavioral mimicry. *Behavior*, *75*, 148–184.
- Schlichting, C., & Pigliucci, M. (1998). Phenotypic evolution: a reaction norm view. Sunderland, MA: Sinauer.
- Scott, D.M., & Ankney, C.D. (1983). The laying cycle of Brown-headed Cowbirds; passerine chickens? *Auk*, *100*, 583–592.
- Scott, T.W., & Grumstrup-Scott, J.M. (1983). Why do Brown-Headed Cowbirds perform the head-down display? *Auk*, *100*, 139–148.
- Selander, R.K., & LaRue, C.J. (1961). Interspecific preening invitation display of parasitic cowbirds. *Auk*, *78*, 473–504.
- Sih, A., Hanser, S.F., & McHugh, K.A. (2009). Social network theory: new insights and issues for behavioral ecologists. *Behavioral Ecology and Sociobiology*, *63*, 975–988.

- Smith, V.A., King, A.P., & West, M.J. (2000). A role of her own: female cowbirds, *Molothrus ater*, influence the development and outcome of song learning. *Animal Behavior*, *60*, 599–609.
- Smith, V.A., King, A.P., & West, M.J. (2002). The context of social learning in brown headed cowbirds: Association patterns in a captive flock. *Animal Behavior*, *63*, 23–35.
- Snowdon, C.T., & Hausberger, M. (Eds.). (1997). *Social influences on vocal development*. Cambridge, UK: Cambridge University Press.
- Wasserman, S., & Faust, K. (1994). *Social network analysis*. Cambridge: Cambridge University Press.
- West, M.J., & King, A.P. (1980). Enriching cowbird song by social deprivation. *Journal of Comparative and Physiological Psychology*, *94*, 263–270.
- West, M.J., & King, A.P. (1985). Social guidance of vocal learning by female cowbirds: Validating its functional significance. *Ethology*, *70*, 225–235.
- West, M.J., & King, A.P. (1988). Female visual displays affect the development of male song in the cowbird. *Nature*, *334*, 244–246.
- West, M.J., King, A.P., & Eastzer, D.H. (1981a). The cowbird: Reflections on development from an unlikely source. *American Scientist*, *69*, 57–66.
- West, M.J., King, A.P., & Eastzer, D.H. (1981b). Validating the female bioassay of cowbird song: Relating differences in song potency to mating success. *Animal Behavior*, *29*, 490–501.
- 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., & Freeberg, T.M. (1996). Social malleability in cowbirds: New measures reveal new evidence of plasticity in the Eastern subspecies (*Molothrus ater ater*). *Journal of Comparative Psychology*, *110*, 15–26.
- West, M.J., King, A.P., & Freeberg, T.M. (1997). Building a social agenda for birdsong. In C.T. Snowdon & M. Hausberger (Eds.), *Social influences on vocal development* (pp. 41–56). Cambridge: Cambridge University Press.
- West, M.J., King, A.P., & White, D.J. (2003). The case for developmental ecology. *Animal Behavior*, *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.
- 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*, 113–122.
- 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.
- White, D.J., King, A.P., West, M.J., Gros-Louis, J., & Tuttle, E.M. (in press). Effects of singing on copulation success and egg production in brown-headed cowbirds, *Molothrus ater*. *Behavioral Ecology*.
- Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Tutin, C.E.G., et al. (1999). Culture in chimpanzees. *Nature*, *389*, 682–685.
- Wynne-Edwards, V.C. (1962). *Animal dispersion in relation to social behavior*. Edinburgh: Oliver and Boyd.
- Yokel, D.A., & Rothstein, S.I. (1991). The basis for female choice in an avian brood parasite. *Behavioral Ecology and Sociobiology*, *29*, 39–45.

*Authors' addresses*

Meredith West  
Department of Psychological and  
Brain Sciences  
Indiana University  
1101 E.10th St.  
Bloomington IN 47405  
USA

email: mewest@indiana.edu

Andrew King  
Department of Psychological  
and Brain Sciences  
Indiana University  
1101 E.10th St.  
Bloomington IN 47405  
USA

email: apking@indiana.edu

Gregory Kohn  
Department of Psychological and  
Brain Sciences  
Indiana University  
1101 E.10th St.  
Bloomington IN 47405  
USA

email: gmkohn@umail.iu.edu

*Authors' biography*

**Meredith West** received her B.S. degree at Tufts University, majoring in psychology and Russian. She received her Ph.D. in psychology from Cornell University. From Cornell, she went to the University of North Carolina at Chapel Hill and from there to Indiana University where she is Chancellor's Professor of Psychology and Biology. She has served as executive editor of *Animal Behaviour* and editor of the *Journal of Comparative Psychology*. Her research efforts have included play and exploratory behavior in domestic kittens, sharing in infant toddlers, prelinguistic behavior in infants, and song and social development in cowbirds.

**Andrew King** received his Bachelor's degree from Franklin and Marshall College. He received his Ph.D. in psychology from Cornell University. From there he moved to a lecturer's position at Duke University, followed by a senior scientist appointment at Indiana University. His research interests include communicative development, bioacoustics, and social network methodology.

**Gregory Kohn** received his Bachelor's degree at the University of Montana in Zoology and Ecology. He then went on to receive a Master's Degree in Behavioral Neuroscience at Utrecht University under supervision of Dr. Simon Reader, researching directed social learning in fish. He is currently pursuing his Ph.D. at Indiana University under supervision of Dr. Meredith West and Dr. Andrew King, investigating the development and function of social signals in Brown-Headed Cowbirds. His main research interests are the ontogeny of social behavior, social learning and evolutionary consequences of developmental plasticity.