

Discovering culture in birds: The role of learning and development

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There are 9000 species of birds in the world; this is a report on two of them, cowbirds (*Molothrus ater*) and starlings (*Sturnus vulgaris*) Bird, 1999). We note the discrepancy in numbers to put into perspective the task of characterizing culture and social learning in ‘birds’ as a group. But as daunting as the task might sound, the diversity of behaviors and ecologies in birds offers a window on social learning, culture, and evolution that is hard to match. Bird species afford diverse opportunities for comparative analysis at the level of peas in a pod; a taxonomic point at which natural and sexual selection operate (King & West, 1990).

Our interest in cultural processes in birds grew out of an interest in birds’ songs: how songs develop and how they are used. Vocal learning and the transmission of song information across generations have been documented in many species (Freeberg, 2000; Kroodsma & Miller, 1996). Song is used in territorial defense and in the attraction of mates. Moreover, there is no question that birds make use of social and auditory learning to craft their repertoires. It is the nature of the crafting process that appeals to us, especially the need for social interactions to build an inventory of vocalizations and behaviors important for reproductive success.

In our minds, culture is a verb; it is the “growing of biological material in a nutrient substance” (Merriman’s Dictionary, 1993). The “material” is the organism along with its behaviors-to-be and the “nutrient substance” is the organism’s developmental ecology. The cultural transmission of behaviors across generations is therefore the emergent product of an active organism and the nutrient substance. Such a metaphor may seem innocuous, but at its core is an assumption we believe is fundamental to theories of

culture or social learning. In the laboratory analogue, we assume different properties of the biological material/organism and of the medium/nutrients in which it is grown. Scientists focus most on changes in the former, not the latter. But what if the material affects the medium, the presumed passive source of growth? In a completely fictional example, what if bacteria being cultured produced heat that then affected the chemical properties of the medium, which then affected the nutrient value of the medium? Thus, the nature of the outcome is neither “in” the organism nor “in” the medium but in the synergy between the two. How could we know this to be the case? We would have to begin by measuring the medium before, during and after the experiment just as we would the properties of the organism.

Scientists of social behavior generally accept the fact of synergy as a given, but that does not make it easier to study (Cairns, 1979). In this chapter, we are concerned with social dynamics and understanding culture in animals. By culture, we mean the social transmission of specific behaviors from one generation to another within a species. The study of culture in animals is a growing field, with much effort directed toward documenting the comparative existence of and behavioral transmission of cultural information by mechanisms such as imitation and teaching (Whiten et al., 1999). While these mechanisms are important, we are most interested in the processes responsible for the emergence of cultural information, i.e., how do young learners come to detect and choose to adopt traditional behaviors? Said another way, what processes lead to selectivity in the specificity of imitation or the learning the informational properties of peers or adults?

Our studies of only two avian species lead us to believe that “cultural information” is not simply there in an environment to be copied or observed, but that it becomes available only by virtue of social interactions by which the needed information emerges. In other words, cultural information, e.g., a certain song variant or a certain way of eating, is not bio-available in all social ecologies because the information is neither in the animal nor the environment. Thus, to study culture, one must first study the social discovery processes by which organisms make the needed information accessible in a dynamic environment. As will be seen, such an approach requires study of many more aspects of the organism’s behavior than the trait of interest, i.e. bird song. One must learn how animals negotiate their everyday social world to uncover and learn the meaning of specific behaviors.

Our plan in this chapter is to describe this social discovery process in cowbirds and starlings with reference to song learning including 1) the acoustic nature of the songs, 2) the function of songs, and 3) nature of the behaviors used by the birds to elicit information from their surroundings. We follow with some thoughts about the role of imitation and culture, whether song is a sufficiently self-contained behavior to support cultural arguments, and whether culture of the whole organism can be studied.

The two species we discuss are ones not often associated with culture, but crime. Cowbirds are disliked because they are brood parasites, laying their eggs in the nests of over 200 different species and subspecies in North America (Friedmann, Kiff, & Rothstein, 1977). This habit elicits quite uncharacteristic attributions from usually staid writers of field guides: “the cowbird is an acknowledged villain, and has no standing in the bird world...No self-respecting American bird should be found in his company”

(Chapman, 1934, p. 359). European starlings earned a nasty reputation after being imported to North America, where their numbers swelled from 200 to 200,000,000 in less than a century. According to Chapman (1934), the species "...is a distinctly foreign element in our bird-life, and seems out of place among the species with which we share the bond of birthplace in common (p. 355). Once in America, starlings had to carve out a niche and carve they did, finding nesting and roosting sites in nooks and crannies in cities and countryside. To them, a parking garage is the concrete equivalent of evenly spaced trees and perching posts. Starlings are now found in every state and province in North America.

Another way to look at these species is that they are extremely successful. Some have attributed that success to their adaptability with respect to food habits as both are omnivores and both show considerable local variation in mating systems. But, our focus is on their social flexibility and how it intersects with the transmission of vocal traditions. In ontogenetic terms, the species represent opposite developmental endpoints, with cowbirds expected to have closed systems for species and mate recognition as they are not raised by conspecifics and with starlings expected to be exemplars of open systems as they show life long vocal learning. But, as we hope to show, when it comes to discovering and attending to the social affordances of their environments, these two gregarious species have much in common.

The cowbird: Vocal athlete at work

The song of the cowbird is a bubbly mixture of notes followed by a modulated whistle, from 300 to 13,000 kHz. Crawford Greenewalt, who produced much of the definitive work on how birds sing, pronounced, "This undistinguished bird... is the

undisputed winner in the decathlon of avian vocalizations.” (1968, p. 119). Among the cowbird’s achievements is use of a wider frequency margin, 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 of a full two octaves; a first introductory note with the most rapid glissando, 5-8 kHz in 4 msec.; 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 (p 120).

Greenewalt captures the vocal challenges for the young cowbird. He also alludes to a social dimension, female cowbirds. We have explored these vocal challenges using many approaches from aviary studies of mating success to acoustic playback of song segments to female cowbirds. Here we will focus on three studies chosen to illustrate the proximate or social dynamics of song learning. First, we give an example of a female cowbird’s potential influence on males during song ontogeny. We follow that with an example of young males learning to sing when exposed to different contexts. Finally, we show how those learning processes play out in richer social contexts.

Female nourishment of song

Some years ago, we studied a cowbird flock over wintering in North Carolina. During the time of year when juveniles’ songs develop most rapidly, i.e. late winter and early spring, we found that juvenile males affiliated with females in small groups of half a dozen birds or so (King & West, 1988). These observations were of great interest because we had accumulated several lines of evidence implicating female cowbirds in the development of song. Her role did not seem to be one of simply providing motivation for males to sing, but rather the role appeared to be one of motivating a male to change what

he was singing (King & West, 1983a; West & King, 1985). How females could do this was puzzling as they themselves do not sing.

We had uncovered her role while, in fact, trying to change her preferences for song (in a perfect example of the effects of synergy discussed earlier). Female cowbirds, when tested by acoustic playback, show reliable preferences for natal song as measured by frequency of copulatory responses given within one second of the song's onset. We attempted to modify female preferences for song by housing a local female with a "distant" adult male, for example, females from Texas TX) with male cowbirds from North Carolina (NC); King & West, 1983b).

These studies showed that it was the males, not the females, who changed, with NC males coming to sound more like Texas males, including different acoustic structures in their songs, structures simply not found in NC males (King & West, 1987). Bird song learning is usually described as vocal imitation: a male hears songs of his species, memorizes them, and later practices them, honing their final songs by counter-singing with other males. Thus, males certainly need access to male stimulation, but how could females serve a meaningful role?

To find out what female cowbirds were doing, we videotaped pairs of young males and adult females housed together. We chose the time of year (March) when the discovery process for the young males is in full gear. At this time in the wild, males and females are on prospective breeding grounds and younger males now have a chance to see what song is all about. The clue to what was happening came from watching the reactions of the males to the females: every once in a while when a male sang, he would suddenly change the pace of his singing, as well as sometimes abruptly move toward the

female. We found that such changes in the males' behavior were often preceded by wing actions by females, movements we called wing strokes. These data suggested to us that female cowbirds used a gestural signal system to communicate about an acoustic signal system and that males had to know how to read these gestures to use the information available. Thus, a male's discovery process was a multi-modal one; he had to look at what happened when he sang a certain song and remember what he was singing when reactions occurred. The males often repeated the song that had elicited the wing stroke, suggesting a means of memory rehearsal (West & King, 1988).

To find the functional value of wing strokes, we employed a playback test during the breeding season to see if females would adopt copulatory postures to songs that had elicited wing strokes as opposed to ones that had not. The answer was clear: wing stroke song elicited significantly more copulatory postures from a different set of females, who knew no more about the singers than their songs (West & King, 1988). These data led us to view song learning as a process of social shaping. Wing stroking was a form of contingent leaning, produced on a partial schedule, serving to bias the male's singing toward more female-preferred signals. But the males had to perform, to sing time and time again, in order for female reactions to emerge. These data on social shaping complement those of Marler and Nelson's process of selective attrition and action-based learning in recognition of the role of male counter-singing in the sparrows they studied (Marler & Nelson, 1993; Nelson & Marler, 1994).

Recently, we looked again at male-female interactions throughout the year, studying young males individually housed with two adult females. We wanted to find out just what parts of male vocal ontogeny females could modulate. Some males were housed

with adult females from their local region to maximize social and acoustic synchrony between the two sexes with respect to local song preferences and timing of breeding. Some males were housed with adult females from a distant population, females with different song preferences and a different time course for breeding readiness (Smith et al., 2000). We found that specific actions of adult females predicted different rates of vocal progress throughout the stages of development. Young males housed with local adult females produced stereotyped song earlier, ceased motor practice earlier, and produced more effective playback songs than did males with females from the distant population. The males with the "distant" females showed slower growth and more variable song well into the spring. The major difference between the groups was that the local females stayed more often when males sang instead of flying away, whereas distant females left, sometimes even before the song was finished being sung. Proximity between male and females gave females the ability to hear more details in the song and gave males an opportunity to inspect female movements more closely (Smith et al., 2000).

From in vitro to in situ

In the work just described the males' songs were the focus of the culturing process; we did not look at the birds themselves and how they behaved. Although we had looked at courtship in wild-caught males, neither we nor other labs had observed courtship in the laboratory specimens of birds housed under restrictive conditions (but see Williams et al., 1993). We chose to take a look at what happens when males face a more competitive and responsive environment. We asked two questions: did they show species recognition at the time of mating and were they successful at obtaining mates? The first study included wild-caught juvenile male cowbirds from South Dakota (SD; *M. a.*

artemisiae), the same population studied in Smith et al. (2000). We housed young SD juvenile males with either SD females (the female housed or FH males) or canaries (the canary housed or CH males) in the laboratory in individual contexts, one male with two females or canaries. Thus, we were using housing conditions we had used many times before to look at species recognition. Moreover, instead of concluding the study when the males' songs were mature, we continued on, asking how males would use their learned vocalizations (Freeberg et al., 1995). By use, we meant would they direct their songs repeatedly to females and would they sing to adult males, as these two skills are necessary to obtain a mate.

First, we observed all of the males when individually placed in a new flight cage with new SD females and new canaries. In the test flight cage, we watched in astonishment as the CH males chased and sang to new canaries. The CH males' persistence was striking in that the canaries offered no incentives and simply evaded their odd consort-to-be. The FH males did vocalize to female conspecifics in the flight cages and ignored the canaries, behaviors that made sense to us. And so, we moved the birds to the next setting, outdoor aviaries with multiple conspecifics and heterospecifics, but no adult male cowbirds. We had thought that once the CH males saw FH males court female cowbirds, some sort of light bulb would turn on and they would adopt typical cowbird courtship. It did not happen, their behavior remained significantly oriented toward the canaries, not toward the female cowbirds.

But their behavior did not represent a case of ignoring available information, i.e., observing competent courters, because the FH males behaved differently in the aviary than in the flight cage. The FH males rarely sang to females and had little success

courting female cowbirds. The major failure was in song use; they did not direct their vocalizations to females, instead singing to each other. After documenting the behavior of the CH and FH males with several sets of females, we introduced adult males to the aviary with FH and CH males to give them competent models to observe. The introduction of the adults had an immediate and positive impact on the females. The day the adults were introduced we saw more social activity by the female cowbirds than at any time prior. The adults successfully courted and copulated with females. But their success did not change the behavior of the FH or CH males, except perhaps to suppress what little courtship we had seen. Thus, learning by observing did not appear to have any effect at this point in development.

By the end of the breeding season, we also knew something about the attractiveness of the songs of the FH and the CH males to playback females. The females had responded significantly more often to the songs of the FH males and the adult males compared to the CH males. Thus, the FH males had learned something from their winter with their female cowbird companions, but it was not enough to make them competitive in the setting we chose because they did not vocalize in the right context.

In past studies, we had assumed that playback females could recognize effective songs, but we had also assumed that males could recognize when to sing such songs. It had simply not occurred to us that song use was a skill in the same way that learning to sing was a skill. Clearly, we were wrong.

In the following two years, we did more work that exposed the multiple layers of learning needed to connect social behaviors, singing and courting, connections that we had not known could be dissociated by social manipulation. Several lessons were

primary. First, the CH males' orientation toward canaries made clear that species recognition is not a sure thing in cowbirds, neither innate mechanisms nor early learning guarantee discrimination of potential mates. Second, the cage and aviary tests revealed the need to consider social proximity as a possible scaffolding mechanism to facilitate learning. The size of the flight cage represented a supportive mechanism for the males as the females could not get very far away and the males did not need to go very far to find a female. We would not have recognized such support had we stopped our studies after observing the CH and FH males in the confines of a flight cage. Without the aviary tests, we would have concluded that FH males showed appropriate recognition and attention to potential mates and we would have been wrong.

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

Breaking away: Cowbirds in flocks

The realization that such practical factors were so important to an individual's reproductive success encouraged us to shift the way we studied social learning. We moved out of the laboratory and studied groups of birds in large outdoor aviaries where we could provide them with social stimulation similar to their natural environment. To begin, we placed a group of 74 cowbirds, differing in sex and age class (young and adult)

into a football-field sized aviary and observed them for a year (Smith et al., in press; Figure 1a & b). We then looked to see how the birds would organize their environment.

The birds quickly self-selected their own social affiliation patterns, organizing themselves by age and by sex. Assortment based on similarity in age and sex persisted throughout the entire year, with separation by sex being stronger than separation by age. For example, some of the young males associated more with adult males than other juveniles males: these males turned out to be more successful in courting females than were young males that associated less with adult males. Also, young males that sang more to females stopped singing earlier; a pattern we have seen in the past that suggests these males progressed to crystallized song faster. The correlations between patterns of social assortment prior to the breeding season and courtship competence in the breeding season show that self-selection affected vocal and social development and reinforced the point that young learners have to act on their social environment to develop social skills, simply “being there” is not enough (Smith et al., in press).

The large aviary experiment showed us that social learning was open to study in complex social environments and differences among individuals could be measured. Moreover, we now had correlations suggesting that self-selected social environments influenced developmental trajectories of functionally important behaviors. The next step was to test these correlations. To do this meant manipulating social composition to obtain a more rigorous assessment of social influences.

We created groups with different social compositions, manipulating the types of social experience that was available (White et al., in review). Thus, in four groups we varied the age class of males present. Each group contained young and adult females, one

group contained both adult and young males (AY group), one contained only young males without adults (Y group), one group contained only adult males without young males (A group), and one group did not contain any males at all. Groups had approximately 24 birds in each. We watched the groups daily from September through the breeding season in late spring. The results showed that for any class of birds - young males, young females, adult females, and even adult males - the social environment in which they were housed influenced their development.

Let's begin with the young males. As the year progressed, the young males in the two different groups developed reliably different courtship and communicative skills. Between August and April, the young males in the AY group assorted by sex and age and frequently sang to other males and to females. In May, during the breeding season, the AY males were aggressive with other males, and courted and copulated with females in patterns typical for cowbirds in the Midwest. In stark contrast, throughout the year, the Y males showed little social structure avoiding other males and females, paid little attention to females, and sang in long bouts of undirected soliloquies. In the breeding season, while males in both groups got copulations, the Y males showed different patterns of courtship and copulation and displayed no aggression with other males. The two groups of young males also developed structurally different songs at different rates, with Y males advancing sooner to stereotyped song and developing song more effective at eliciting females' copulatory responses than AY males. But, in the aviaries, the Y males did not show much interest in following females and directing their songs to them. Without adult males, either to challenge the young males or energize the females, or both, the Y males settled into a highly stable state of atypical social patterns.

Differences in male behavior across the conditions also related to differences in female behavior across conditions. The large aviaries gave females the space to meter their social proximity with males and with other females. They could engage in or avoid social interactions by choice. In the A male condition, females assorted with males far more than in the other two conditions that contained young males. In the Y male condition, females rarely came near males, affiliating mainly with other females. Females assorted by age class in the three conditions where they were housed with males, but not in the one condition where they were housed without males. In the breeding season, the females housed with Y males produced fewer eggs and destroyed more of them than AY and A females (West et al., in review). Why females react so differently in response to the different males is unclear. It seems that females are stimulated by male-male competitive interactions and may use them for mate assessment.

Finally, there were differences in adult male behavior. It is generally thought that there is little modifiability in adulthood, rendering development and learning of little importance. For most of the year, this conceptualization held true for the A males in our study; there were few differences between the two groups of adult males (housed with or without young males). Both groups sang approximately the same amount. The clearest difference was that A males sang more songs to females over the year, probably a result of the females remaining closer to these males. In the breeding season, we brought the two groups of adult males together in a new aviary, allowing them to compete directly against each other for access to a new group of females. Here a difference between adult males from the two groups became stunningly apparent. The AY males vastly out-competed the A males. Every single AY male got copulations faster than the A males. In

fact, only one of the A males ever managed to copulate. Young males, constantly exploring their physical and social environments, while not knowing the rules of social interaction provided the AY males with constant challenges. As a result, living and interacting with young males kept the competitive abilities of AY males honed (White et al., in prep).

We have now studied the origins of the effect of adults on juvenile male development (White et al., in press) and have also followed the Y males into their second breeding season. The Y males' patterns of atypical behavior persisted into adulthood and were resistant to our making changes to their social environment by exchanging the females in their group. The next step will be to use the Y males as adults for a new generation of young males and chart the development of this F1 culture of males exposed to adults displaying atypical behavior.

These new experiments in socially complex aviaries have revealed that some of the emergent information necessary for development may not be available in simpler social contexts. Moreover, the different cultures that emerged from differences in composition of the groups demonstrate how different opportunities for learning are catalyzed.

One result that impressed us most from watching these different groups was how social behaviour could serve as a variation generator. Social groups rapidly diverged from one another as different behaviors became common in the different groups. In some groups, males focused on singing only to themselves, in others, to other males and/or to females. In some groups males adopted fighting as a response to confrontation, others did not. In some groups males guarded females, in others, males simply moved on to other

females. And there were also reliable differences in song potency and song structure across groups. The differences we saw throughout the year translated into differences in mating success with direct implication for survival of phenotypes.

These data support the idea that cowbirds have a facultative system of development, with variation in behavioral outcomes reflecting differential phenotypic responsiveness to local ecologies. 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 distinction to be made in our work is that the environments differed based on the presence or absence of other individuals in the group. Therefore, just as there is an individual’s norm of reaction that reflects how the individual differs in response to the environment, so too is there is an environmental norm of reaction that reflects how the environment differs in response to the individuals within it. This interconnectedness between the environment’s effects on development and development’s effects on the environment results in the merging of developmental and cultural trajectories.

Part of the above-mentioned definition of reaction norms stresses the importance of the biological relevance of the environment. Cowbirds provide an excellent species to explore different social ecologies because as a species they are second to none in being successful in just about every type of ecology available. When cowbirds over winter in flocks, they sometimes find themselves with other species and/or in mixed age and sex classes of cowbirds, but field data also report all female flocks or flocks of juvenile males (Friedmann, 1929). It is at this level, within the range of normal contexts, that phenotypic

plasticity evolved and yet it is at this level that we still know the least. In cowbirds and other songbirds, for example, some young males reliably hear song in their first summer and others do not (Kroodsma & Pickert, 1980; Nelson et al., 1995; O’Loghlen & Rothstein, 1995). Such environmental variation may have led to the evolution of multiple modes of information transfer and differential dependence on mechanisms such as imitation or trial and error learning.

Cowbirds are brood parasites and have often been expected to be exemplars of closed programs of development, i.e., they were not supposed to have open programs highly dependent on social learning, nor would theorists have predicted the amount of geographic variation found in modes of learning across cowbird populations (Lehrman 1970; 1974; Mayr, 1974). But, after several decades of research have shown, the conceptual pendulum has swung. Ironically, in recent reviews of our work, the idea has been put forth by reviewers that the cowbird probably is an exemplar of an open program of development because they have to rely more on learning to make up for their odd early environment! And so, we turn to a more traditional parental species, the starling, and to quite different methods to expose the role of the kinds of social learning seen in cowbirds.

Starlings: Composers at work

Let us begin by providing some perspective. An adult male cowbird with a large repertoire has seven seconds of sound to call his own, give or take a few seconds for whistles. This output would produce a paper portfolio of 7 pages of 1.2 sec sonograms. A starling, in contrast, has a basic song consuming up to one minute, 60 times longer than the average cowbird song. And starlings have many songs, requiring not a slim file folder

or sonograms but an entire book, complexly indexed to capture their ability to repeat, improvise, and acquire new material. And if the male cowbird's ability to traverse several musical octaves is impressive, so is the starling's ability to sustain and organize singing for periods over minutes. Adult male starlings have repertoires of 60-80 song units called motifs, a subset of which appear in individual songs. Motifs are most comparable to note clusters in cowbird song; they are arranged and rearranged into predictable sequences to configure songs, often repeating motifs at least once. The mimicry of an entire cowbird song qualifies as a single motif. Motifs depend on the learning of many sounds including conspecifics, heterospecifics, and inanimate and non-avian sounds (cell phones are fashionable right now). An entire repertoire may consume 10 or more continuous minutes of song, a 600-fold increase over the average cowbird song.

Like cowbird song, the major proposals for the function of starling song include mate attraction, in addition to individual recognition and male-male competition. There is a growing consensus that the size of the repertoires and perhaps aspects of song delivery (rate of vocalizing) are products of sexual selection, with female preferences driving male song learning toward larger repertoires (Ball & Hulse, 1998; Mountjoy & Lemon, 1991).

With respect to song development, studies using restrictive housing, usually birds in individual isolation have shown that young starlings housed without adults produce smaller and atypical repertoires. Young starlings housed with peers do better but still show smaller repertoires than do wild starlings. Starlings copy tutors beyond their first year, with a sensitive period occurring between 6 and 15 months (Chaiken et al., 1993; Chaiken et al., 1997). Starlings keep most of their repertoire from year to year and simply

add to it and there is growing evidence suggesting that a starling's social ecology affects its vocal repertoire throughout its life (Hausberger, 1997).

Life with starlings: an insider's view

But how does the social environment guide the repertoire building process? We were fortunate to stumble on evidence suggesting strong links between repertoire content and social histories between individuals, as well to find a method to watch how sounds morphed from one acoustic state into another as starlings went about the "processing" of sounds. To accomplish both goals, we used ourselves and other humans as potential sources of sounds and placed the birds in different human contexts to see how social interactions affected vocal composition.

Starlings appear to have a long history of association with humans; the Latin scholar Pliny reported that he taught starlings to repeat Latin and Greek phrases. Mozart owned a starling that produced notes from one of his concertos. He had the bird for three years and accorded him a funeral, complete with a poem written by the composer (West & King, 1990).

Our first experience with starlings came about by accident; we were actually studying his companion, a male cowbird. Until the bird uttered something that sounded like "Good Morning" we were unaware how much the starling had observed us: we knew nothing of their mimicking abilities. This starling muscled his way into our psyches before we knew what was happening. Rex (so named because as a baby he looked like a dinosaur) simply insisted on being part of our affairs: he shared our morning coffee, vocalized to music and songs whistled to him, chattered at lab meetings, and perched on

the shower curtain watching events inside. But it was when he uttered the phrase, "Does Hammacher Schlemmer have a toll free number?" that we paid attention.

We knew he only heard this phrase once and we knew the context. From this unlikely start, we thought we had a way to trace the origins of mimicked phrases, as utterances such as Hammacher Schlemmer have a high signal to noise ratio for humans compared to the sounds of other birds or even the sounds such as squeaking doors, microwave ovens, coughing and sneezing, and sounds so familiar we filter out. Thus, we saw Rex's assimilation of sounds with a known history as a way to trace the selectivity and flexibility of vocal mimicry much as one might use a radioactive isotope to watch its course through some physiological system (West et al., 1983).

Rex's mimicry and that of the other birds we went on to study suggested to us that the motivating conditions for vocal learning were not simple: sounds heard most frequently by the birds were not present in their mimicry (such as "no" or "here's your food") and sounds only rarely heard seemed over represented (such as "defense, defense" chanted after observing a televised basketball game).

Most importantly, we found that social interaction with humans was necessary for human mimicry of words or whistles or any other human-derived sounds (e.g., clearing of the throat). We also housed some starlings in homes in cages with another bird but instructed the caregivers to provide good care but no extra interaction. Thus, the birds heard human sounds as often as the birds that also experienced human social interaction (West et al., 1983). Although these birds mimicked extensively, none of them copied human sounds.

Quantifying sociality

To add to our observations, Marianne Engle (2001), undertook a longitudinal study of starlings raised under several conditions varying the amount of human interactions as we had. She also recorded local, wild birds to gather baseline information. Two of her findings are relevant here. First, she operationalized the social relationship between the human caregivers and the birds by using a behavioral protocol to gauge degree of social interaction. The major variable was degree and duration of social proximity, the same variables we had found to be important in cowbirds. To be scored as interactive, the bird had to (1) attend to the caregiver, (2) approach, (3) create contexts for interaction by (4) getting near the caregiver or (5) attend to a novel object to provide a topic. The more of these acts completed, as well as some others, the higher the bird's score. Engle found significant correlation between protocol scores and human-derived mimicry for both males and females.

Here was another social discovery-based system. Starlings appeared to throw out a sound and follow what happened: we dubbed the system, social sonar (West & King, 1990). The repertoires of the birds contained greetings, farewells, conversational fragments, and time-locked sequences (from the starling's point of view), such as 1) squeaking door, 2) dogs barking, 3) dishes clinking, 4) mimicry of "good morning." Events 1-4 represent the morning sequence for that household. All of these mimics stress social attention and emphasize events where humans and starlings were apt to interact on a routine basis. The rules for social learning by starlings seem to be compounded from degree and duration of proximity and what happens during proximate interactions.

Engle's work also provides an instructive perspective on the developmental data from other laboratories cited earlier. Chaiken et al. (1993) found that birds deprived of adult male companions or deprived of any social companions developed smaller repertoires than wild males. While Engle's starlings were equally deprived of starling input, as were Chaiken et al.'s (1993), their social surroundings were far more complex, albeit atypical. Engle's birds developed repertoires overlapping in size with wild males from her sample and from Chaiken et al.'s (1993). Engle also found, as had we, that non-interactive exposure to humans did not lead to the use of human sounds for mimicry (West et al., 1983). Engle's home-based, interactive birds did show some similarities to isolated birds in lab studies, though, in their failure to produce certain wild-type sounds such as the distinctive "click" trains. The home-based starling also differed in the preferred duration of their song production, generally shorter segments than wild birds, perhaps being influenced by the average length of speech utterances heard in their homes.

Starlings are vocal mirrors, reflecting back exactly what they hear, with no filtering. Their mimicry of human sounds included the sounds of human speech production: our lips smacking and swallowing. Despite the accuracy of the imitation, the mimicry lacked contextual elements that are usually associated with social transmission. First, no vocal contingencies developed. Even if a human immediately repeated the sounded mimicked by the starling, the bird was unlikely to respond in kind. Second, the mimicked sounds were used in many contexts not associated with their original context. Among our home birds, one screeched, "I have a question" when held to have her toenails clipped. During an agonistic encounter over suet, all sorts of mimicries seemed literally squeezed out of the very excited birds, as is often seen in the wild at a feeder. If

we were to sample the behavior of our starling only at breakfast and suppertime, we would be led to conclude that they use sounds referentially, as 15 minutes or so before those times, the starling increases his mimicry of feeding-related utterances, such as “breakfast” or “ hi guys” or imitations of the microwave. But, if one were to visit the same birds at other times, the chances are high of hearing the very same sounds mixed into the potpourri. It may be the case that what distinguishes the feeding times is the possible greater focus on specific mimicries, but that important distinction remains to be tested. Thus, in our view, vocal imitation is a cheap way to acquire potential song material, with the particular selection of sounds to be imitated influenced by social learning.

Whiten (2000) lists “social knowledge” as one of the components of social intelligence in primates, i.e., “ a store of social information about their companion’s characteristics and past behavior, which they can apply to novel situation” (p. 193). The selectivity of the starling’s mimicry to those humans who interact with them suggests an analogous ability, but one humans can learn about if they know the animal’s social history. Imitation is a way of storing and expressing social knowledge. Thus, the transmission of culture in starlings involves imitation, but imitation guided by social learning.

What is the nature of avian culture?

What we have outlined is a different way of thinking about culture, not limited to transmission of compartmentalized innovations in a population (potato washing or termite fishing for e.g.) or isolated species-typical traits such as bird song, but an approach that encompasses the development of the whole animal (becoming a cowbird).

If, as we argued at the outset, culture is a process, then it may be too narrow a view to look only for domain-specific instances. We originally compared the process of culture as the growing of biological material in a nutrient medium under controlled conditions. As we review what we have written here, we make one amendment, the biological material is the whole organism, it is not the song or any behavior separated from the bird. In study after study, for example, we have shown that cowbirds must learn how, when, and to whom to sing.

In a review of culture in non-human primates, Whiten et al. (1999) document innovations among different groups of primates to reveal the diversity of cultural innovations found. They distinguish primates from other taxa based on the number of cultural processes reported, suggesting that cultural processes typically exist for only single behavior patterns in other mammals and birds. We would suggest this might be an artifact of the compartmentalized way in which culture has been studied in other taxa. Birds raised in socially barren conditions cannot show any other potential forms of culture. With respect to bird song, it is not only the song that is affected but also other behaviors of the singer and the perceiver. Let's consider the starling first. In order for a novel form of behavioral transmission to occur, incorporation of human sounds, the starlings a) were raised from an early age with heterospecifics (humans); b) lived in the heterospecifics' environment meaning that even basic resources were delivered in new ways (food from a human's dish, water from a faucet); c) absorbed an ambient visual and auditory world biased toward human activity; d) physically interacted with humans allowing extreme proximity; e) became attuned to a temporal schedule different from that of wild conspecifics and f) were deprived of aggressive feedback for almost any action

(not including someone throwing a sock at the cage to quiet them down). In Hausberger's (1997) work with wild starlings, the control parameter predicting song and whistle sharing is close contact. But in order to achieve close contact, all of the processes we saw in the home that lead up to directing song to a neighbor must also fall into place.

Thus, the object/subject of the culturing is the animal, not simply one of its behaviors. In cowbirds, we have shown that the following behaviors, which are obligatory for song to be used as a mating signal can be altered by postnatal experience: species and mate recognition, that is, to whom to affiliate and sing; male-male relationships including counter-singing and dominance; vigilance to potential mates especially after copulation; and populational selectivity in mate choice. When viewed in this context, the male cowbird's total seven seconds of song is embedded in a far more complex series of events that must occur and must occur in a certain order and in a certain time frame. Lehrman (1970) noted, "nature selects for outcomes"; the same is true for culture, as outcomes determine what is transmitted.

We have focused here on the processes that can give rise to cultural transmission. The orthodox cultural researcher would correctly point out that the true test in thinking about culture and whole organisms comes, however, by asking if we can actually affect generational transfer of behavioral traditions experimentally by following the methods and assumptions outlined here. We have data for cowbirds, but not yet for starlings. Todd Freeberg (1996, 1997, 1998) provided the data for cowbirds. Freeberg put together knowledge from previous work to propose a strict test of cultural transmission: could he alter mating preferences and would his subjects carry on the tradition for him? He collected cowbirds from South Dakota. All the birds lived in large aviaries where they

could interact with other juvenile birds from their original population and adults of one of two experimental populations. The first experimental adult population was birds from the same geographic area as the juveniles: the other population was adults from Indiana, a population 1500 km away. The young birds, male and female pupils, were randomly assigned to these conditions. Thus, from the young bird's point of view, there was no designated model: all of the adults were potential models and from the young bird's point of view, so were the other juveniles. The test worked: young males and females preferred as mates birds from their postnatal experimental context. Moreover, in the next year, the birds, in the absence of any "true" models, transmitted their culture to a new group of South Dakota juveniles.

The change in female preference was the most striking from the point of view of the history of our lab's work. With one exception, we had not found a way to modify female cowbirds' natal song preferences even if they were hand reared and exposed only to males from a distant population. And so why did females from South Dakota develop a preference for Indiana males and their songs when they could also hear and interact with other South Dakota males, albeit juveniles? We believe the answer lies in the social context provided: we gave females other females, as well as males. Although we have not tested the idea, we now wonder if housing females alone with males is stressful for them, as they seem to always be on guard, aware of the male's proximity to them. Nadler et al. (1994) showed striking differences in chimpanzees (*Pan troglodytes*) if they could regulate access to males. Perhaps female cowbirds need the sense of self-regulation to allow them to absorb information from adults or maybe they need to see both male and female adults. Female starlings are also less likely to sing if males are present, suggesting

social inhibition of learned behaviors (Hausberger, 1997). As a field, we may have to approach questions of male and female modifiability from different perspectives. Recent work on stress in humans documents different stress regulatory styles, with females showing a distinctly more social approach, labeled “tend and befriend” as opposed to the male pattern of “flight-or-fight” (Taylor et al., 2000).

Summary: A test of culture as a social enterprise

We have provided abbreviated tales of song learning in birds as examples of how cultural transmission may come about. We have focused on the role of social interaction and feedback as a guiding mechanism. Michael Goldstein (2001) completed studies of human infants in our lab where he tested some of our ideas about cultural transmission as an emergent property of social interactions. Imitation and teaching play an obvious role in the learning of speech sounds, but many theorists have denied any role for social learning, proposing development advances automatically via biologically privileged mental modules (Pinker, 1994; Wexler, 1990). We began our study by borrowing two methods from our avian studies. First, we carried out playback experiments with mothers, recording how they categorized the infant sounds of babbling, which occur over many months in an infant’s first year. Mothers reliably identified specific information in these quite variable sounds, even when listening and looking at very short videotape clips of unfamiliar infants (Goldstein & West, 1999). Moreover, as infants made more phonologically advanced sounds, mothers relied more on sounds than facial expressions to determine meaning. Next, we asked if infants’ babbling was sensitive to social stimulation from mothers, much as we had asked how young male cowbirds respond to stimulation from adult females. In an ABA design, after a baseline play session, mothers

provided non-vocal stimulation to infant sounds when directed to do so by an experimenter. An extinction period followed where mothers were told to behave as they had in the first trial. Compared to baseline, the 7-8 month old infants used more mature forms of infant speech during the interactive session and retained many of these sounds in the extinction phase. A control group of infants, given the same stimulation but not linked to their vocalizations, did not show the developmental changes in their babbling, although they vocalized as much as the experimental group. The infants' interest in social contingencies thus led to the emergence of the most advanced sounds in their repertoires, sounds then bio-available for further shaping in the course of the mother's and infant's play. These results are the first to show the sensitivity of the phonetic trajectory of babbling to social stimulation; previous work found no such relationship but previous research did not employ a design allowing for social interactions to occur. Much like the starlings' use of social sonar, the babies threw out sounds, acted on their immediate consequences, and produced a new sound. The tendency to use developmentally more advanced sounds may have been due to arousal and/or the infant's association of more advanced sounds with more maternal attention. Only more research can distinguish these possibilities. But these data are an example of how the social environment can influence an important developmental skill through social learning that is based neither on imitation or teaching, but based on social discovery of contingencies. Thus, the emergence of cultural information through social interaction begins much earlier in our own species than is assumed by many linguists (Goldstein, 2000; Goldstein & West, in prep.).

In summary, the study of even two species birds reveals a potentially important mechanism for many taxa: the role of social interaction to elicit feedback that helps the

young learners to identify cultural information. Culture or traditions are not simply passed on as one might pass on ownership of a home to an heir. Social knowledge is earned by organisms acting on their particular social surroundings to probe its properties. Although skills can come from imitation and teaching, these mechanisms ultimately depend on successful social performance and the feedback it engenders.

Thus, studying the behaviors by which animals uncover culture is a critical next step. The uncovering of culture involves attention to social detail, knowledge of the social properties of conspecifics and of one's own behavior, and pragmatic skills to manipulate another's behavior within a group. For those accustomed to thinking of these characteristics as existing only in big-brained mammals, think again. The next time you see a flock of blackbirds projected against the sky, we hope you can see beyond the grace of their flight to their social intelligence writ large, a collective brain, as it were, over our heads, but not beyond our grasp.

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Figure Captions

Figure 1a. Schematic depicting the large aviary complex studied in Smith et al. (in press).

Figure 1b. Scale diagram of housing conditions for the various studies mentioned.

Smallest box the size of sound attenuating chambers (1m^3 ; e.g. West & King, 1988). The next larger box is the size of the flight cages (e.g. Freeberg et al., 1995). The next larger box is the size of our typical aviaries (e.g. Smith et al. in press) and the largest box is the size of the aviary complex studied in Smith et al. (in press).

Figure 2. A male and female cowbird.(photograph by Andrew King).

Figure 3. A male starling (photograph by Andrew King).

