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Science lies it way to the truth...really.

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Summary/Abstract

In science today, the study of behavior seems to be something someone does to get to somewhere else. Behavior affords a gateway to physiology, neuroscience, and genetics. The quality of such integrative work thus begins and ends with the quality of knowledge about behavior. How do we assay behavioral quality and its integrative potential? We ask this question because we believe many beliefs about the nature of behavior are wrong, albeit wrong in a right way, a scientific way. In this chapter, we illustrate some of the issues in the study of behavior to be considered before its transport into new domains. We call for renewed emphasis on the tasks actually confronting organisms as they develop and learn and on the social context in which behavior typically occurs, a context too often excised and ignored in current work. Without a focus on task and context, we cannot connect knowledge about biology to knowledge about behavior. Without such a focus, we cannot prevent a cascade of changes in the meaning, relevance, and utility of behavioral knowledge as it is subjected to the process of integration.

In Africa a thing is true at first light and a lie by noon and you have no more respect for it than the lovely weed-fringed lake you see across the sun-baked plain. You have walked across that plain in the morning and you know no such lake is there. But now it is there absolutely true, beautiful and unbelievable (Hemingway, 1998).

Introduction

In 1988, for this first edition of the Handbook, we wrote about the nature and nurture of behavior (West, King, & Arberg, 1988). We described what we saw as a neglected element in discussions of ontogeny, the inherited niche, i.e., the physical and social contexts that accompany genes. It was a promising theme we thought, outlining ways to weave ecology firmly into ontogeny. Since then, we have seen our "nature-nurture-niche" notion surface here and there (e.g., Drickamer, Vessey, & Meikle, 1996; Michel & Moore, 1995). But, the converted already believed it, and the unconverted remained unaware of it. It was a message in a bottle that did not travel far. But, unbeknownst to us, we were floating our modest idea at a time that a super tanker of an idea, the human genome project, was about to be launched. As we write this in 2000, the "HHS Genome" has already reached an important port of entry, human chromosome 22, and will soon reach others. All the maps from these journeys are to be published in a book projected to be as tall as the Washington Monument (550 feet). One of the

project's captains has dubbed the monumental work, "the book of life" (Collins, 1999, NPR interview). Our bottle hugs the shore.

The arrival of the genomics deserves grand words and even grandiose opinions because the revolution in our knowledge about molecular biology is astounding. But, as students of behavior and development, we believe that the interest in the molecular has come at the cost of interest in the non-molecular. Such neglect would not matter if the non-molecular level could now be discarded as one might dispatch with outer packaging. But the multidisciplinary mergers do, however, include behavior, either as a probe to explore another level or as a phenomenon to be explained by finding previously unseen physiological or genetic roots (Wilson, 1998). Moreover, integration of molecular and non-molecular systems included animal models and humans. The stakes are high in getting the payoff matrix right between the benefits of using behaviors simple enough to study at many levels and the costs of compromising the integrity of the behaviors we seek to understand. The stakes are also high because the science of the future forces us to revisit some of the most entrenched and darkest ideas about behavior at a molar level. What theory will guide bioengineering of organisms, bio-cleansing of "flawed" genotypes, or biological determinism made simple?

Despite these perils, common sense tells that we may be taking the state of progress of science too seriously. The gaps in knowledge within areas of science are still great enough to make talk about domesticating genetics or decommissioning evolution just talk. Moreover, although science involves big successes, it also involves big mistakes, hence, our title, "Science lies its way to the truth." Scientists take concepts and methods; ones known to be only partly right, and create a narrative to frame their theories and their work. Thus, the trial and error that define the scientific process leads us to regard the hoopla about the human genome project as enjoyable, but not intoxicating. It is early in the day.

As we look ahead, however, our wariness stems from the real possibility that the human genome project or other grand multidisciplinary enterprises may end up pursuing mirages. If, as we propose, the solidity of many behavioral phenomena is being assumed without sufficient questioning, linkages between different levels of integration become troublesome. We start with the premise that it is hard not to link a behavioral layer with a genetic layer. Progress to this point has depended heavily on reductionism. Molecular biology is not only the dominant field in biology, but also the predominant metaphor for science. When bringing together knowledge from different levels, we will have to be selective and sensitive to which phenomena can survive disconnection and reconnection. What metrics should we use? And what is really being connected? Although genes are now visible and amenable to dissection and manipulation, the kinds of behavior-gene connections proposed are of two kinds. First, there is the search for the concrete, i.e., "biological" genes, specific patterns of proteins that match up to specific changes in behavior. Second, there are "abstract" or "evolutionary" genes, of which memes are most famous, that fend for themselves in a theoretical struggle for survival (Griffiths & Neumann-

Held, 1999). The specific locus of their functions is not the issue for the latter, but is for the former. The distinctions made by Griffiths and Neumann-Held between biological and abstract genes is much like that of D. O. Hebb, who made an analogous distinction between the conceptual nervous system and the central nervous system. He did so to distinguish thinking about what we assume the nervous system must do and what we actually know it to do (Hebb, 1949).

A conceptual frame for abstract genes and behavior can overlap with biological genes and behavior, but the excitement at present is about latter, biological linkages, how G, C, A, T, in all their combinations, link to higher systems. Our focus here is on the nature of that pursuit. How do biological genes map to real behaviors? The use of genes in a more metaphorical way is of less concern to us here. But the potential for confusion between the two is great. The never-ending debate about the genetics of IQ caricatures the possible downside of inattention to the nature of measures and the kinds of linkages being made. At times, both geneticists and psychologists have had to remind the other of the frailty or outright falseness of one another's measures. Even more dubious connections now fill the popular media, in the syntactic frame of "genes for X". There have been reports of genes linked to the wearing of flannel shirts all the way to the ability to form the plurals of nouns (Gopnik, 1997). In the case of genes for plural nouns, what was remarkable was how easily people overlooked the far more pervasive language deficiencies of the families; plural nouns were far from the root of these families' biological problems.

Errors or exaggerations in science are, of course, routine, that is what science is all about -- today's fiction is yesterday's truth. But there is no mechanism in science to evaluate the currency and meaning of data for those outside of the specialization that created them. And given the number of specializations, the problem becomes one of monumental scale. Moreover, people and textbook or popular science writers tend to fossilize good stories, either because they do not know they are wrong or because good, simple stories sell. A finding true at first light may get lots of attention, but not the finding making it a lie by noon. Less spectacular data may not make it into print, let alone into a textbook's second edition! But, by then, the now outdated original information from the first edition may have skipped across integrative borders into other texts and other research programs. Such error-prone transfers of knowledge are even more likely given the particulate nature of knowledge: who can possibly embrace so many parts?

From textbook biology to a social task biology

The path to integrative progress means changes in basic behavioral approaches, especially laboratory-based models. We need an ecologically based method of choosing and defining robust scientific problems on which to use integrative methods. We need such a method because the organisms and genomes we seek to understand developed in response to ecologies filled with

contextual demands. Most laboratory work does not, however, take those ecologies or demands seriously (but see Timberlake, 1993,1994 for a model paradigm).

Of even more importance is that many of the species we study also evolved in worlds where stimulation, information, and knowledge are socially constrained. We contend that many individuals do not have direct access to potential stimulation (thermal, tactile, visual, olfactory, taste or any cross--modal connections among these). Nor do organisms often have direct access to proximate reinforcement systems to consolidate and shape perceptual experiences. Instead, for many species, these basic resources are delivered via a "social gateway" in which older organisms or peers facilitate or constrain sensory exposure, timing, and duration. Of even more consequence is that some stimulation is not even available to a single conspecific, but must occur in an aggregation of conspecifics -- thermal regulation in a rat huddle is an elegant example (Alberts, 1978). The social gateway, however, has been bypassed in most laboratory research in perception, cognition, and neuroscience. We shuttle the animal through the social gateway even before the work begins! Consider a very simple example. Golden hamsters (*Meseocricetus auratus*) are not considered particularly social animals. But adult females can be taught a novel means of obtaining food, a fishing technique in which they use paws and teeth to reel in a chain with food attached at the end. They can learn this by experimenters' shaping the response through 10 days of extensive training (Previde & Poli, 1996). The pups of trained mothers show the entire response in only one day of observation if a trained mother is present and using the response. Pups of untrained mothers do not show the behavior at all; they try whatever technique their untrained mother tries. In the life of a small rodent, a difference of nine days in learning efficiency is huge. But, by and large, studies of observational or social learning are rare in comparison to the number of studies of individually shaped or conditioned animals. Because of the bias toward the latter approach, the search for the genetic roots of learning ability is aligned to the model of individual learning. While such data are important in that the capacity to learn individually is abundantly apparent, it unfortunately bypasses the question of what might be the evolutionary preferred or selected route for learning. This is hardly a new point in comparative psychology: as Harlow (1953) noted, " the Skinner box enables one to demonstrate discrimination learning in a greater number of trials than any other method "(p. 98).

Thus, as we discuss the idea of task biology, we highlight two features. We argue for a change in the basic unit of analysis from "behavior" to "task." By task, we mean a functionally rooted set of acts performed by one or more organisms in an actual ecology, tasks ranging from foraging to reproduction to communication. Second, we assume that many functional outcomes, such as successful foraging, cannot be genetically dissected by looking only at animals as individuals. The very existence of certain phenomena depends on the social composition of a species and the pattern of interaction among individuals (Giraldeau et al. 1994).

As a way to illustrate some features of tasks and social dependencies, we provide several examples below of "textbook knowledge" based on familiar laboratory practices. We do so to expose the inherent frailty of many behavioral explanations when the behaviors have not been grounded in an ecological context. We do so as well to show how the light of day can change lovely truths into misleading mirages.

Imprinting as a family phenomenon. Imprinting refers to the tendency of newly hatched precocial young to form a rapid social attachment, an attachment often thought to be irreversible. Who can forget the pictures of ducklings paddling behind Konrad Lorenz? In part, it is the recognition factor of the behavior that made it endure and in part, it was the finding itself. At that time in history, the dominant theory of learning consisted of the laws of classical or operant conditioning. Imprinting did not fit with such general laws of learning and thus broke important new ground (Gottlieb, 1971; Sluckin, 1965).

Although few still believe in the irreversibility of imprinting, now even the basic phenomenon is under scrutiny. When the door was opened to let in some of the behaviors' natural complexity, the simple story cracked under social pressure. As it turns out, imprinting unfolds quite differently when the young hatchlings have access to their siblings, with whom they have had auditory contact as egg mates. The ages at which ducklings learn and remember the experimenter-designated stimulus of model hens, for example, are not the same if ducklings receive sibling stimulation (Gottlieb, 1993; Johnston & Gottlieb, 1985; Lickliter, Dyer, & McBride, 1993; Lickliter & Gottlieb, 1987). Exposure and time with siblings can also promote or delay maternal imprinting. Indeed, if the mother is not seen frequently, siblings imprint on one another. Thus, despite first appearances, reliable imprinting on the mother is dependent on other social contingencies, a more fragile a process than often portrayed. Interactions with siblings occur at the same point in developmental times, as interactions with the mother. It is the dynamics of the co-occurrence of these two tasks that needs to be emphasized to understand imprinting as it actually happens.

Look again. Stories about the evolution of a behavior are especially vulnerable to textbook ossification if the original story is intuitively logical. The tendency to fall for "just-so-ism" or more formally, the "adaptationist programme" (Gould & Lewontin, 1979) is widespread. When things make sense, we are lulled into complacency. The moth that is becoming a myth serves as an elegant example of the dangers (Majerus, 1998; Millar & Lambert, 1999). The peppered moth, *Biston betularia*, showed changes in wing coloration during and after the industrial revolution from light to dark to light again. These changes are cited in many textbooks as an example of natural selection in modern times, as the tree trunks the moths were presumed to rest against also turned from light to dark to light as a result of changes in sources of pollution. The correlated changes in color were thought to have been favored as a mimicry response to prevent predation by birds. But questions about the phenomenon have come from many directions, including problems with replication, knowledge about vision in birds,

and about the actual resting places of moths. The story assumes moths rest against the lichen on the bark of the aforementioned tree trunks. But, in a triumph for context, scientists cannot find peppered moths on tree trunks; no one is actually sure where the moths rest (the undersides of branches seem more likely). But how then would mimicry work to deter predation? The true story may be more complicated, involving fluctuations in moth and bird populations, or what the pollutants do directly to the moths? In any case, the task for the moth and for the predator no longer can be captured in the bold strokes of black and white theorizing.

Whose error? At a certain age, human infants make what is called the "A not B" error. Infants are shown two locations, A and B, and then are shown or allowed to reach for a toy at point A for several trials. The object is then placed at point B. Under many conditions, infants then reach at A, not B. It is a very reliable phenomenon for infants of a certain age, good enough to bank on for class demonstrations, etc. It has also been the subject of countless experiments and permutations to provide a coherent explanation. Some have said it shows the absence of certain mental structure, glitches in an emerging theory of mind. But simple tests can change the error rate, manipulations that focus on the idea that the baby's mistake is born out of time-linked patterns of perception and action, not absent mental modules (Smith, Thelen, Titzer, & Mclin, 1999). Babies repeat the arm movement to A, when it "should" go to B because their arm keeps going where it has been going. If procedures are used to make the baby more aware of arm movements or if the arm movements are made less familiar, perseveration greatly decreases. Within the same session, it is hard to argue for mental structures that simply come and go within the same child, but changes in the proprioceptive feedback from a limb are highly plausible. Thus, the "A not B" test can have vastly different developmental explanations. A baby's reach in space is not independent of context. The issue is the experimenter's theoretical reach. If we do not first analyze the tasks we create for our subjects, we cannot hope to explain bigger things such as mind or the structure of knowledge, or at least not seriously (Thelen & Smith, 1994).

Psychology's black rat. Some textbook illusions come from the tendency to persist not with the same task or setting, but the same animal. Few would dispute that the "white rat" has mascot status in psychology. Most associate the white rat with how individual animals learn in a Skinner box or maze. But rats as a phyletic group are highly social and highly successful, generally outwitting humans' attempts to contain them because of their ability to learn socially (see Galef's 1982; 1996 work on social learning of food preferences). The social part of rats' normal task biology is much less widely communicated in our basic texts, if mentioned at all, it is in a special section on observational learning, which is treated as the exception, not the rule. Studies of social learning in black rats are probably even less often cited as textbooks tend to jump from phyla to phyla, not rat to rat.

In the 1980's, Terkel and his associates discovered that black rats (*Rattus rattus*) could strip the bark off the cones of Jerusalem pine trees, trees planted during the 20th century (Terkel, 1996). That the rats were in such a habitat at all was also a surprise and represented an opportunity to watch animals exploit a previously unavailable niche. Terkel discovered that adults from another population never exposed to cones did not learn the skill of pine cone stripping by handling the cones or by observation, and that young rats from the population had to learn to strip cones. In a series of laboratory experiments, the role of the mother became clear as she could demonstrate the behavior, as well as provide materials for trial and error. Although learning from the mother was important, it also turned out that access to partially stripped cones was enough for some adults to acquire the habit and to facilitate the learning in the young. Thus, pine cone stripping is a social behavior available for the "taking" if one has access to adult demonstrators and the materials.

What prevents its spread to new species such as wood mice or squirrels, species also found in the new niche of the pine forest? The spread is constrained because the behavior is enmeshed in a social safety net. In all their years of work, the investigators have never found partially stripped cones lying about in the wild. Access to these learning tools comes only through interactions with one's mother from whom cones can be snatched. Thus, a social task one would think to be feasible, learning by finding half-eaten cones, is not available. Another species or population would have to steal the social system, mother, pups and all, to get the behavior. That is the power of a social system of distributed intelligence, a system not visible at all in the laboratory world of the "model" species, the white rat, or in the tasks we typically ask it to perform.

Bypass surgery? What holds these examples together is that each demonstrates that need to view behavior within a system and to understand the task from the organisms' point of view. In each case, when only part of the behavioral whole is accentuated, or if others parts are too highly discounted, we are led astray. Connecting information made up of excised parts often leads to frustrating examples of integration, producing cubist images, an eye here, a leg there, half a body somewhere else.

In a recent Science report, Iacoboni et al. ask about cortical mechanisms of imitation (Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999). Using fMRI techniques, they present data suggesting enhanced signal intensity in three areas of the brain (area 44 and parietal cortex) when human adults are asked to imitate a finger movement as opposed to watch a finger movement or perform one as a result of specific instructions. The authors take these data as evidence of the presence of a cortical "imitation mechanism," an internal module tuned or resonant to the perception of "matching" the behavior of another. The conclusion requires evaluation, however, in light of the tortuous course taken. First, the original example of imitation given by the authors, the premise for a neural resonance mechanism, is neonatal imitation of human facial and manual gestures. Newborns have been reported to imitate tongue

protrusion in response to seeing an adult perform it. It is a textbook favorite and those outside the field seem to wholeheartedly embrace it (Wilson, 1998). The problem is it may be a mirage. Jones (1996) has shown that one can also elicit similar rates of tongue protrusion when babies see a set of randomly blinking lights. Thus, it is not clear that infants really do imitate at very young ages. As a result, the rationale stated by Iacoboni et al. imitation is really a leap of faith, not a step forward based on solid facts: imitation must be a very simple neural mechanism because newborns can imitate. But Iacoboni et al. not do study young babies. They ask adult subjects to do something quite different from the babies-- to follow instructions about when to imitate. But, in keeping with Jones's finding, the conditions for imitation, as opposed to observation, were perceptually more dynamic. Thus, with more controls, it is not clear what the task really is from the subject's point of view.

The authors also bring to bear data from non-human primates (where the kind of motor imitation is not described) to argue for the particular location of the neural substrate they believe to be implicated and invoke another kind of imitation, children learning language, as another behavioral premise to help delineate the neural search. And so, we have three kinds of imitation, all of which are very different tasks. But, all are now connected in cubist fashion to create a picture of the underlying substrate for imitation and to support the idea of a "direct matching mechanism" to effect imitative learning.

It is important to follow the trail of substitutions used to produce an integrative picture. Babies are hard to study and even harder to use in fMRI procedures, and so adults and a new kind of imitation were substituted, a common bypass technique in integrative work. There is no problem as long as the reader knows that to keep the conceptual patient alive, there was the need for such surgery. But, if the investigators themselves do not know that the starting premise, neonatal imitation, has another explanation, just what is being integrated? This study is not unusual in the number of biological proxies employed or the number of generalizations from different levels of analysis.

Thus, to summarize, as we look over the decade since the last Handbook, we have serious concerns about the possibility of veridical vertical integration through levels of analysis. Perhaps, the image is beautiful, but the pathway to its realization is tortuous. But, as the unrelenting accumulation of facts goes on, new reasons emerge making the need for some new kind of organization necessary. We now face an obesity of bite-sized facts, unaccommodated by current theoretical structures. Perhaps, it is the sheer volume of scientific stuff that is at the root of calls for multidisciplinary work. It is a call for help.

Our proposal to focus on tasks suggests ways to change the kind of informational units as they are generated to allow them to cohere and form robust, but manageable units. Task biology is a way to embed behaviors within an ecological framework and thus exploit natural structure (Gibson, 1969; Gibson, 1966; Lehrman, 1970; Oyama, 1985; Thelen & Smith, 1994). In the preceding paragraphs, we have talked at the general levels of the nature of science and

nature of behavior about the problems of ignoring context. In the next section, we explore specific experiences, in particular, a scientific "lie" of our own making. We want to recount how hard it can be to edit a mirage. Our plan is to describe old and new studies and show how the more recent social approaches altered previous conclusions about the nature of productive units of analysis in the study of communication. These experiences should help to explain our growing interest in a task-oriented approach and our skepticism as to how such an approach fits with the prevailing images of integrative work.

Early in the day

When we began to explore vocal development in the 1970's, we had two goals. First, we wanted to focus on naturally occurring early experiences. Second, we wanted to track how a developmental system worked when things went right, not when things went wrong. Both of these goals were reactions to then popular developmental paradigms in which the early experiences imposed on animals were quite alien for the species involved. Moreover, the more frequent practice was to remove, rather than add, social experiences, so as to disable development and then try to rehabilitate it (e.g., Harlow's studies of attachment or lack thereof (Harlow & Harlow, 1962). In contrast, we sought a system where the constructive properties of development were visible but one in which developmental change occurred at a slow enough pace (not the one day window of imprinting) to allow us to see the process.

We chose to focus on song learning. Singing is something a bird naturally does but depends on certain kinds of experiences. Singing is conspicuous but the nature of its ontogeny is not (Kroodsma, 1978; Kroodsma, 1996; Slater, 1983). Learning to sing is compounded out of the acts of vocalizing, socializing, discriminating, attending, imitating, improvising, rehearsing, and memorizing, to name only the most obvious. The study of birdsong is also natural for a task-oriented biology, as there is a clear outcome, how song affects the organism's ability to reproduce, an outcome with implications for understanding incipient processes of speciation. Singing is also an example of social learning, as species-typical songs pass from one generation to the next.

The last decade of study of birdsong has been productive but as overwhelming as the rest of science. Although Tinbergen's questions of cause, development, function, and adaptive value remain the mantra, the field has followed the trend of science in general of increased specialization. Thus, to get answers to all four of Tinbergen's questions for the same species is difficult. Part of the problem is that a major outcome of the last several decades has also been one that does not easily fit into Tinbergen's schema, the finding of tremendous inter- and intraspecific diversity. Even among the less than 5-10% of all 4000 or so songbird species that have been well studied, each new fact seems to halve or quarter the scope of a previous generalization. Some birds sing many different melodies, others just one; some birds share songs with neighbors, some do not; some species imitate, others improvise; some learn only when

young, others for much longer, some birds that learn song are technically not songbirds, but parrots or parakeets. Thus, even this single sea of facts has risen to daunting size.

One rule appears to hold: young learners (typically males) need to hear adults sing to develop species-typical song (Kroodsma, 1982; Kroodsma & Baylis, 1982). This statement is also true for the species we have studied: the brown-headed cowbird, *Molothrus ater*. But, to read our own early work and others' reports of our work up to and including the present, the cowbird would seem to be the exception to the rule. The textbook story of the cowbird, which we have helped to create, often reads as if cowbirds are the exception to the rule, i.e., when reared without adult males, young males produce a species-acceptable song, unlike the ontogeny of other songbirds. What is the truth?

Because cowbirds are brood parasites, it has always been easy to suppose that their song development differed from that of other passerines (see Lehrman, 1970; Lehrman, 1974; Mayr, 1974). The species had originally appealed to us as its upbringing suggested that it might display exceptions to common developmental rules as the young are not raised by their own species, but by a variety of host species (Friedmann, 1929). We thought that viewing exceptions would more clearly demarcate general rules and the conditions supporting them; others had expressed similar opinions (e.g., Lehrman, 1974; Mayr, 1974).

In 1977, we published data suggesting that we had found such a difference (King & West, 1977). In that study, we had hand-reared naive male cowbirds, which had never heard adult male song, and recorded their songs when they reached sexual maturity. The songs the naive males produced differed on several acoustic dimensions from a sample of over 400 songs of wild males from the same geographic area. Thus, the naive males appeared to be like other songbirds. This was not what the idiosyncratic cowbird was "supposed" to do. But we also played the songs back to female cowbirds, along with the songs of other species and control songs from a wild male. As expected, females responded more to cowbird songs than those of other species. The surprise was that the females responded most to the atypical songs of the naive males. Thus, although naive male songs were abnormal, to females, they seemed supernormal.

Now here was a good story: cowbirds naturally deprived of early experience have just the fail-safe mechanism a brood parasite should have! As we wrote, here was "an independent system designed to insure identification during the most important context, the breeding season..." (King & West, 1977, p. 1004). Maybe their songs are atypical, but they work. The mechanism seemed quite simple: nature had innately endowed young males with sexy song elements. The "just-so-ish" gist of the story undoubtedly acted as a magnet to hold the parts together and worked against us when we tried to pull it apart.

As it turns out, we were wrong on three counts. First, across playback experiments, on average, female cowbirds do not find atypical songs of acoustically naive males more stimulating than the songs of wild, successfully breeding males (West, King, & Freeberg, 1994). We had unwittingly created conditions favoring the naive males' songs, as is discussed below. Second,

we now know that socially and acoustically naive males cannot obtain actual copulations with their atypical songs, even if the songs are acoustically potent (Freeberg, King, & West, 1995; West, King, & Freeberg, 1996). Third, the social experience of females affects playback responsiveness and mate choice and thus may change which songs they find attractive (Freeberg, 1996; Freeberg, 1997).

Concerning the first point, years of playback tests of females housed without males have revealed that females' copulatory responsiveness changes with the range of song stimulation presented. Thus, if females only hear the songs of acoustically naive males, they may respond on roughly 50% of the trials, as given their male-deprived state, these songs are the "best" available. But, if species-typical songs from wild males are introduced into the same playback set, responding to the songs of the naive males quickly drops relative to the wild males' songs, with only some overlap between the least effective wild songs and most effective naive songs (West, et al., 1994). The relativity of female responsiveness could have affected the original 1977 experiment. The 1977 females probably responded more to the atypical songs of the naive males because we did not test the full range of variation in wild cowbird song. The songs of the naive males may not have been supernormal; the songs of the wild males we played back may have been subnormal. Hand-reared acoustically naive males produce a much wider range of variation than do wild males, thus some naive males' songs can be among the very best, others, among the very worst. We will explain more about the second and third count subsequently, but in general, as we learned more about the actual task of courtship and mating, we saw ever increasing limitations to our proposition about an innate safety net.

We have written many times about these facts-turned-fictions, but we still find the old facts in new places (Ball & Hulse, 1998; Michel & Moore, 1995). Part of the reason is our own doing: we often discussed the seemingly anomalous nature of the original finding, supernormal song in naive males, in an attempt to focus attention on the need to understand more current work. Our strategy did not work: what was remembered was the possibility of supernormal behavior, the mirage, and not the possibility of contextual relativity. Even after a paper entitled, "Innate is not enough," we found our colleagues dubbing cowbirds as exceptions of songbirds' developmental rules (West, King, & Duff, 1990). In that paper, we recounted the many studies after 1977 showing that such males could not succeed because females used characteristics other than song to choose mates, such as dominance and courtship persistence. We also showed that adult males attended to very effective songs from young males and would attack naive males singing such songs. Thus, supernormality, even if it did develop, could be detrimental. These males were like Kuo's rat-loving kittens or other in-vitro preparations (Kuo, 1967). Like others, we had created animals with behaviors that had no context outside the laboratory. But, still, the message was not clear.

The play's the thing...

During the last few years, we have taken a more direct approach to understanding the task of song development by focusing on its goal, successful courtship. At the same time, we have used contexts in which the animals lived in groups or were tested in groups to begin to incorporate the social composition of learning. To see what social and vocal skills males must have to succeed, we have looked at the parts of the story in a more connected manner. Thus, we carried out a series of studies in which the major players were naive male cowbirds. We followed them from 75 days of age until two or three years of age. We exploited social surroundings to look directly for any fail-safe system based on vocal behavior. The findings summarized below come from three longitudinal studies, measuring the effects of social experience on vocal outcomes (Freeberg, 1996; Freeberg, et al., 1995; King, West, & Freeberg, 1996; West, et al., 1996; West, King, & Freeberg, 1997). We have omitted many details in favor of synopses of the studies. All the details are published. In writing up the studies, however, we found that the conventional elements of style for journal writing did not capture the dramas we had watched unfold. Although each year's study was a true experiment with independent and dependent variables, it seemed more like a summer theater production, with us as producers, not experimenters. That sense came from the considerable backstage efforts we needed to introduce more elements of social settings into each scene and because the script was organic and dynamic. We did not know what the major players would do: in this case, young male cowbirds being asked to use their song outside the confines of a sound chamber.

To create male cowbirds with different social and song histories, we housed young male cowbirds individually in sound-attenuating chambers. Half of the males were provided with several female cowbirds from their local area (Fmales). The other half we housed with canaries (Cmales). By the time, the action took place in the spring, the young males had had extensive social exposure to either their female cowbird or canary companions, but had not been exposed to the sights or sounds of adult male cowbirds since they were fledglings.

The first act took place in early May after we had removed the young males from their female or canary companions and put them in two flight cages by group. To look at the males' behavior when faced with new cage mates, we watched each male, in two separate sessions, while in a test flight cage with two unfamiliar female cowbirds and two canaries. Thus, we retained much of the simplicity of their original housing, but allowed the males more choice. Would the males discriminate their species and spend more time with cowbirds than canaries? Would they court the females? In this context, we began to see unfold what our playback methods could not reveal. The Fmales sang and courted the female cowbirds, albeit only haphazardly compared to what normally reared males would do. But the Cmales appeared to

court the canaries. Even when females approached and solicited courtship, the Cmales' attention was on the new canaries. We saw no safety net for species identification during the breeding season, the time period we had targeted in our 1977 explanation. Moreover, the core behavior, the male's song, began to differentiate before our eyes: singing to a female appeared very different from singing to a male or singing directed to no individual.

The subsequent acts occurred in large aviaries, where life was very different for the previously sheltered C and Fmales. In the aviaries were various classes of birds: canaries, starlings, female cowbirds from two geographic areas, and eventually adult male cowbirds from the same respective populations. There were, of course, many other differences including rich opportunities for foraging to encounters with resident frogs in the aviaries' ponds. Thus, the C and Fmales could do many things, many of which had nothing to do with courtship. In these socially rich conditions, we looked to see if the Cmales would give up their unreciprocated pursuit of the canaries and to see whether the Fmales could court female cowbirds selectively. Would the Fmales show more attention to unfamiliar females from their own population as opposed to females from a distant area? And, what would the males do with one another? We gave the birds time to show us what they could or could not do. These were not 20-minute tests, but 2 or 3 hours of observation 7 days/week for 6 weeks.

The Cmales showed no measurable changes in their social orientation; indeed, it seemed all the more amazing to watch in the large expanse of the aviaries. The Cmales would fly by female cowbirds with no more attention than they gave to the starlings. But the Fmales, who had attended to females when in the confines of the flight cage, now focused most of their attention on each other. They reminded the observers of teenagers at a dance where the boys talk together across the room from the girls. Some of the Fmales did sing to females but were rarely successful in obtaining a copulation or maintaining the persistent following and accompaniment of the female as seen in nature or in our aviaries with wild caught males. The Fmales also showed no selectivity toward their own population. Were the females making the yearling males look bad? Unlikely. The females were responsive when sung to and did copulate with the two males who sang the most to them. They also attended to wild males who were attracted to the goings-on in the aviary and sang to the birds through the wire. Thus, the F and Cmales' lack of interest in females did not appear to originate in actions by the females.

We wondered if role models would help and so midway through the breeding season, we brought in adult males. The setting re-organized almost immediately, but not to the young males' advantage. Females that had been rarely seen were now highly visible in front of the adult males. We saw typical courtship and strong patterns of mate assortment by geographic population, but only among the newly added adults. When we repeated the entire production over the next two years with a new cohort from a different population, we saw essentially the same thing, naive male cowbirds appeared largely uninterested and highly non selective when attending to females (although we saw less overt attention to canaries). Even when females did

adopt copulatory postures, males did not mount. About 40% of the time, males sang and only watched as females solicited in front of them. In today's vernacular, the males didn't get it.

We wanted to publish the data from the first cohort in bold print as "COWBIRD COURTS CANARY" to end any argument about the flaws in the 1977 study. The new studies were sweeping dismissals of our original proposition of the existence of a built-in identification program geared especially to mate recognition. Under the social conditions present in the more complex settings, we saw that behavioral pieces did not suddenly or gradually snap into place, an image fostered in many ethological works by connotations of terms such as innate releasing mechanisms. Prior to this work in the aviaries, we had focused on whether the birds could develop the appropriate behavioral forms in the first place. It had not occurred to us to ask if the animals would know how to connect the behaviors to appropriate goals. These data also put the female playback procedure in a new light: we realized the importance of the seemingly innocuous tasks that we carried out on behalf of the males, i.e., choosing a song and getting the song close to a female before playing it. The importance of proximity is paramount. Indeed, we had learned by using the playback bioassay that even very small changes increasing the distance at which songs were recorded greatly depressed female responding. The song is a close distance communication signal: the male is often less than a foot away singing at about 85-90 dB... hardly, a whispered sweet nothing.

In sum, what we did by creating a more social setting was to join together many potential parts of a young male cowbird's ecological world and put him in its midst. By parts, we mean the social tasks possible with different classes of individuals. Thus, in the aviaries, we had different species, different ages and sexes of cowbirds, individuals varying in experience and geographic background. We also changed the social dynamics periodically by adding or removing birds as we tested courtship competence. Thus, when asking the males to do more than one thing at a time, we were specifically requiring that song be placed in a realistic contextual state, allowing us to see how much power it did or did not have as a single behavior, a different kind of bioassay than playbacks to females. After using that setting, it is even difficult to call song a single behavior because whether it is directed to males or females or no one produces different immediate consequences.

What was missing among our subjects was the ability to connect behaviors to outcomes. Lorenz (1957) called the presence of such automatic connectivity, "the hereditary teaching machine," and considered it essential to understanding how innate behaviors worked, i.e., how behavioral pieces were shaped to fit together and work as a unit. He assumed the connectivity was also innate: in cowbirds, it was the connectivity, not the behaviors, what was missing. What the birds did not seem to know was what to do with their behaviors. In fact, the arrow-like progression does not always work in stickleback (Bolyard & Rowland, 1996; Rowland, 1994). Like cowbirds, social learning and perception of context affects recognition and response to cues so

that behaviors are directed in other ways. Even the famous red belly of the female stickleback does not always elicit courtship from a male.

The female bioassay of song: Buyer beware.

In telling this story before, it is at about this point that someone usually says, "OK, so males can learn, but isn't the safety net in the female? Maybe, you were closer to the truth than you thought." The answer is no, the female does not have a genetically constrained safety net for mate recognition. There are three parts to the female's story. First, we must say more about the functional cornerstone of so much of our work, the female bioassay. Then, we discuss her actual role in song development. As it turns out, looking at males and females as a unit does suggest a safety net of sorts, but one woven experientially out of social interaction between the sexes. Third, we will show how the system might work in a study of cultural transmission.

Thorndike noted that scientists, being human, are quick to see the marvelous rather than the mundane (Thorndike, 1911/1965) The result of this tendency may be to read more into what is actually there in a single measure if it at the marvelous end of the continuum. Certainly to us, the bioassay of song function we were using resided at the marvelous end. The response is rapid and unambiguous: the sound goes in the female's ear and down her spine, sometimes before the song is even over. At the time we began using the bioassay, the only alternative was to judge the normality or typicality of males' songs by looking visually at sonograms of song structure. While this measure has many uses, it is functionally constrained because our eyes are not tuned to female cowbirds' ears. Indeed, the parts of the song that first struck us as most atypical turned out to be ones that did not influence female responsiveness. We judged the terminal whistle to be the most differentiating feature, but females' copulatory postures happened before the whistle.

Playback tests have now been carried out for a number of songbird species, but we suspect that we hold the record for continuous use of the song bioassay, having done at least one playback study of female cowbirds every year from 1973 to 1997 (Searcy, 1992). We have gained an extraordinary appreciation for the experimental context and task demands. We now know that female responsiveness to song in the context of playback testing has limitations that must be well understood to interpret outcomes. For example, responsiveness is relative to the kind and amount of stimulation received, as noted earlier. For example, we have done playbacks to learn about specific acoustic dimensions of song where all we have played to females are songs from another cowbird subspecies, they respond frequently in this context (King & West, 1983a). They would not, however, respond as frequently, or at all, if they also heard songs of their own subspecies. Thus, the bioassay only gives the "relative appeal" of a song in that single context. Thus, one must identify what aspects of playback responding carry across contexts.

We have identified one parameter of female responding that may tap a stable form of individual variation, a female's pattern of choosiness. In the 24 years of testing, we find stable

patterns of individual variation among females within and between experiments. Some females are highly responsive, some less so, and each year, one or two never respond at all out of a sample of 20 or so. To calibrate the females across yearly cohorts, i.e. to see if the range of responsiveness is similar, we have often used the same set of playback songs across some years. To do so, we created a special playback set composed of six songs we knew were consistent winners and six that were consistent losers. In the lab, it became known as the good-bad test tape. We found extraordinary stability across sets of females in their reactions to the songs, each agreeing with previous years' females with correlations above $r_s = +0.80$ (if all the females were from the same geographic population) (West & King, 1986).

As we studied the problem, we realized, however, that females expressed their preferences differently: some responded very frequently, and thus, although they responded more often to good songs, they also responded on a number of trials to bad songs. Other females responded less often in general, but when they did respond, it was to the same good songs as the other females, and rarely to bad songs. The latter females were thus more "choosy" or more selective, conserving copulatory energy for the best songs. It took several years to realize that every year we saw these two "types" of females. We were also led to this measure of choosiness because we had watched some females in the playback context and in breeding aviaries. The females that seemed most reactive to song, the least choosy, were often the ones not systematically courted by the males. Whereas the females that looked as if they were made of granite when males came near were vigorously pursued.

These individual differences were then used in a study of the anterior forebrain pathway within the song control system (Hamilton, King, Sengelaub, & West, 1997). We were especially interested in one nucleus, IMAN, as it has been implicated in initial song acquisition in male songbirds and was thus a logical candidate for receptive song acquisition in non-singing females (Bottjer & Arnold, 1986; Bottjer, Halsema, Brown, & Miesner, 1989; Nixdorf-Bergweiler, Lips, & Heinemann, 1995). It also was monomorphic between male and female cowbirds, an unusual finding relative to other songbirds where the female does not sing. We measured the volume of IMAN in a set of females following playback of the good-bad test tape. Selectivity or choosiness was highly positively correlated with volume of IMAN. Subsequently, the effect has been replicated in a second set of female cowbirds, from another geographic area using different "good-bad" songs.

No other significant correlates of choosiness were found with other song-related structures. Thus, non-singing female cowbirds possess a "song" nucleus typically described as necessary for initial acquisition of song in singing males and its size is comparable across sexes. Moreover, consistent individual differences among females mapped extraordinarily well onto neural variation in IMAN, providing an anatomical validation of the playback assay as tapping a reliable source of variation among females. Moreover, it taps variation in perceptual selectivity

at the level of individual differences in songs from males within a population, the level at which the discrimination occurs in nature.

Despite these elegant biological correlates, the female song bioassay simply cannot bear the burden of explanation that we originally assumed. It is a beautiful behavior and seductively believable, but true only in some light. It can be used profitably and reliably to learn much about song structure, the measure we wanted it to replace or supplement. Thus, we can use it to identify the kinds of acoustic properties that are necessary (but not sufficient) for a stimulating song to lead to copulation. But, no matter how much we learn about its neural structure or variation across females, it alone cannot predict copulatory success of males in the actual social task nature has set. Indeed, when one watches females in such a social setting or in the wild, one would wonder if females ever respond so positively or animatedly to a male. Thus, the power and concomitant danger of the female bioassay is its deceptive simplicity. It has fine features but fine print.

Mum' s the word: Breaking the female wall of silence.

These limitations of the use of the bioassay still leave unanswered questions about the development of female preferences, whether measured by playback or by watching courtship. In 1983, we concluded that females possessed an experientially "closed" system, a conclusion that was premature, and constitutes the second reason that the safety net cannot be assumed to be genetically provided (King & West, 1983b). We made the statement about lack of modifiability on the basis of a traditional laboratory design in which we housed acoustically naive, hand-reared female cowbirds with males from their own area or from another subspecies: 25 of 26 females preferred playbacks of their own populations' songs. The songs of the two subspecies differed acoustically in several ways, including the presence or absence of certain song elements altogether. We did find one population in Oklahoma, which is near a subspecies border, where similar housing did broaden females' preferences (King, West, & Eastzer, 1986). But, in general, under these conditions, social experience most often had no effect on female discrimination in playback tests of geographically distant song variants, a level of discrimination we admit may be ecologically irrelevant. But, our reason for now believing in an open system for females does not rest on having studied only populational preferences. It rests on having misconstrued the nature of the task of the female as primarily a listener and social bystander during song development.

The first major clue to the active nature of forming perceptual preferences was when we realized the procedures we had used to modify females had had the opposite effect. We discovered that the males we had been using as potential modifiers of female preference were in fact being modified by the females: their song repertoires were changing during the period of time the males were employed to affect female perception (King, et al., 1986; West & King, 1985). The females were not hearing stable renditions of the songs of the other subspecies of

males, but were gradually exposed to changing sounds as males began to include the song elements found in the female's home population. When male cowbirds were housed with canaries during the same time period, such changes did not occur in the males' repertoires (King & West, 1988). What were males and females doing? What was the task from their point of view?

This finding led us to study social interactions during development, well before the time of mate choice. We found that female cowbirds have the capacity to respond socially to emergent acoustic patterns from males (West & King, 1988a). We have found the effect in three populations representing the three subspecies of cowbirds. The most conspicuous evidence of social shaping was the discovery of the female's use of brief wing movements coincident with the male's singing of certain songs. Songs receiving wing strokes were more likely to be retained by males and to be more potent releasers of copulatory postures, relative to other songs from the same male not receiving wing strokes.

Wing strokes and other social actions of adult females are associated with different rates of progress through stages of vocal development of the young males. We have found that greater social interaction between the sexes leads to faster acquisition of stereotyped songs, earlier cessation of practice, and more potent song types. A major component of the social interactions is whether females stay when males sing or fly away, sometimes even before the song is finished being sung (Smith, King, & West, Submitted). Female proximity gives males an opportunity to receive more social feedback to individual songs and conversely, gives females more chances to shape content by more subtle cues such as wing stroking or beak or body movements.

Discovering the wing stroke and female shaping of song was a major breakthrough because it demonstrated beyond all doubt that female birds that do not sing can still affect the song learning process. Thus, imitation could not be the only route to song learning as had been proposed. The data showed that operant learning or shaping now had to be brought back into the picture, having been banished from the birdsong field at about the same time it was ruled out for imprinting (see also Marler & Nelson, 1993; Nelson & Marler, 1994). The discovery of female signaling is also a neat story because it also reveals a communication system embedded within the vocal learning system, a gestural system in which the female is the sender and the male is the receiver. But we hoped we have learned something in two decades and do not want to isolate wing stroking out of the entire system of yearlong social interaction. For our purposes in this chapter, the wing stroke is most appropriately viewed as a symbol of the kinds of ongoing, organizing processes that have often been missed in developmental studies because the actual nature of social interactions have been inferred, not investigated.

But the fact of female shaping still begs the question of possible female modifiability. Wing stroking and other responses could reflect innate or socially modified female perceptual biases. They probably reflect both. Female cowbirds appear to need no postnatal experience to show preferential responding to cowbird song as opposed to the song of heterospecifics, a

broad level of discrimination that may not come into play at all when birds breed, having been together in flocks for almost a year (West & King, 1988b). But, although females appear to discriminate cowbird song with no postnatal experience, the prior work does not rule out that social experience naturally changes or fine-tunes their preference, females show wide variation in choosiness. Is selectivity affected by social experience?

We are accumulating evidence suggesting that social experience does affect female song discrimination. For example, we compared the preferences of juvenile and adult females for atypical versus typical song from males of their local population. Adult females made finer distinctions among songs than did yearling females. These data suggest that juvenile females may not give as specific or fine tuned feedback to males, a proposition we still need to test (King, unpublished data). Ongoing work with adult and juvenile females in aviaries shows some effects: young males housed in an aviary with adult females were more successful at obtaining copulations with unfamiliar females than were males housed with yearling females (Schlossberg, unpublished data). Thus, there are differences in perceptual skills that seem related to experience.

Biasing female mate preferences: Opening the closed program

Powerful evidence of the implications of such plasticity comes from studies of mate preferences, not simply song preferences, carried out in our lab. In a two yearlong study, Freeberg (1996, 1997) studied the mate preferences of females given typical and atypical song stimulation. In a longitudinal design, he showed that social preferences of juvenile females for potential mates differed when the females were given different social experiences during their first year. The contrasting social experience consisted of residence in large aviaries with other young females and males from their own local population and with male and female adults either from their natal area or from a distant area. But the young females were not forced by physical constraints to be near the adult males or females, or the other juveniles, for that matter. Moreover, they could hear and see wild birds outside of the aviary. In the original work, the sound attenuating chambers offered none of these liberties.

Under these conditions, Freeberg found female mate preferences were predicted by social experience, not by geographic/genetic background. His design ruled out mate copying and another experiment reinforced the direction of effects: it is the female, not the male that controls whether copulations occur. But another test of the durability of the social effect followed. More remarkably, the learned differences in preferences were transmitted to a new generation of young males and females whose models were the former pupils from the original study, the experiential F1's.

Freeberg's work has several important implications. First, it shows the power of a social context. We had assumed in the 1983 study that housing females for almost an entire year with males from another cowbird population in triads in sound attenuating chambers would increase

the chances of finding malleability, perhaps even malleability not normally seen because of the unnatural context. Our assumption was in part intuition and part tradition. The conventional procedure for testing innate preferences in many animals is housing of the sort we used. Instead, we found malleability when females were faced with a seemingly more complex setting. Thus, failures in other species to find malleability may reflect hitherto unrecognized inhibitory effects of standard isolate housing (but see Payne et al. 2000).

Second, Freeberg's data show that female copulatory responsiveness toward males is malleable and male responsiveness to females is malleable. If that is the case, where is the net? What holds the system together? To understand this question again requires we step back and consider function. What are the advantages of a) female shaping of male song and b) social shaping of female preferences to reflect local experience?

Necessity is the mother of vocal invention

A critical task for all females, but especially in parasitic species or in species where males offer no resources, is mate assessment. What can a female cowbird use? Is it to her advantage to have an epigenetic stake in song ontogeny? We suggest that her involvement in song ontogeny allows her to implant quality detectors to be used by her local population later on.

We begin with the repeated finding from playback and mating studies that female cowbirds from local populations share preferences for specific song types. The work on choosiness was based on the finding that females show extremely high concordance within a set of songs. They "agree" as to the best and the worst and even in between show only moderate variation. The level of concordance among local females in responsiveness to song suggests that they are listening to or for the same acoustic features across different males. As it turns out, recent work looking at the specific acoustic features affected by female social interactions with males during song development show that across males, the same acoustic properties are affected even when males are with different females. Moreover, females that are most choosy (reserve all of their responding for only the best songs) have a different effect on males than do females that are less choosy. The males with the choosier females ultimately develop smaller repertoires of high playback quality than do the males with the seemingly more responsive but less selective females (King & West, 1989). We suspect that this effect is a simple form of partial reinforcement: males learn to pay more attention to feedback from choosy females because it occurs less often and thus has a higher "signal to noise" ratio. Thus, given social shaping by females, high homogeneity in preference should foster high vocal homogeneity among local males, at least for the parts of the song that elicit copulatory responding (the first half of the song).

If the acoustic features that females use in song or mate discrimination are ones that females can influence during song ontogeny, females would then be choosing males that display the most past attentiveness to female signals. But, and this is a critical feature, the

attentiveness need not be specific to a given male, i.e., we, in no way, mean that females prefer or even interact with the same individuals they may have interacted with earlier in the year. Indeed, in playback testing, we find no evidence at all that females respond more or less to the specific males they have been housed with than other males in the same experimental condition, but they do discriminate by condition (West & King, 1980). This is an effect we have seen in over 20 cohorts. Thus, the female's effect is generic.

But, as local females share a percept, the males most attentive to females in the spring, should show evidence of a widely shared percept in their songs. Thus, song becomes a potential index of male sensitivity to females. In the case of the cowbird, for a male to be affected by females' ontogenetic signals, he needs to do more than simply sing, as we have shown in several studies. He needs to be alert to changes in a female's behavior to connect his immediate behavior to her immediate response. Males that, for whatever reason, do not direct songs to females from close proximity do not develop potent songs.

Our studies of captive males' courtship show that some males, even with potent songs, fare poorly in courtship if they do not also display active attention to females (chasing, approaching, coming back for more after being pecked or ignored) and active attention to males (dominance, aggressiveness, and defense of females) (West, King, & Eastzer, 1981; West, et al., 1996). The latter form of interaction is equally important, although we have not emphasized it in this chapter. As noted earlier, males also discriminate potent songs and attend differently to males according to their social and vocal behavior. Thus, the female-implanted song structure is a potential handicap and as such, only serves the females' interest more completely as she assesses how males handle their vocal legacy.

Thus, when a female is courted by a male whose vocalizations contain female-shaped features (e.g. potency) and male-shaped courtship skills (e.g. dominance), she is using his compounded history of successful learning. This history can be operationally defined by measuring how effective males are at courting and copulating with the same females over time (consort persistence level or CPL). CPL is measure of the number of days in which a male meets a criterion of directing a certain number of songs at close proximity to the same female during a sampling period, divided by the number of days in the aviary (Eastzer, King, & West, 1985). CPL is thus implicitly assembled out of song structure, song use, and social vigilance to males and females, and all of these behaviors are assembled out of the nested parts we have been discussing. Not all males in our aviaries, even wild caught ones, seem to bring all of the parts together. For example, there are males that do not court but whose songs turn out to be highly potent releasers of copulatory postures. There are other males who sing and chase females frequently but also sing and chase males. In both cases, these males' CPL's are low. Thus, the female's part in stimulating social learning is one means to assay the degree of social learning.

How does social malleability in the female seen in Freeberg's work fit into this scenario? We suspect that Freeberg's effect rested on females' opportunity to see adult males and

females interact with one another and then with adults and juveniles. These experiences may have narrowed the female's preferences because the narrower vocal output correlated with social output of the males preferred by older females. In Terkel's studies of black rats, the only access to partially stripped pine cones (to practice stripping) came through the mother-pup bond. In cowbirds, the only access for young females to see the full range of song and its effects may come from life in a flock, in the company of other females, something we could not simulate in the prior work using small enclosures.

These data also suggest that CPL is the kind of unit on which females may assess males. The data also suggest the importance of visual attentiveness to that unit. The latter might seem obvious and not that noteworthy but most theories of song learning and its neural substrates have not looked for visual involvement because they were focused on a vocal part, not the social whole. If we are right that individual components of CPL such as potency or repertoire size (number of song types) or directing of songs to males or females must be assimilated into larger units, perhaps we should be able to see evidence of such integration in the song control region of the avian brain, in the same way we saw that choosiness mapped onto female perception. If so, it might add credibility to the practice used here for the CPL of "lumping" rather than "splitting," something many fear to do because it often smacks of a cover-up rather than a discovery.

The avian forebrain in songbirds contains two connected pathways formed by a series of discrete nuclei that appear to have differentiated roles in the motor production and sensory perception and learning of song. It is a distributed system with complex connectivity, perhaps in keeping with the complexity of the compound nature of the function of vocal behavior. To be brief, we studied the brains of adult males whose song and courtship histories were known in detail, with data from several years of each male (Hamilton, King, Sengelaub, & West, 1998). We looked at the traditional measure of song used in many such studies, song repertoire size, and found no correlations with any nucleus. We did find a strong but negative correlation between song potency and Area X, a nucleus thought to play a role in assimilation of developmental experience, perhaps in the winnowing of song to fewer patterns. But we also looked at visual areas in light of the knowledge of male's visual attention to females. Nucleus rotundus (Rt) is the largest nucleus in the avian visual system. Rt has been implicated in visual processing of texture, motion, shape, and color in pigeons (*Columbia livia*) (Shimizu & Karten, 1993; Shimizu, et al., 1997; Wang, et al., 1993). These qualities are clearly key components of social attention to conspecifics and thus could affect attentive singing behavior. Volume of Rt was most positively correlated with CPL (with less strong, but reliable correlations with potency and directed singing but none with repertoire size). The data are the first to implicate a visual nucleus in song use and to show that the utility of compound measures such as CPL. It is further anatomical validation of the role of social learning. Thus, male's visual attentiveness, the skill we believe unlocks his ability to learn from females and males, is important throughout ontogeny

and through the period of actual reproduction. And a female's assessment of a male's visual attentiveness may be facilitated when he uses vocal patterns males and females mutually shape. Thus, the safety net is not prebuilt into either sex, but socially built up between them.

These inferences lead to certain predictions about social life in cowbirds. Our data suggest that birds pay attention to age and sex of individuals, and can learn different things from such attention. Do the birds show any signs of attention to these dimensions? The data also suggest that social access to different age or sex classes may be important at certain points in the year. In the laboratory experiments, we provided the access, but what if the birds are left to themselves? We are now beginning to answer these questions using more complex social settings. We are completing an investigation of social context in a setting even more unstructured than Freeberg's. We spent a year watching a group of 74 cowbirds, juvenile and adult males and females, in a very large aviary (the aviary is as long as a football field, with multiple roosts, perching, and foraging areas). We measured social assortment by gathering data on "nearest neighbor" patterns, tallying which birds were within one foot of one another during sampling sessions. We also measured singing patterns and social context during singing. Would we see order at group and individual levels? Would we see the possibility of social transmission in patterns of proximity (Smith et al., in preparation)?

Briefly, we saw strong social assortment by age and by sex: young birds perched near each other, adults with each other, and the sexes segregated as well. Thus, we saw order at the level of attention to age and sex. There were some departures from these patterns, however, and these departures indicate windows of access for learning. First, in the late winter, young and adult males were found together much more often than in the fall when the ages remained apart. Second, throughout the year, adult females showed the least assortment by class. Said another way, they had more neighbors from all the classes, meaning juvenile males had access to them from the beginning. The adult females' pattern of sociality suggests that the social niche exists in more socially complex settings for the kinds of learning we saw in lab settings. Third, the young birds were more social, they were found in the company of some other bird more often than were adults. But, among the juveniles, the frequency of social contact still varied greatly. We followed the young males through their first breeding season looking at courtship competence. Even though all the young males had the same general social access of adult males and females, their CPL's ranged from 0 to 1. Thus, the opportunity for social interaction does not always translate into action or consequences. And, as hoped, we found correlations between social assortment and breeding success: juvenile males who associated more with adult males and juvenile males who showed more frequent social contacts had higher CPL's.

These data thus begin to lay out an epigenetic landscape created by the birds themselves. Given multiple access to food, shelter, perches, and roosts, the design of the aviary did not force the social order that appeared. The kinds of social dynamics we saw are

also found in wild avian populations. The observations also suggested that learning is available only through negotiating a social structure set by age and gender biases. In follow up work, we are looking at aviaries where not all ages and classes are present. One of the current aviaries is composed only of adult and juvenile females. With no males around, the ambient social atmosphere does not involve reacting to song. Throughout the fall and early winter, we have not seen segregation by sex, adult and juvenile females intermix freely. Thus, attention to age may depend on attention to gender. It is hard to resist seeing the females as living a relaxed life, as they experience a context with no competition for males or by males. But will the young females have learned to be discriminating listeners? That is the next question on the agenda.

A call for task biology: An interest in reality

Consider the fruit fly, *Drosophila melanogaster*, which thousands of geneticists have studied. For over 80 years, it has been at the center of genetic research.... That effort has paid off... we can do astounding things: we can clone fly cells and remove and insert genes at will.....But after all that investment and knowledge we still do not know how the fruit fly survives through the winter. (Suzuki & Knudson, 1989, p. 21-22, cited in Michel & Moore, 1995).

By reviewing our work in detail, we hope to have demonstrated that the question of the reliability or quality of behaviors used as focal points in research must be guided by ecological principles. Once behaviors are taken too far afield of their natural settings, the nature of the knowledge acquired loses functional value. What unites the cowbird work to the earlier textbook examples is the danger of studying behavior without attention and respect for the contexts present in the environments of species. Hence, the challenge before us is for ecological task biology to trace connections between the tasks on which we base our knowledge and the contexts in which organisms actually display them. Establishing task biology, i.e., paying closer attention to what animals really do, is, however, not enough. We have to look at more animals doing more things. We need to expand horizons on the tasks and on the organisms we study. When Charles Darwin took his voyage around the world, he was shaken as much, if not more, by the variation he saw in human form, as opposed to the varieties of animal and plant forms (Rozzi, 1999). How could he reconcile the mannerisms of his English colleagues with those of South American tribesmen? To Darwin, the latter acted like animals, sexually exuberant and morally vacant primates. Here was the literal "descent of man" in the flesh. Had Darwin not left England, he would not have witnessed variation that struck so important a chord. What Darwin witnessed was an assembling of the parts of human behavior in a manner and to a degree he thought not possible for one and the same species. It was culture shock writ large.

When conceiving of task biology, Darwin's experience looms large in our thinking. We believe that some of the inertia to adopt contextual approaches comes from fear of having to reconcile the variations in behavior one sees when contexts shift. It is not easy to introduce change into paradigms. Just try to shake researchers loose from college sophomores or white rats, let alone direct them to South America! In 1989, Kroodsma pointed out possible problems with playback designs used to test songbirds' responses to the songs and suggested changes, changes requiring wider sampling of behavior across different populations of songs and birds (Kroodsma, 1989). These changes were important because of the ongoing debates about the existence and function of song dialects, acoustic variation among songs within neighboring populations of the same species. Many of the concerns he expressed eventually led to needed changes in methodology and less reliance of studies of single populations. But, not, we should note without a fuss. The original article was published in *Animal Behaviour*, as were the many short communications from those who felt wounded by the article or who simply disagreed on other methodological grounds. Several editors of the journal began to call it the "Kroodsma" section of journal. We recommend readers take a look because it shows how hard it can be to introduce change, especially when the changes contain the implication that some past work could not now be considered true or definitive. And keep in mind that the journal published only the most mannerly end of the continuum (Kroodsma, 1992).

We have made suggestions comparable to Kroodsma's about the asocial conditions of the tradition of work termed "animal learning," work that now forms the basis for many conceptualizations of the workings of the central nervous system. If Kroodsma temporarily hit a stonewall, we continue to hit the rock of Gibraltar. We do not know what argument to use to persuade researchers that a wider sampling of the conditions in which animals learn is essential. Perhaps, the decline in the numbers of researchers interested in such paradigms reveals the ultimate answer, if we are patient, their students will see it themselves. But knowledge about social learning exists now and already shows the need to consider how the narrow use of tasks employed in animal models could serve to defeat integrative goals.

The study of learning is thus at a decision point. We can continue to learn about parts, in even more exquisite technological detail, or we can study animals in social contexts where animals must do more than one thing at a time. A contextual or task biology has to begin with actual tasks and guard against oversimplifying the animal's options. More of the behavioral parts, the separated abilities, must be looked at the same time in the same settings, and then in different settings at different times. One of the great surprises we have found in putting animals in larger groups and giving them more social freedom is that it has not deprived us of the ability to see or measure developmental change. Behavior and its ontogeny are a complex system, as the term is formally used in the lexicon of adaptive systems or complexity theory. A fundamental finding of such research is the imbalance between effects on the behavior of an excised part and the system from which it was excised. The greatest effect is on that which is

removed and not on the system from which it was removed, e.g., think of cutting a leaf from a plant or taking a single worker ant from a colony (Bar, 1997). Isolating individuals from the social system in which they normally live and from the environment to which they are adapted can produce the same imbalance and lead to distortion in theories. The new approaches vastly increase the burden of description to the point that new technological tools are needed to increase feasibility. Fortunately, video and audio technology, biological telemetry, behavior-based robotics, voice recognition data collection, computational models, and oceanic amounts of raw computing power are now here to assist in handling what may seem like added complexity, but which in the end, may be a restoration of order. Thus, we may be able to use the newly available computational power to find patterns in social settings hard to see with the naked eye and then to vary these patterns in simulations to guide the empirical steps (Schank and Alberts, 1998).

End of the day

It is easy to look, but learning to see is a more gradual business, and it sneaks up on you by stealth, the sign that it is happening is the fact that you are not bored by the unspectacular. (Hughes, 1999)

We stated at the outset that the study of behavior had become a transfer station for many scientists, not a place to take up permanent residence. In a "drive-thru" age, simple, particulate behaviors, with no social or ecological strings, are the easiest to package and sell. We hope to have made some progress in these pages in stimulating interest in arranging longer visits and creating bigger bundles. Such changes are needed to address what is disquieting about current integrative science. It is not the idea itself, but its present instantiation. That instantiation includes a remarkable confidence in downwardly spiraling reductionism, with only a nod toward the possibility that behavior in context is poorly studied and poorly understood.

And it is on this very point that the mission of the "HHS Genome" causes concern. We cannot expect molecular geneticists to know the fragile state of behavioral knowledge about concepts such as intelligence, aggression, imitation, or risk taking. These constructs may be especially attractive to molecular geneticists because they seem structurally similar to diseases, constructs with which the field is already familiar. Although diseases are softer categories than many might believe, they are clearly robust entities compared to behavioral phenomena. If those using genomics do not understand the fragility of behaviors, they may not only be wasting time seeking things that are not there, but they may also place society in a perilous state. The call for more behaviorists to work directly with geneticists will help but the behaviorists will need a real backbone to resist restricting the range of phenomena and even the organisms (use mice, not rats, we are told) to those geneticists see as tractable (Azar,

2000). If we use mice, we should use mice (plural) with work to do, with the tasks tapping the workings of ecology and evolution. Honeybee genomics is setting a fascinating example, as the natural busyness of bees has not been separated from the business of science (Page & Robinson, 1991).

We have argued strongly for creating methods and measures that capture socially emergent phenomena, behaviors co-defined by settings and by individuals. The reality of emergent outcomes is not hard to illustrate. Consider the matter of producing RBI's (runs batted in) by a hitter in baseball). RBI's require hitting ability but also a pitcher, fielders, catcher, umpires, AND the performance of the previous batters. The matter may sound trivial when couched in terms of baseball (but see Gould, 1996 for evolutionary analyses). An RBI, however, is a direct measure of social dynamics and many of the measures of human behavior we seek to understand bear analogous properties. Now consider whether there could be a gene or genes for hitting RBI's. Specifying the task dynamics for such a search swiftly exposes the asocial and nondynamic assumptions of the HHS Genome. The never-ending discussion among true sports fans of a player's or team's "statistics" reveals a respect for natural history we need to recover.

An emergent measure we discussed earlier in cowbirds, persistence in courtship (CPL), requires singing ability but also requires receivers and rivals whose roles and abilities are as differentiated and as necessary as baseball teammates are to achieving an RBI. Ecological, temporal, social, and individual probabilities must combine to afford the possibility of the outcome. Thus, another way to state our reservations about the mapping of genes to behaviors, even in a metaphorical sense, is to suggest that it perpetuates the very dangerous idea that functional behaviors are literally self-contained. We believe that this is the mirage luring some would-be mappers onto the HHS Genome -- the illusory view that the behavior we see before us is a property of the individual organism. We may be focusing at one moment in time on only this organism, but the contributions of those we are simultaneously ignoring are no less real.

And so we return to our original message in a bottle. Genes inherit a nested set of environments that lead to a succession of biological products, some of which are mappable to familiar categories such as cells, limbs, organs, reflexes, movements, etc. But, at all of these stages, effects, from other organisms and environments co- occur -- hidden correlates with stealth-like properties easily missed if we are not looking. But the effects are real and measurable. To abide by contextual rules will require an active effort to restructure our science. Part of that process will be looking at past work to see how the original need to simplify, reduce, or take out of context has affected knowledge as a whole. Part of the process will be recognizing that the lives of real organisms have somehow slipped out of the big picture. Part of the process will be the willingness to collide with present paradigms. At times, the forward momentum of big science makes these goals seem as improbable as being able to hold back an ocean with one's hands (Seaton, 1992). But the history of science is also a story of

highly improbable successes and extraordinary amounts of effort. Confronting an ocean, however hard, is what science is about...not maintaining a mirage...however lovely, however grand.

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