

Behavioral Science, Engineering and Poetry Revisited

By: George F. Michel

[Michel, GF](#) (2010). Behavioral Science, Engineering and Poetry Revisited. Journal of Comparative Psychology, 124(3), 336-341. [DOI: 10.1037/a0017355](#)

Made available courtesy of the American Psychological Association. This article may not exactly replicate the final version published in the APA journal. It is not the copy of record.

Abstract:

Forty years ago, Lehrman (1971) identified 2 orientations to the study of animal behavior. The natural history orientation conducted field and lab research designed to reveal how animals cope with the circumstances of their natural environment. Such research reveals the diversity among different types of animals and differences between the world of animals and the world of humans (i.e., “poetry”). In contrast, the anthropocentric orientation studies animals either to generate animal-derived general laws applicable to humans or to provide experimental information that, for ethical and practical reasons, cannot be acquired from human research. The primary motivation for the anthropocentric orientation is to provide workable models for investigating specifically human problems (i.e., “engineering”). Evidence is presented from the study of bird song that demonstrates the contribution that the “poetic” approach can make to anthropocentric (“engineering”) concerns.

Keywords: psychology | comparative psychology | animal models | behavioral science | bird song | ethology

Article:

Forty years ago, Lehrman (1971) argued that there were two legitimate orientations to the study of animal behavior. These were described subsequently as the anthropocentric orientation and the natural history orientation (Michel & Moore, 1995). The goal of animal behavior investigations from the anthropocentric orientation is to solve human societal problems such as eliminating mental illness, controlling aggression, improving education, understanding psychosomatic diseases, combating stress, and so forth. This goal would strike most of us as an appropriate and fundamental justification for the activities of those scientists studying animal behavior. According to Lehrman, a scientist, like an engineer, is engaged in trying to understand the world, partly for the purpose of gaining control over it and being able to manipulate it, partly to make it over... [and thereby]... bettering the conditions of human life. (Lehrman, 1971, p. 471)

Two types of investigation of animal behavior may be distinguished in the attempt to achieve the goal of the anthropocentric orientation. One type is designed to investigate animal behavior so as to reveal and define the general principles, or the general mechanisms, of behavior that apply to

most, if not all, animals (or, at least, all mammals). Identification of such general principles or mechanisms of animal behavior would lead to their use in attempts to solve human behavioral problems. This is analogous to the identification of general principles or mechanisms of physiology, derived from animal research, which then may be used to address human biomedical (physiological) problems.

A second type of investigation is designed to identify an animal model for certain aspects of human behavioral functioning so that experimental manipulations may be conducted on that animal model which cannot be conducted ethically on humans. In this case, general principles or mechanisms need not be assumed—only a good correspondence between the animal model and human condition. Of course, this begs the question of what constitutes a “good correspondence.” Animal models of human conditions are always a compromise between those whose mechanisms have too close a correspondence (thereby failing to operate as a simpler to understand and manipulate mechanism) and those that have too distant a correspondence (thereby not accurate enough to serve as a model).

Modern neuroscience uses selected animal behavior model systems to identify mechanisms that may operate similarly in humans (e.g., specific mouse models for schizophrenia, autism, depression). The animal model provides the experimental information about causes that, for ethical (especially in neuroscience) or practical reasons, cannot be acquired from human research. In both types of anthropocentric-oriented investigation, the primary motivation for studying animal behavior is to provide workable tools or models for investigating specifically human problems in psychology. However, species that are considered good models of a particular behavior may prove to be not particularly good models when their behavior is more fully examined within the natural history-oriented frame.

In contrast to the anthropocentric orientation, the perspective from the natural history orientation is that the behavioral life of the animal itself poses problems for the investigator. The scientist is motivated to study those behaviors that enable animals to cope with the circumstances of their natural environments. Therefore, they study behavior either in the setting within which the animal evolved (field research) or in a more controlled “laboratory” setting that would permit relating the results of their investigations to the field setting. An implicit goal of the research is to understand how an animal's behavior is related to evolutionary and ecological processes. This approach, most often associated with the science of ethology (cf. Kruuk, 2003), considers the specific character of individual and group behavioral functioning to be embedded in complex social and ecological frameworks that differ among species. The animals' behavioral characteristics adapt them to different natural ecological and social conditions. Therefore, the units of the behavior studied may be considered “natural” units (i.e., those behaviors expressed in the animal's natural habitat).

The natural history-oriented scientist is interested in how the animal's behavior contributes to both the construction and exploitation of its world. Perhaps influenced by his close association

with many ethologists (cf. Rosenblatt, 1995), Lehrman proposed that such investigators typically express genuine wonder and curiosity about animals and their worlds. These scientists are sensitive to the striking diversity in the worlds of animals. Within this orientation, the contemplation and appreciation of the complexities of nature can be valuable human aims (much like art), independent of their immediate usefulness for improving human life. Therefore, although the results of the research may not reveal anything of direct use for resolving the problems of human behavior, they expand our understanding of animal behavior in nature and illuminate the characteristics of our own unique place therein.

[I]n addition to (or instead of) serving a function like that of an engineer, the scientist can also serve a function like that of an artist, of a painter or poet... [to see] things in a way that no one has seen them before... This function is that of widening and enriching the content of human consciousness, and of increasing the depth of contact that human beings, scientists and nonscientists as well, can have with the world around them. (Lehrman, 1971, p. 471)

Because of the troubled state of our society and our concern with understanding ourselves so as to improve human life, the anthropocentric orientation has had wide appeal on pragmatic grounds and the natural history orientation may appear to be a luxury. This is especially true when expensive animal research must rely on public support. Support is contingent on the degree to which research focuses on human problems. Such pressure forces even those scientists with a natural history orientation to cast their research within the frame of an anthropocentric orientation. Although knowledge gained from the anthropocentric orientation has obvious relevance to humans, the general fund of knowledge gained through studying the extraordinary diversity in the animal kingdom can be applied in numerous and often unexpected ways to these same ends (cf. Michel, 2001; Michel & Moore, 1995).

Michel and Moore (1995) identified four broad areas of human psychological research which have benefited from the incorporation of research conducted from a natural history orientation. These areas experienced a transformation of such concepts as “attachment,” “critical period,” “aggression,” and “abnormal” as a consequence of incorporating information derived from natural history-oriented research. Although these concepts are derived from human experiences created within the frame of language and sociocultural conditions, they acquire new meanings when forced to account for animal behavior, which lacks such a frame. Moreover, these new meanings take on even greater diversity when each concept is placed in the context of the socioecological frame relevant to the species being studied.

Natural history-oriented empirical research reveals how the specific pattern of interaction among the behavioral characteristics of the participants in an encounter prompt adoption of the descriptors “attachment” or “aggression” (Cairns, 1972a, 1972b). Concepts such as “attachment” and “aggression,” when applied in natural history-oriented animal research, become descriptors of patterns of interaction among two or more individuals rather than attributes characteristic of a single individual (as they are used in human and anthropocentric

research). Similarly, “abnormal” is also not an aspect of the individual but rather takes on meaning only as the individual's behavior relates to the range of variation in behavior observed among other species members within their typical socioecological frame (Gollin, Stahl, & Morgan, 1989). Within natural history-oriented research, “critical period” becomes less associated with time (or the age of the individual) and acquires a more developmental meaning involving multiple pathways and questions of “equifinality” (Michel & Tyler, 2005).

The natural history orientation also permits identification of the special features of human development including imitation, play, and culture. Although many species exhibit imitation (Galef, 1988), only humans combine imitation with explicit modeling to form deliberate teaching. Humans deliberately model and reinforce specific behaviors for their young to acquire, and this likely forms the basis of culture and society. Moreover, although many species exhibit play behavior (Burghardt, 2005), only humans expand such behavior into adulthood to create phenomena such as competitive and noncompetitive sports, entertainment (theatre, music, literature, poetry), art (musical composition, painting and sculpting, architecture), and hobbies. Then, in turn, humans impose such activities (in a somewhat modified form) on their developing offspring. These activities, too, form the basis of culture and society. For humans, society becomes a set of relationships and interactions among group members governed entirely through abstract principles and notions that constitute a culture. These are just a few of the ways in which knowledge obtained from a natural history orientation can illuminate human psychology.

The general fund of knowledge gained by studying the extraordinary diversity in the animal kingdom can be applied in numerous, and often unexpected, ways of resolving human behavioral problems. Indeed, if provided with robust support, a natural history-oriented comparative approach complements that of the model system research technique to provide a better understanding of the neural mechanisms underlying the diversity of behavior. This understanding is essential to bettering the conditions of humans. Of course, it is impractical to insist that all species be investigated from a natural history orientation. Instead, my argument is that natural history-oriented research should be supported to the same level and accorded the same attention as anthropocentric-oriented research.

In support of that argument, I describe briefly the study of birdsong, because scientists have investigated this behavior using both orientations and it nicely illustrates the differences in knowledge and perspective that the two orientations generate. Birdsong is a “natural” pattern of behavior rather than the kind of contrived behavior that is more commonly used in the engineering approach. However, by importing birdsong into the engineering approach, its “natural” character has been distorted in the process. The importation has necessitated the adoption of specific model species (convenient because of the simplicity of their song and ease of rearing in the laboratory), which has truncated the range of song-learning processes found in nature. I propose that the specific model species used to study birdsong fail to reveal important differences among song species and, hence, weaken their value as models of either birdsong in general or any human trait (e.g., speech acquisition or early learning).

However, by combining information derived from natural history-oriented research with that derived from the model species, we can achieve greater insight into the mechanisms (and their development) that govern the diversity of birdsong. This insight may help reframe our investigation of human traits in ways that may improve our understanding of their development and control. My brief description of the phenomena of birdsong draws heavily from recent publications by Brenowitz and Beecher (2005), Catchpoole and Slater (1995), and Williams (2004).

It is generally assumed that the neural systems that are involved in song learning in songbirds are a valuable model for studying general neural mechanisms of learning, particularly imitative vocal learning (Brainard & Doupe, 2000). Therefore, research on birdsong exhibits both types of anthropocentric-oriented investigation. It is a model system for revealing general principles and mechanisms of early learning and memory, and it is a model of a specifically human phenomenon (i.e., imitative vocal learning of speech and language). As a model in the latter sense, birdsong is characterized by three features: (1) Several species have well-defined sensitive periods for learning song similar to the presumed sensitive periods in the acquisition of language by humans; (2) song learning and song production seem to be dependent on discrete, well-defined neural circuits, as is presumed for human language; (3) song learning often requires social input for effective development, much like human language. Thus, because the neural structures involved in learning and production are fairly well known for a few “model” species, birdsong has been proposed as a good model for examining imitative vocal behavior in general (including human speech). “Birdsong is a complex vocal behavior learned during early life in a process similar to the learning of human speech” (Hessler & Doupe, 1999, p. 209). “Recent data from the birdsong system, the best model for human speech, indicate that sleep has a critical role in vocal learning” (Crandall, Adam, Kinnischtzke, & Nick, 2007, p. 232, emphasis added).

Note, however, that there are two aspects of birdsong that are not considered when they are used as a model for human speech: (1) Birds obviously remember songs of other species that they do not, and in many cases cannot, imitate because they recognize and respond to them in territorial disputes (Catchpoole & Slater, 1995). Little work has been done to determine how birds acquire these memories, but this would be equivalent to humans acquiring memories for the languages of other cultures but not being able to express them. (2) Many nonsongbird species engage in complex vocal behavior that are directly relevant for understanding the neural mechanisms of songbird vocalizations (Cheng & Durand, 2004). This latter aspect would be equivalent to considering ape and monkey vocalizations as relevant for understanding the neural mechanisms of human speech. Perhaps, these two aspects of birdsong highlight some of the differences that make them a weak model for human speech and learning.

Birdsong also has attracted the attention of those scientists with a natural history orientation because song is essential for reproductive behavior of songbirds and it permits the study of the neural basis of a learned behavior in a naturalistic context. Moreover, there are more than 4,500 species of song birds (about 45% of all bird species) exhibiting a wide diversity of tonal,

structural, and learning characteristics (Brenowitz & Beecher, 2005; Williams, 2004). Consequently, birdsong automatically generates curiosity about the contributions of evolutionary and ecological diversity to the neural and developmental mechanisms involved in its acquisition and production (e.g., Boncoraglio & Saino, 2007; Byers & Kroodsma, 2009; Lachlan & Servedio, 2004).

Despite the diversity of songbirds, 70% of studies of the brain correlates of song acquisition have been done with only three species: zebra finch (*Taeniopygia guttata*), canary (*Serinus canaria*), and Bengalese finch (*Lonchura domestica*). Indeed, 51% of the neurobiology of birdsong derives from the study of only one species—the domesticated zebra finch (*T. guttata*). The domesticated canary (*Serinus canaria*) represents another 14%. Therefore, “much of what we know about birdsong neurobiology is based on the study of a very small subset of the relatively small number of species whose singing behavior has been studied in any detail” (Williams, 2004, p. 4).

Because the song structure and acquisition trajectories of zebra finches and canaries differ somewhat, their comparison is considered sufficient to identify commonalities in the neural mechanisms of learning. The zebra finch is considered a “close-ended” learner because, once achieved, the adult song exhibits little plasticity. The canary, in contrast, is considered an “open-ended” learner because it exhibits seasonal plasticity in brain and song. Their commonalities are presumed to operate similarly in all related species, if not all instances of vocal learning. However, neither canaries nor zebra finches have (1) repertoires with multiple song types, (2) repertoires defined as dialects that are associated with specific geographical regions, or (3) the ability to mimic recently heard sounds or prune songs based on the behavior of conspecifics (action-based learning; cf. Williams, 2004). Moreover, these two species do not even begin to represent the range of mimicry (ability to produce accurate imitations after hearing one or only a few exemplars of a sound) of such species as mockingbirds (*Mimus polyglottus*) and mynahs (*Gracula religiosa*). These limitations alone make the zebra finch and canary problematic models for understanding birdsong in general. This also raises questions about their use as models for human speech.

Consider the notion (based on the commonly studied species) that songbirds exhibit four stages of acquisition: early sensory learning, subsong, plastic song, and postpubertal crystallization. The zebra finch is proposed to have an innate crude “template” that guides the memorization of the conspecific song heard during an early sensitive period. Exposure to the conspecific song converts the template into a more complex acquired template (early sensory learning). Young birds convert the acquired template into a sensorimotor pattern by comparing the auditory feedback from their initial poorly constructed song to the memorized model (subsong and plastic song). Eventually, a crystallized adult song is achieved, consisting of a repertoire of elements, notes, syllables, phrases, motifs, or songs.

Research on the model species provides a very sophisticated account of the neural mechanisms involved in song (cf. Zeigler & Marler, 2004). There appear to be neural mechanisms involved in acquisition that do not operate during eventual production, and it is sometimes presented as though these mechanisms operate as relatively isolated neural circuits with restricted functions. For example, Hessler and Doupe (1999) reported that the pattern of singing-related neural activity in several high-level neural areas (L-MAN, Area X) specialized for song learning (but not production) depends on whether the zebra finch sings alone or to another zebra finch. Also, multielectrode single-unit recording in juvenile zebra finches identified single HVC (high vocal center of the forebrain) neurons that appear to integrate sensory and motor information during the sensorimotor phase of vocal learning (Crandall, Aoki, & Nick, 2007). This suggests that the premotor HVC is part of the circuit involved in the sensorimotor shaping through activity-dependent mechanisms characteristic of song learning. Recent evidence (Day, Kinnischtzke, Adam, & Nick, 2008) suggests that the HVC affects song variability rather than song features.

However, studies show that many song characteristics of zebra finches (e.g., syllable order) can vary depending on how syllables are defined by an experimenter. Kojima and Doupe (2008) intentionally used different syllable definitions in the same song to reveal different mean syllable durations and that the syllable order selectivity of each bird's neurons varied depending on those durations. Moreover, Meitzen, Thompson, Choi, Perkel, and Brenowitz (2009) demonstrated that measuring either song quantity or quality alone does not provide a complete picture of how song behavior changes during seasonal transitions in breeding physiology. Song rate, song phonology, and song syntax changed on different time scales in response to changes in breeding condition. Thus, although seemingly simple in character, the particular definitions that a researcher chooses for defining the zebra finch song alters how the song is related to neural and endocrine mechanisms.

Because the definitions used to characterize the phonology, syntax, and rate of expression of the zebra finch's song can create much variability in the relation of the song to neural and endocrine mechanisms, it would not be surprising that consideration of the diversity of song acquisition patterns, as derived from natural history-oriented research, would dramatically alter our models of human language acquisition and learning. The diversity derived from the natural history-oriented research that applies to the human situation includes the following:

- (1) Timing. Song learning can occur early (as in the typical model systems) or remain lifelong (European starling [*Sturnus vulgaris*] and pied flycatcher [*Ficedula hypoleuca*]), as is typical of human speech.
- (2) Repertoire size. A species may sing only one song type (the white-crowned sparrow male has only a single, simple, stereotyped song that is monotonously repeated) or, several, in contrast yet similar to the human situation (the mockingbird, the Australian lyrebird, and the European nightingale have extensive repertoires of several hundred song types, with the brown thrasher [*Toxostoma rufum*] singing more than 1,000).

(3) Mimicry pattern. A species may closely mimic a conspecific song (as in the zebra finch) or, in contrast, improvise (as happens with humans) by modifying song elements to create novel songs (e.g., sedge wrens [*Cistothorus platensis*]).

(4) Modeling pattern. A species may require early exposure to a model (as in the zebra finch) or, in contrast, develop the song in isolation (e.g., gray catbirds [*Dumetella carolinensis*] and sedge warblers [*Acrocephalus schoenobaenus*]).

(5) Constraints on mimicry. A species may copy tutor material only if it fits tightly constrained species-typical parameters (chaffinches), or a species may copy nearly anything heard (e.g., northern mockingbirds [*Mimus polyglottus*] and Marsh warblers [*Acrocephalus palustris*]).

(6) Choruses and duets. Choruses are most associated with communal breeding species, and both males and females sing. For the white-browed sparrow weaver, each bird can produce the song of the whole chorus on its own. Duetting is common among members of a mated pair, and each sings different notes alternately (antiphonal singing), which may be important for pair bonding. Matched countersinging is the coordinated singing between territorial neighbors. Territorial rivals may imitate one another's songs in countersinging (e.g., indigo bunting [*Passerina cyanea*], meadowlarks [*Sturnella magna*], nightingales, song sparrows).

Although for many species, young birds acquire the song of their parents and neighbors, Wheelwright, Swett, Levin, Kroodsma, Freeman-Gallant, and Williams (2008) showed that most male Savannah sparrows acquired their songs from neither their biological nor their foster-reared “social” father but rather from breeding-year neighbors. Moreover, Beecher, Burt, O’Loughlen, Templeton, and Campbell (2007) reported that young song sparrows (*Melospiza melodia*) learned from two kinds of adult “song tutors”: one with whom the subject interacted vocally and one whom the subject only overheard singing with another young bird. Unlike zebra finches, song sparrows learned more than twice as many songs from the “overheard” tutor. Thus, in some species, birds may learn more by eavesdropping than by direct interaction. In contrast, some model species (e.g., zebra finch) require an interactive relationship either with an adult bird or with just a key that needs to be pecked to produce the playback from a speaker, whereas others (e.g., canary) acquire song just from hearing it through a speaker.

Within species, adult individual variability reflects differences in the sources from which the song was acquired, how the song was assembled during acquisition, the responses of adult listeners, the levels of circulating hormones, and sensitivity to those levels. Moreover, song is a consequence of certain acoustical and structural properties of the bird and the specific properties of the salient tutor, as well as improvised aspects. Thus, there may be no “typical” songbird developmental process other than a need to compare auditory feedback from self-generated song to some internal model (Brenowitz & Beecher, 2005). However, the extraordinary diversity of song learning processes in songbird species provides the opportunity to discover mechanisms of

developmental acquisition of species-typical sensorimotor behaviors that could illuminate aspects of development in humans.

Moreover, as Williams (2004) argued, the way that the neurobiology of song is investigated in the laboratory can distort understanding of the development and control of birdsong. Williams noted that many species broadcast their song accompanied by visual stimulation (displays). These changes in the behaviors associated with the displays have consequences on the sounds produced. For example, an open beak emphasizes higher frequency sounds; inflation of interclavicular air sacs (a component of song respiratory behavior) causes the throat feathers to be projected outward. Dance movements may be distributed throughout the song (it is interesting that, in zebra finches, the dance pattern represents that of the tutor). The coupling of displays and movements with singing means that the traditionally defined song circuitry engages other motor patterns involving respiratory and extravocal sensorimotor pathways. These mechanisms are rarely, if ever, examined in laboratory investigations of song.

Consider, also, that zebra finch and canary neurobiology suggest that neuronal addition (neurogenesis) to the HVC of the brain is related to song learning. However, song sparrows' acquisition of song is limited to their first year, but they exhibit seasonal changes in neural recruitment in HVC that is equivalent to canaries, which add new song syllables as adults when this recruitment occurs. Thus, this comparison reveals that neurogenesis might be necessary for song acquisition, but it is not sufficient. Moreover, Strand, Ross, Weiss, and Deviche (2008) found that photoperiodic condition and social context may modulate the effects of testosterone and its metabolites on brain song control regions (SCRs) and singing behavior in adult male house finches (*Carpodacus mexicanus*). Providing testosterone and its metabolites to males in the fall (in contrast to the spring) did not increase volume of SCRs or increase singing.

Variation in song stereotypy may reflect variations in motivation, and that often means variations in hormonal secretions and/or sensitivity. This influence of hormones and motivation shows that song circuitry is linked to hypothalamic and other limbic mechanisms (Cheng & Durand, 2004). Again, the natural history orientation to birdsong provides an important perspective by which the strengths and weaknesses of the model systems become very apparent.

It is not the intent of this article to propose that the engineering approach to bird song (or indeed any animal model of the human situation) is wrong. Rather, the intent is to demonstrate that the natural history orientation toward the study of bird song has much to contribute to the engineering approach. However, without adequate public support and general education about the value of natural history investigations of animal behavior, such research may serve only as a minor irritant and the occasional cautionary note to the anthropocentric-oriented investigators. Just as the investigation of birdsong can gain from the expanded investigation prompted by the natural history orientation, so too can the investigation of all aspects of animal and human behavior.

For example, research intended to model the impact of parental care on the social and emotional development of offspring has focused on domesticated rats and mice or certain species of monkey. Unlike the human situation, in neither rodent nor many species of monkey does the male parent contribute to parental care. There are species of rodent (e.g., CA mouse, (*Peromyscus californicus*) prairie vole) and monkey (e.g., marmosets) in which the male parent contributes to the care of the offspring. Examination of these species has begun to alter our understanding of the parental factors affecting offspring development (Michel & Tyler, 2007). Human play behavior may be understood from the natural history orientation (Burghardt, 2005). Also, Michel and Moore (1995) identified the areas of attachment, critical period, aggression, and abnormal behavior in human psychological research as having benefited from the incorporation of research conducted from a natural history orientation.

It is time to shift the direction of animal behavior research away from the myopic perspective of the anthropocentric orientation. This shift can be of immense benefit for understanding human behavior and our place in nature. “Human behavior has its own place in this broad framework but that place cannot be established by finding similarities between human and animal behavior on the basis of seemingly similar phenomena” (Lehrman, 1971, p. 471). The natural history orientation is valuable for understanding animals and their worlds. To achieve this understanding, the scientist is forced to change perspective and re-examine and reframe his or her concepts and notions. Once our concepts and notions are reframed, on the basis of the improved understanding of animal behavior in natural context such changes provide, this reframed understanding can provide a richer foundation for resolving human behavioral problems.

Indeed, when we attempt to examine ourselves, we must be able to generate a frame of reference that is not completely dependent on the original object of examination (i.e., ourselves). We must expand our understanding of other species so as to challenge and break our anthropocentric frame of reference. When we approach the study of animal behavior with the intent to discover the animal's “world” rather than our own, we can achieve a perspective on both the animal's world and our own that is less biased by our socially and culturally derived self-reflective intuition. That is, attempts to understand the animal in its world (poetry) will challenge our attempts to cast it as a simplified form of human (engineering) and will better illuminate what is unique about us. It is from this comparative perspective that we can come to better understand ourselves. It is the spirit of preserving and expanding this natural history orientation to the study of animal behavior that makes it appropriate to revisit, in 2009, Lehrman's (1971) thesis.

References

Beecher, M. D., Burt, J. M., O'Loghlen, A. L., Templeton, C. N., & Campbell, S. E. (2007). Bird song learning in an eavesdropping context. *Animal Behavior*, 73, 929– 935.

- Boncoraglio, G., & Saino, N. (2007). Habitat structure and the evolution of bird song: A meta-analysis of the evidence for the acoustical adaptation hypothesis. *Functional Ethology*, 21, 134–142.
- Brainard, M. S., & Doupe, A. J. (2000). Auditory feedback in learning and maintenance of vocal behavior. *Nature Reviews Neuroscience*, 1, 31– 40.
- Brenowitz, E. A., & Beecher, M. D. (2005). Song learning in birds: Diversity and plasticity, opportunities and challenges. *Trends in Neuroscience*, 28, 127– 132.
- Burghardt, G. M. (2005). *The genesis of animal play: Testing the limits*. Cambridge, MA: MIT Press.
- Byers, B. E., & Kroodsma, D. E. (2009). Female mate choice and songbird repertoires. *Animal Behaviour*, 77, 13– 22.
- Cairns, R. B. (1972a). Attachment and dependency: A psychobiological and social learning synthesis. In J. L. Gewirtz (Ed.) , *Attachment and dependency* (pp. 29– 80). New York: Wiley.
- Cairns, R. B. (1972b). Ontogenetic contributions to aggressive behavior. In F. J. Monks, W. W. Hartup, & J. de Wit (Eds.) , *Determinants of behavioral development* (pp. 395– 400). New York: Academic Press.
- Catchpole, C. K., & Slater, P. J. B. (1995). *Bird song: Biological themes and variations*. New York: Cambridge University Press.
- Cheng, M. -F., & Durand, S. E. (2004). Song and the limbic brain: A new function for the bird's own song. *Annals of the New York Academy of Sciences*, 1016, 611– 627.
- Crandall, S. R., Adam, M., Kinnischtzke, A. K., & Nick, T. A. (2007). HVC neural sleep activity increases with development and parallels nightly changes in song behavior. *Journal of Neurophysiology*, 98, 232– 240.
- Crandall, S. R., Aoki, N., & Nick, T. A. (2007). Developmental modulation of the temporal relationship between brain and behavior. *Journal of Neurophysiology*, 97, 806– 816.
- Day, N. F., Kinnischtzke, A. K., Adam, M., & Nick, T. A. (2008). Top-down regulation of plasticity in the birdsong system: “Premotor” activity in the nucleus HVC predicts Song variability better than it predicts song features. *Journal of Neurophysiology*, 100, 2956– 2965.
- Galef, B. G., Jr. (1988). Imitation in animals: History definition, and interpretation of data from the psychological laboratory. In T. R. Zentall & B. G. Galef, Jr. (Eds.) , *Social learning* (pp. 3– 28). Hillsdale, NJ: Erlbaum.

Gollin, E. S., Stahl, G., & Morgan, E. (1989). On the uses of the concept of normality in developmental biology and psychology. *Advances in Child Development and Behavior*, 21, 49–71.

Hessler, N. A., & Doupe, A. J. (1999). Social context modulates singing-related neural activity in the songbird forebrain. *Nature Neuroscience*, 2, 209– 211.

Kojima, S., & Doupe, A. J. (2008). Neural encoding of auditory temporal context in a songbird basal ganglia nucleus, and its independence of birds' song experience. *European Journal of Neuroscience*, 27, 1231– 1244.

Kruuk, H. (2003). *Niko's nature: A life of Niko Tinbergen and his science of animal behavior*. New York: Oxford University Press.

Lachlan, R. F., & Servedio, M. R. (2004). Song learning accelerates allopatric speciation. *Evolution*, 58, 2049– 2063.

Lehrman, D. S. (1971). Behavioral science, engineering, and poetry. In E. Tobach, L. R. Aronson, & E. Shaw (Eds.) , *The biopsychology of development* (pp. 459– 471). New York: Academic Press.

Meitzen, J., Thompson, C. K., Choi, H., Perkel, D. J., & Brenowitz, E. A. (2009). Time course of changes in Gambel's white-crowned sparrow song behavior following transitions in breeding condition. *Hormones and Behavior*, 55, 217– 227.

Michel, G. F. (2001). A developmental psychobiological approach to developmental neuropsychology. *Developmental Neuropsychology*, 19, 11– 32.

Michel, G. F., & Moore, C. L. (1995). *Developmental psychobiology: An interdisciplinary science*. Cambridge, MA: MIT Press.

Michel, G. F., & Tyler, A. N. (2005). Critical period: A history of the transition from questions of when, to what, to how. *Developmental Psychobiology*, 46, 156– 162.

Michel, G. F., & Tyler, A. N. (2007). Can knowledge of developmental processes illuminate the evolution of parental care? *Developmental Psychobiology*, 49(1), 33– 44.

Rosenblatt, J. S. (1995). Daniel Sanford Lehrman: June 1, 1919–August 27, 1972. *Biographical Memoirs*, 66, 3– 21. Washington, DC: The National Academy of Sciences.

Strand, C. R., Ross, M. S., Weiss, S. L., & Deviche, P. (2008). Testosterone and social context affect singing behavior but not song control region volumes in adult male songbirds in the fall. *Behavioural Processes*, 78, 29– 37.

Wheelwright, N. T., Swett, M. B., Levin, I. I., Kroodsma, D. E., Freeman-Gallant, C. R., & Williams, H. (2008). The influence of different tutor types on song learning in a natural bird population. *Animal Behaviour*, *75*, 1479–1493.

Williams, H. (2004). Birdsong and singing behavior. *Annals of the New York Academy of Sciences*, *1016*, 1–30.

Zeigler, H. P., & Marler, P. (Eds.). (2004). *Behavioral neurobiology of birdsong*. (*Annals of the New York Academy of Sciences*, Vol. 1016). New York: New York Academy of Sciences.