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Bird Song Research: The Past 100 Years

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In charting the course of progress in the scientific study of bird song for the past 100 years, two differing time trends are apparent. A slow increase of knowledge over time characterizes the history of developments up to the middle of the 20th century. Although from the 1700s on there were truly remarkable and prophetic insights into bird song gained by a relatively few creative naturalists and experimentalists, ornithological work was taken up more by cataloging descriptions and distributions of species than by detailed studies of behavior, certainly of vocal behavior. A dramatic change in the pace of advance in song research, characterized by a steep rise in the time course of growing knowledge, began to emerge through the 1950s. This was precipitated in large part by the tape recorder, which had become increasingly available somewhat earlier, and the sound spectrograph, a device developed for military applications during the war years and capable of transforming tape-recorded vocalizations into detailed visible portraits of sound. The new horizons in bird song studies opened by these technological innovations must be similar to the new world of organisms revealed by the first microscope. Since the middle of the 20th century, the field of bird song biology has undergone enormous growth in studies of song learning: its ontogenetic aspects at the organism level of organization, its neurobiological basis, and its natural history consequences at the individual and population levels of organization. A review of progress in these areas is presented in this article. In bird song research, the emphasis has indeed been upon the many species that learn their songs. One reason is that vocal learning is fascinating in its own right, raising interesting questions about how this process occurs and why it occurs, and doing so for organisms that are so readily accessible observationally and experimentally. Another reason is because ornithologists came to realize that in the animal world we humans are virtually alone with the songbirds in the manner by which we obtain our auditory communication signals, the fascinating processes of vocal learning. Like human speech dialects and languages, the first sign of cultural heterogeneity among populations of a songbird species is hearing different song dialects. How birds generate sound in the syrinx, however, is a unique mechanism differing from how humans produce speech sounds, and a description of progress in understanding of syringeal function is presented here as well. The research emphasis on birds that learn their songs is not likely to change in the near future, but already there is a nascent trend to bring other taxa of vocal learners, such as parrots and hummingbirds, into the comparative biology picture. Throughout the 20th century, and increasingly so as the early years ticked by, the principles of Darwinian evolution have steered the observations, hypotheses, and experiments aimed at understanding the biology of bird song. By the mid-1900s, the search for an evolutionary understanding of animal behavior in general, ethology, had developed a widespread appeal and included investigations of animal communication signals, such as bird songs.

Singing behavior thus became just one focus in the general study of communication in the natural social lives of birds. The Darwinian perspective, with its emphasis on comparative biology, appears almost certainly to remain the standard in the next 100 years as researchers probe ever deeper into bird song behavior: the ontogeny of song, the physiological and neural mechanisms of song learning and production, and the roles of singing and other vocal signaling in avian societies. Many specific subdisciplines within the general field of bird song have emerged as well, and it is likely that this trend will continue as new problems are discovered and new questions arise.

Behavior *Birds* *Communication* *Dialects* *Evolution* *History* *Learning* *Neuroethology* *Song* *Syrinx*

By the turn of the 20th century, the broad outlines of many of the areas of bird song research that were to occupy ornithology to the present new millennium had been established. From Kircher's (1650) early attempts to describe bird song by transcribing it as musical notation (illustrated in Armstrong, 1963, p. 232), to Barrington's (1773) song learning experiments with hand-raised birds; from Newton's (1896) reference to song "dialects" and geographic vocal variation, to Hudson's (1892) speculations on the effects of habitat structure on shaping vocal patterns; and from Altum's (1868) insights on the roles of song in territorial and mate choice behavior, to Witchell's (1896) application of Darwin's theory of sexual selection to the evolution of song, we readily identify many of the pioneering directions that have inspired the field to the present day. Of course, these several students of bird song themselves often had predecessors with suggestive ideas, and others were to follow who achieved even deeper insights or made more brilliant syntheses than these few mentioned here as early pioneers.

The primary emphasis in this article concerns the historical development of selected areas of bird song biology, events of the 20th century that set out major advances in understanding, but I found it instructive and satisfying to look occasionally and briefly back to particularly important and insightful earlier work. The astute observations on the biology of bird song that were made in the distant past sometimes came through to me like the light from long dead stars. Secondly, I will try to indicate the current status of the selected areas of research in the field of bird song and speculate on potential issues and directions of the future. In 1929, A. A. Saunders remarked on the paucity of information about even the most common of bird species and noted that, "Yet what we know about the song of the Robin or the Chipping Sparrow or any equally common species has merely placed the first drop in the bucket" (pp. 179–180). It is fair to ask: how full is our bucket of knowledge about bird song at the dawn of a new millennium?

In the following review, I have divided bird song biology into broad areas for treatment: (a) development of methods to describe bird vocalizations, (b) development of song in the individual, (c) the syrinx: organ of vocal production, (d) brain mechanisms and the vocal control system, (e) population consequences of song learning, (f) bird song as a communication system, and, (g) the evolution of song and of vocal learning.

Developments of Methods to Describe Bird Vocalizations

Word descriptions that attempt to imitate sounds are apparently the most ancient method of bird song notation, dating in the literature at least to the 13th century, but doubtless residing in unrecorded antiquity. Whether it is the "Tic-tic-tic-tic-a-tee'ze" of the corn bunting (*Miliaria calandra*) rendered by Morris (1925) or "Drink-your-tea" to represent the eastern towhee (*Pipilo erythrophthalmus*), the onomatopoeic method of description has had some staying power in spite of its shortcomings. Unsuitable as scientific description, onomatopoeic notation is useful to beginning birders of any age, and it serves as a helpful memory aid even to experienced field ornithologists.

Also very early on, bird songs were described in musical form. Composers preceded naturalists with this method. Davison and Apel (1949) illustrate the

songs of birds inhabiting the music of the late medieval period (1300–1400). "Summer Is Icumen In" (c. 1310) contains vocalizations of the cuckoo, and Oswald von Wolkenstein (1377–1445) musically rendered vocalizations of nine different species in "Der May." Kircher (1650) was clearly taking a naturalist's view in trying to employ standard musical notation to describe bird song, and this method and various refinements were to engage the efforts of ornithologists to the middle of the 20th century. Consistent attempts to capture song on the musical staff were apparent in Flagg's (1858b) publication, and some of the more sophisticated modifications of musical notation were quite workable, especially for some species. Flagg (1858a) noted, however, that, "There are not many birds whose notes could be accurately described upon the gamut" (p. 288).

To adapt the musical descriptive approach to certain "nonmusical" bird songs, ways were invented to alter conventional music notation, contending with bird song notes of indeterminate pitch, irregular rhythms, and the necessity of providing verbal descriptions of the instrument-like tonal qualities (timbre) of bird sounds. Saunders (1915), for example, developed a system that indicated time, pitch, and intensity features and additionally used phonetic descriptions and words to convey vocal quality. Some of the depictions resulting from his "graphic" method gave visual results much like illustrations produced by modern analysis equipment (i.e., "voice prints"). This phase of song description enjoyed spirited exchanges among advocates of various methods (e.g., Hunt, 1923; Moore, 1915, 1916; Saunders, 1916a, 1916b, 1924). In spite of these concerted discussions, progress was slow, and the study of bird song occupied a tiny fraction of ornithological research in the first half of the 20th century. As Saunders put it in 1929:

> In the early days of ornithology in America the describing of species was a great enough task to take all the time of the ornithologist. Now that such preliminary work is reasonably complete, the study of the live bird out-of-doors has taken more attention. Even here, however, the studies of nesting habits, migration, and distribution have occupied the majority of workers. Bird song has been one of the last subjects to receive serious scientific attention. . . . (p. 132).

He later asked: "Can a bird song be described accurately and exactly? No, nor can anything else" (p. 133).

As if answering this challenge, Albert R. Brand, having secured his economic future through arbitrage on the NY Stock Exchange by age 39, and departing this activity mere months prior to the 1929 crash, took up the study of ornithology at Cornell University in 1930 under the supervision of Arthur A. Allen. Brand focused his attention on the recording of bird songs on movie film and transferring these sounds to phonograph records. One of Brand's most useful efforts resulted in the development of a Fox-Movietone film recorder altered to obtain the higher frequency sounds of bird songs, and he published the first visualizations of songs derived from film soundtrack (Brand, 1935). This tedious process entailed examination, with a low-power microscope, of the acoustic record evident as tiny lines, perpendicular to the long axis of the film, along the edge of the film strip. Given the known passage rate of the film, the number of lines per unit time was counted, and a calculation gave results in cycles per second. Thus, a graph of a song could be constructed, revealing "pitch" (cycles per second) on the ordinate and the duration of notes and silent intervals on the abscissa. Brand ultimately recorded vocalizations of over 300 species. Illustrating the tenacity of his research drive, Brand, assisted by A. O. Gross of Bowdoin College, Maine, once used short-wave radio to transmit the vocalizations of Leach's petrel (*Oceanodroma leucorhoa*) from Kent Island to his sound truck 3 miles distant on Grand Manan Island (A. A. Allen, 1941).

In this same time period, magnetic tape recording devices were invented. Fritz Pfleumer took out the first patent on audiotape in 1929. A tape recorder/playback device, called the magnetophon, was produced by a German electronics company in 1935 and was used to make the first public tape recording in 1936 of the London Philharmonic orchestra in Ludwigshafen (McGrath, 1999). From this nascent condition the materials and equipment available for recording bird vocalizations rapidly proliferated and evolved into increasingly better quality instrumentation.

Given the wide variety of microphones, tape recorders, and recording tape offered by a worldwide set of vendors, it became useful to the bird song community for expert recordists to supply guidelines and advice on the sorts of choices one needs to consider before obtaining recording machinery and supplies. One of the earliest publications in this re-

gard was by P. P. Kellog (1960), who at the time headed the Laboratory of Ornithology at Cornell University, site of one of the foremost archives of bird songs in the world. Somewhat later, Fisher (1977) and Gulledge (1977) provided detailed advice for those engaged in recording bird vocalizations for research purposes. A very thorough and readable treatment of equipment considerations for the recordist is a chapter by Wickstrom (1982), although its main emphasis is on analog recording to magnetic tape. We are currently in the transition to digital recording, which seems destined to replace the more traditional equipment, as long as funding allows investigators to upgrade. Advantages of the digital format are the long-term storage on CDs, floppy discs, or hard drives, ease of transfer of data over the Internet, and no losses from signal transductions once the songs is recorded. Nevertheless, no matter what equipment is used there will remain important considerations about equipment choices that require careful attention to technical specifications. Even though analog recorders may be replaced by digital machines, one still needs a microphone to capture the pressure waves of a sound source and convert them into electrical current for conversion to digital form by the recording device. Similarly, many broadcast "playback" research applications will still require retrieval of the digitized song to drive a loudspeaker. Thus, important elements of the "old" technology will remain as important factors affecting quality in this domain.

Following Brand's efforts, the next advances in translating sound into visual patterns began in the war years from 1941 on when scientists and engineers at Bell Telephone Laboratories embarked on developing equipment that could assist in code breaking. As coded communications often involved time and frequency shifts, a device that could examine such patterns was sought. Other military applications for the analysis and visual display of sounds, the "visual translation of sound" as it was expressed, were the examination of sound signatures of propellers of ships and planes, and later of rockets. The war years kept the emerging devices out of the public eye. By 1943, however, the sound spectrograph, or sonagraph, as it came to be known, was made available for use by researchers wishing to develop a means by which a deaf person could visually "read" speech, such as when answering a telephone or listening to the radio (Potter, Kopp, & Green, 1947), and to assist the deaf in the learning of speech by adding visual feedback monitoring to kinesthesis. In the early stage of development, the sonagraph was limited to producing a short segment of sound on paper, but by 1944 a "direct translator" was available, which was essentially a continuous spectrum analyzer that enabled an observer to view ongoing speech. The ultimate goal of this technology was to allow a deaf person to read the "words" in real time from a screen. The first reproductions from the sonagraph were soon published (Potter, 1945), emphasizing the human speech applications but also containing illustrations of songs of northern cardinal (*Cardinalis cardinalis*), American robin (*Turdus migratorius*), northern mockingbird (*Mimus polyglottos*), brown thrasher (*Toxostoma rufum*), and eastern screech-owl (*Otus asio*), about which Potter remarked:

> . . . these song patterns are obviously revealing and illustrate well the possibilities of sound portrayal. With such patterns as these it will be possible to analyze, compare, and classify the songs of birds, and, of even more importance, it will be possible to write about such studies with meaningful sound pictures that should enable others to understand the results. (p. 470)

By 1947, Bell Labs was receiving requests from the acoustic research community for the sound spectrograph. Sometime earlier, Bell Labs engineers Harry Foster and Elmo Crump had left to start their own company to produce radar and television test equipment. While at Bell, Crump had a hand in developing circuits for the early sonagraph designs. Bell Labs now approached this new company, Kay Electric Company (Kay was a daughter of Crump), and offered them the commercial rights to the sound spectrograph. Kay Electric soon released a commercial version called the Sona-Graph™ in 1948. The Crump family continues to operate the company today, renamed Kay Elemetrics.

Ornithologists soon began to make great use of the Kay sonagraph. Early papers by Bailey (1950), Borror and Reese (1953), Collias and Joos (1953), Kellog and Stein (1953), and Thorpe (1954) ignited the field of avian bioacoustical research, which has grown immensely since the 1950s. Thorpe's paper was particularly significant for its insightful and creative use of the spectrograph, going beyond the mere display of songs by using sonograms to illustrate

the developmental stages of the song learning process in the chaffinch (*Fringilla coelebs*). Soon, such application became common as the sonagraph became a tool routinely employed by students of bird vocal communication. The Kay sonagraph was essentially unchanged from 1947 to about 1977 when it underwent alteration from an analog to a digital device. In 1986, Kay Elemetrics introduced the Digital Signal Processor, a sophisticated instrument capable of carrying out a number of analyses and functions not available in earlier models.

A second line of spectrographic devices was initiated with a machine developed in 1969 by Bernard Miller, a graduate student at Columbia University. Over the course of the next 2 years, he and fellow graduate student William Stern improved the original device and formed Unigon Industries to fulfill a growing demand by both the military and scientists for their spectrum analyzer. Military applications ranged from antisubmarine warfare to analysis of vibrational signatures of trucks on the Ho Chi Minh trail during the Vietnam war. Early scientific users of the Unigon spectrum analyzer were bird song researchers at the National Zoo in Washington, DC, and the Rockefeller University Field Research Center near Millbrook, NY. The Uniscan spectrum analyzer continued to be available until about 1995, often found in the research laboratories where animal vocal signals were the subject of interest. At about the same time that the Unigon spectrum analyzer was developed, a second device was being put together, also at Columbia University. This was a time-compression analyzer marketed by Federal Scientific, and named the Ubiquitous Spectrum Analyzer, a digital device for analysis of animal vocalizations that displayed sounds continuously in real time, and with the addition of a camera produced a film record of the scope display as well (Hopkins, Rosetto, & Lutjen, 1974).

A number of different hardware and software systems are now available for bird song analysis and virtually any researcher with the least bit of interest in vocalizations has such a device as standard laboratory equipment. Having songs reside in digitized form in computer memory allows one to perform various manipulations with considerable ease, such as filtering, or cutting and pasting to rearrange song components. New developments in analysis procedures now allow quantitative evaluations of the similarity of pairs of songs, useful in several research domains such as comparing songs of neighboring territorial males or the song of a tutor with that of a pupil in developmental studies. One approach is a spectrogram cross-correlation technique developed by Clark, Marler, and Beaman (1987) and marketed as "Canary" software (Cornell Laboratory of Ornithology). A more recent method employs spectral analysis to examine four acoustic features: Wiener entropy, spectral continuity, pitch, and frequency modulation (Tchernichovski, Nottebohm, Ho, Pesran, & Mitra, 2000). As noted in their report (Tchernichovski et al., 2000), the authors offer the software ("Sound Analysis") free to researchers in the hopes of encouraging standard methods for comparisons between vocal patterns.

The detailed visual patterns of song production in birds necessitated a set of descriptive terms that could be used to discuss the features of songs. Problems in defining the various vocal utterances of birds and describing their acoustic components or patterns of delivery have had a persistent and largely unresolved presence for most of the 20th century. Even a definitive concept of song has proved elusive. Barrington (1773) defined a bird's song "to be a succession of three or more different notes, which are continued without interruption during the same interval with a musical bar of four crotchets in an adagio movement, or whilst a pendulum swings four seconds" (p. 252). Saunders (1919) said, "Bird song is a vocal performance produced by the male bird during a definite season of the year, that season including the time of courtship, mating and nesting" (p. 149). Nicholson (1929) described song as "properly a sustained more or less uninterrupted repetition of one or more notes conforming recognizably to a constant specific type, and used by the male as an expression of independent sovereignty" (p. 41). Armstrong (1947) noted difficulties in defining song but referred to it as "The frequent, loud, sustained and more or less melodious utterances with which we are all so familiar" (p. 294), but he pointed out that from a functional viewpoint there may be no way to sharply distinguish songs from other vocalizations commonly referred to as calls.

Tinbergen (1939) viewed the great diversity in songs and calls of species and found no defense for separating them on either duration or aesthetics, instead taking a functional approach to defining song as "a loud sound, given by a bird of one of the two sexes especially at the beginning of the reproduc-

tive period, that serves to attract a sex partner, to warn off a bird of the same sex, or both" (p. 80). Thorpe (1956) made a distinction between songs and calls, the latter being of more brief duration and simpler acoustic structure than songs. Catchpole and Slater (1995) say simply that songs "tend to be long, complex, vocalisations produced by males in the breeding season" whereas calls "tend to be shorter, simpler and produced by both sexes throughout the year" (p. 10). Textbook authors (e.g., Gill, 1995) point out the arbitrary distinction between calls and songs but acknowledge that the terms are probably not going to go away. Thus, songs are considered to be vocal displays usually of a complex set of notes that are repeated and, in north temperate regions, are typical utterances of males defending territories during breeding season. Calls, by contrast, tend to be shorter and of simpler structure than songs and are commonly given by both sexes. Acoustic features of typical songs are amplitude and/or frequency modulated pure tones, lacking in broadband characteristics such as noise or harmonics, whereas calls often have these broadband traits.

In a sense, all the definitions of song proposed are correct but at the same time all are wrong. They are correct because a general synthesis, as summarized above, conveys a sense of the criteria that capture the essence of our experience in observing birds engaged in what the ordinary person refers to as singing. The definitions are also often incorrect when viewed from the perspective of particular species where vocal behavior does not quite conform to any of the definitions either alone or in concert. Thus, in some species songs may not be confined to a particular season, may be as short as many calls of the same species, can be of simpler acoustic structure than calls, can be rich in harmonics, and may be uttered routinely by both sexes. These exceptions often derive from increasingly more knowledge of birds around the world.

Students of bird vocalizations, whether the signals are songs or calls, have also generated a variety of terms used to describe the structure of vocal signals. There are two meanings of the term "repertoire" in bird song research. One is used to describe the vocal repertoire of a species population, all the kinds of vocalizations produced during the life history of an individual male and female (e.g., Hailman & Ficken, 1996). Of this set of vocalizations, usually one is referred to as song, and typically for most north-temperate breeding species of songbirds this is the loud vocalization of territorial proclamation, which itself can serve more than one function, as previously noted. In many songbird species, an individual male may have several different versions of this territorial song and this set is referred to as a song repertoire. Some bird species have a single kind of song that is repeated over and over. A white-crowned sparrow (*Zonotrichia leucophrys*), for example, sings a song that is about 2 s in duration, and a territorial male may repeat this song at a rate of 4–6 times per minute from one or more song perches for several hours each day primarily in the reproductive season. Other species may have multiple forms of song, anywhere from two to dozens or more, and this set is referred to as a repertoire. A song sparrow (*Melospiza melodia*), for example, may have as many as a dozen different versions of its territorial song, each about 2 s in duration, and these song types are sung in a manner much like the white-crowned sparrow. Studies have shown that these different song types classified by human observers are perceived as discrete categories by the birds themselves (Searcy, Nowicki, & Peters, 1999). Many variations on these two examples of species differences in song variety have been described, and there is also great variety in the sequential and temporal patterns with which repertoires are broadcast in different species.

Within a particular song type we also find conventions for identifying components of the song. Thus, terms like note, syllable, or phrase are commonly employed in descriptions of songs (Fig. 1). A note (also commonly called a "phone"), for example, usually refers to the smallest acoustic unit, a single sound, and leaves a continuous trace on a sound spectrogram. A syllable (also commonly called a "figure") can be composed of a single note or a few notes that always occur together in a group. A phrase may be a single note repeated a number of times or a syllable repeated a number of times. These three terms are in fairly widespread use, but other terms exist and no single standard has been adopted by the bird song research community. The terminology proposed by Shiovitz (1975), following a detailed review, has rather wide acceptance. He proposed nine terms to describe the components of bird songs, which was a compression of 19 different terms he identified in the literature. Nearly 20 years later, Thompson, LeDoux, and Moody (1994) reviewed the problem of terminology and concluded that the

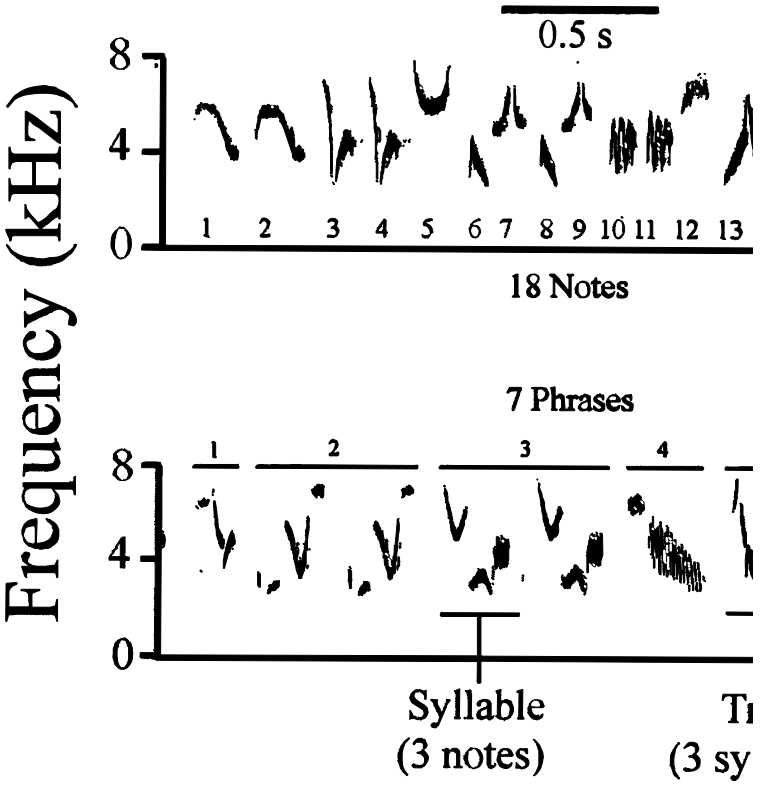

Figure 1. Terms commonly used to describe basic features of bird songs. Illustrated are sonograms of two songs of buntings (*Passerina*). The principal basic units of sound produced by the bird are syllables. A syllable may be a single sound revealed as a continuous trace on the sonogram, a note, or composed of two or more notes that always occur together as a complex. In the upper sonogram, notes #6 and #7 constitute a syllable, and this syllable is repeated (notes #8 and #9). An example of a three-note syllable is illustrated in the lower sonogram. In these songs, characteristic of buntings, most syllables (e.g., except #5 and #12 in the upper sonogram) occur as repeated units. Groupings of syllables are called phrases, a term that also applies to single syllables as well. The term phrase allows one to describe the number of different kinds of syllables seen in a song, regardless of repetitions. The term "trill" is often employed to describe rapid repetition of three or more syllables.

situation had worsened; they found a total of 28 identifiers for the units of songs. These latter authors proposed a song formula, in analogy to a floral formula, as a method of describing the set of components of a song in a hierarchical format. This method deserves consideration, but so far has not been adopted by many workers. In actual practice, in good descriptive papers, one often sees an illustration of a song of the species under study with the component parts labeled with the terms by which the researcher will discuss the content of the study. While this may seem somewhat wasteful of journal space, in fact it is usually handled efficiently and has the obvious benefit that there is no confusion in the reader's mind.

Reflecting back to the development of the sound spectrograph, which gave rise to the need to develop ways of talking about the details of bird songs, it is clear that as Potter et al. (1947) prophesied "permanent patterns of bird song can be examined in great detail. . . . If detailed analysis of song patterns is possible, there would seem to be a wide new field of study open to the ornithologist" (p. 411). One such field of study, as Thorpe (1954) had so well introduced and was busily exploiting, was the ontogeny of song.

Development of Song in the Individual

Passerine birds represent about 5000 of the world's 9000 bird species, and within the passerine

order the songbirds (oscines) comprise about 4000 species, the remaining 1000 designated as sub-oscines. Evidence to date indicates that all songbirds learn their songs (Kroodsma & Baylis, 1982; Mundinger, 1982), and a limited number of studies suggest that sub-oscine passerines do not (Kroodsma, 1984, 1989c; Kroodsma & Konishi, 1991). Among non-passerines, vocal learning occurs in parrots (c. 332 species) and hummingbirds (c. 319 species), although far fewer studies of vocal development have been conducted in these latter two taxa.

It was noted at least by 1720 by von Pernau (Stresemann, 1947) that songs of many birds were acquired by listening to other individuals. Fifty years later the pioneering experiments of Barrington (1773) clearly demonstrated the role of experience as a modifier of song, yet this finding too lay dormant for over a century more. Barrington hand-raised nestling linnets (*Carduelis cannabina*) in the presence of singing adults of other species and found that these young learned to sing the song of their tutor. He also noted the occurrence of a species filtering effect, by which in nature the young birds attended preferentially to learning model songs of their own species and disregarded other species' songs when both were available, and he was the first to draw attention to the analogy of the early singing attempts of the young bird to be like "the imperfect endeavor in a child to babble" (p. 250). A dedicated experimentalist, Barrington even had a castration performed on a Eurasian blackbird (*Turdus merula*) to see if the pitch could be altered, in the manner of the "Italian eunuchs," but the bird died from the operation.

Experimental work on song development was taken up in 1895 by Scott (1901) in his studies of Baltimore orioles (*Icterus galbula*). He hand-raised two birds in the absence of experience hearing the songs of any bird species. These birds sang unique improvised songs as adults and then served as models, passing on their unusual songs to four other hand-raised nestlings. This was one of the first experimental demonstrations of a cultural transmission chain, although von Pernau (1716, in Stresemann, 1947) seems to have made a very similar observation on chaffinches. He tutored his subjects on tree pipit (*Anthus trivialis*) song and they in turn passed the tree pipit song on to a new set of chaffinches. In any case, by 1904 Scott had raised 16 species for his observations on the effects of depriving developing songbirds from hearing conspecific model songs.

With their experiments, Barrington and Scott had moved the field of vocal learning forward only a modest degree. Probably extending back to unrecorded history, observations had been made of avian vocal learning, certain birds being able to learn vocalizations of other bird species, as well as human speech or other sounds, from the environment (mimicry). Parrots, for example, seem to have caught the attention of a number of early naturalists. In Book X:LVIII of *Natural History* (Rackham, 1943 translation), Pliny the Elder (A.D. 23–79) observed:

> Above all, birds imitate the human voice, parrots indeed actually talking. . . . It greets its masters, and repeats words given to it, being particularly sportive over the wine. Its head is as hard as its beak; and when it is being taught to speak it is beaten on the head with an iron rod. . . . (pp. 367–369)

Aelian (A.D. 170–235; Scholfield, 1957 translation) made similar observations (Book XIII), noting that in India the Brahmins considered parrots as sacred, and with good reason, "for the Parrot is the only bird that gives the most convincing imitation of human speech" (pp. 18–19). And in 1800, Alexander von Humbolt visited the cemetery of the extinct Atures Indian tribe in the Orinoco basin of Venezuela and tells of the "parrot of Mapures" that was the sole repository of the language of the dead culture (Humbolt, 1814–1825, translated by J. Wilson). Thus, although the imitation of sounds by various bird species undoubtedly was noticed and encouraged for centuries, not a great deal of genuine research activity occurred in the field of vocal learning until the middle of the 20th century.

Aside from the isolation experiments of Barrington and Scott, it was not until 1940 that there were sufficient technical developments to encourage a more sophisticated probe into song learning. Metfessel (1940) raised canaries (*Serinus canaria*) from the egg in sound-proof chambers, leaving some isolated from hearing songs while tutoring others with various speeds of pulsating vibrato from an electrical oscillator. Later, these birds were recorded on phonograph discs and the vocalizations transferred as sound waves to paper by a kymograph. The results indicated that the subjects raised without hearing songs produced normal canary song, and those

tutored by the oscillator reproduced the tutoring tones.

It was Thorpe (1954), however, who firmly established the modern protocol for developmental studies in the field of vocal learning through his careful and thoughtful use of tape recordings and sound spectrograph documentation. Several of the research problems Thorpe tackled had been addressed to a degree by others somewhat earlier, but the lack of tape recordings and sonagraphic illustrations resulted in their lesser impact. Poulsen (1951), for example, had made many of the same observations on song development in chaffinches as Thorpe, independently and beginning in 1946, but was able to provide only verbal description.

The detailed description made possible by the sonagraph led to meticulous illustration of the time course of vocal ontogeny through subsong, plastic song, and crystallized song (Marler, 1970; Marler & Tamura, 1964; Thorpe, 1958), the investigation of sensitive phases in the timing of song learning (Immelmann, 1967, 1969; Nottebohm, 1969b), the recognition of variation in what sorts of learning models are acceptable (Lanyon, 1957; Marler & Tamura, 1964), and the identification of auditory and motor learning processes (Konishi, 1965a, 1965b; Nottebohm, 1966).

Species exhibit variation in their song ontogenies, some passing through the learning phase in very early life, others able to learn much later in life. At the ends of a spectrum of ontogenies, species with age-limited learning have an early sensory learning phase that closes out quickly, whereas open-ended learners may continue to acquire new song forms well into adulthood, if not throughout life. An age-limited learner like the marsh tit (*Parus palustris*), for example, may perform subsong immediately upon fledging and is in fully developed song at 8–10 weeks of age (Rost, 1987). Other species falling into the category of age-limited learners are song sparrows (Marler & Peters, 1987) and white-crowned sparrows (Marler, 1970). At the other extreme, species such as the canary (Nottebohm & Nottebohm, 1978), common starling (*Sternus vulgaris*) (Bohner, Chaiken, Ball, & Marler, 1990), Eurasian blackbird (Thielcke-Poltz & Thielcke, 1960), and greenfinch (*Chloris chloris*) (Güttinger, 1977) are essentially open-ended learners with the potential to develop new songs through their entire life.

Several species are now known to acquire more songs during an early learning phase than they actually sing once established on territory. Described in swamp sparrows (*Melospiza georgiana*) by Marler and Peters (1982a, 1982b), such overproduction apparently occurs with the memorization of several auditory models and then later, during male–male interactions and territory establishment, some of the songs are discarded from use (Nelson, 1992). This late attrition of songs from a library of song forms learned earlier, known as "action-based learning" or "selection-based learning," appears to be a way a young male attempting to establish territory can match songs with neighboring males, possibly increasing the effectiveness of its songs in such contests. The action-based learning model has implications for the biology of song dialects, which will be treated more fully in a later section. Choice of the terms "action-based learning" or "selection-based learning" may have been somewhat unfortunate, but as they seem firmly established in the literature they will be used in this review. That a bird does not produce all the songs or song components it learned might be more usefully called selective production or selective forgetting (Nottebohm, personal communication). Selective production may indeed result from social influences, such as counter-singing with others during establishment of territory, but songs and song components learned earlier may still be retained though not frequently used in current circumstances (Baptista, 1975).

There is also variation among species in what songs are acceptable learning models. Some mimicry species routinely incorporate elements of other species' songs into their own song structure (superb lyrebird, *Menura novaehollandiae*: Bell, 1976; northern mockingbird: Wildenthal, 1965) whereas others appear to have species-specific preferences that focus their learning on conspecific models (swamp sparrow: Marler & Peters, 1977; white-crowned sparrow: Marler & Tamura, 1962; chaffinch: Thorpe, 1958). Sometimes it is possible to provide extreme laboratory circumstances of social tutoring and deprivation from conspecific songs, which overcome the conspecific preferences, as had been accomplished in white-crowned sparrows (Baptista & Petrinovich, 1984), but the occurrence of wrong-species song learning in natural populations of this species is rare and probably of little populational consequence. Hybridization experi-

ments between breeds of canaries (Mundinger, 1995) and between canaries and greenfinches (Güttinger, Wolffgramm, & Thimm, 1978) show that some features of song (e.g., duration, maximum frequency) are genetically programmed. Furthermore, species differences in songs are manifest in birds raised in isolation from conspecific vocalizations (Marler & Sherman, 1985). Learned song features are therefore constrained within the heritable species-specific range. Little quantitative work of this type has been conducted and further studies would constitute a major contribution to the field.

Recent advances in understanding the song learning process have come from a blend of laboratory experiments and field studies (Kroodsma, 1996; Nelson, 1998, 1999). Laboratory experimental studies of song learning have the great advantage of controlling many of the variables attending song learning in natural social circumstances. While there is always the potential for laboratory song learning results to fail to provide the entire and final story, there is little doubt that such experimentation has been an enormous driving force of progress in understanding song learning. This progress is illustrated by the pioneering song learning work of Thorpe (1954) and Marler and Tamura (1964). A recent example (Tchernichovski, Lints, Mitra, & Nottebohm, 1999) illustrates some of these points. This study noted that young male zebra finches develop accurate copies of their father's song when kept in dyadic father–son pairs, but imitation is poorer when several male siblings are present with the father. In such a group, some young develop song before others and therefore provide song models for their siblings additional to the song of the father. This led Tchernichovski et al. to hypothesize that too many song models may cause incomplete imitation. This was tested in a tutoring experiment in which the number of model songs heard by each juvenile was controlled by presenting songs over a loudspeaker to each individual housed separately. The results showed that the highest quality imitation occurred when the youngster heard 40 repetitions of the tutor song; more repetitions led to poorer imitation. While an interesting result in isolation, the many additional questions raised by the study will doubtless produce an enlarging set of increasingly interesting results in the future. That some of the future results may modify the present picture has been a recurring theme in song learning research, but the process of observation, hypothesis, and test in both laboratory and field situations has advanced our understanding of song learning a great deal in a short time.

Field studies of song learning present a formidable challenge because it is necessary to follow a known individual from early life throughout song ontogeny, recording what songs it had been exposed to all along, and then upon initiation of singing during territorial establishment, complete the sequence by recording the subject and its neighbors. Remarkably, Beecher and colleagues (Beecher, 1996) have made progress in obtaining this sort of information for a song sparrow population in Washington state, verifying, for example, the occurrence of action-based learning by young males and the consequent formation of song-sharing neighborhoods. As a result, song learning in song sparrows in the field has been described, and the emerging view differs somewhat from the laboratory-based song learning results on this species. However, it remains to be seen if migratory song sparrow populations, or other species, follow the same pattern as the resident population of song sparrows studied thus far. It has been noted, for example, that song sharing by neighboring male song sparrows occurs at a high frequency in the population studied by Beecher, Campbell, and Stoddard (1994) but only at low levels (Hughes, Nowicki, Searcy, & Peters, 1998) or rarely (Harris & Lemon, 1972) in other populations.

An interesting variant case is the long-distance migrant Gambel's white-crowned sparrow (*Z. l. gambelii*), which overproduces songs during the plastic song developmental period but arrives on the breeding grounds in the arctic taiga with a single crystallized song (Nelson, 1999). Thus, these birds do not form small clusters of neighborhood song sharing on the breeding grounds as a consequence of selection-based learning. However, this subspecies, as do a number of other migrant species, exhibits territorial counter-singing at stopover sites along the northward migration route prior to arrival at the breeding areas. During counter-singing interactions on these "floating" and temporary territories at refueling stopovers, action-based selection of overproduced songs may occur.

Action-based learning, if found to be widespread among species, may make generalizations more difficult because such vocal plasticity, which responds to social influence much in the manner of operant conditioning, implies that wherever or whenever

reinforcement conditions change, so too may vocal ontogeny. Thus, conclusions about the "where and what" of learning could well vary intraspecifically, from a disturbed population in a city park to one in a more pristine habitat, from a dense population to a sparse population, or from a migratory population to a resident one. As Kroodsma (1996) suggests, ecological factors could well have a large effect on many features of bird song learning and production. This may be a caution to those anxious to find their results more definitive than those of other studies.

Other patterns of more deterministic song learning also occur. In a number of Galapagos finch species (*Geospiza*), there is a strict father-to-son cultural transmission of song pattern details (Grant & Grant, 1989, 1997). *Geospiza fortis, G. fuliginosa, G. scandens*, and *G. magnirostris* all follow the father-to-son inheritance pattern. Over a 20-year period, cases of hybrid pairings among several of these species apparently were the result of females of one species choosing males of a different species because they sang songs like those of the father of the female mate (Grant & Grant, 1997).

The phenomenon of vocal learning has led in two major directions of research. On the one hand, workers with a field orientation have devoted their efforts to understanding the communicatory, population, and life historical consequences of vocal learning; these subjects will be addressed following the next two sections. Others have adopted a reductionistic approach in an attempt to understand the physics and physiology of the organs of vocal expression and to reveal the brain mechanisms of vocal production and perception. These latter two directions of research are considered next.

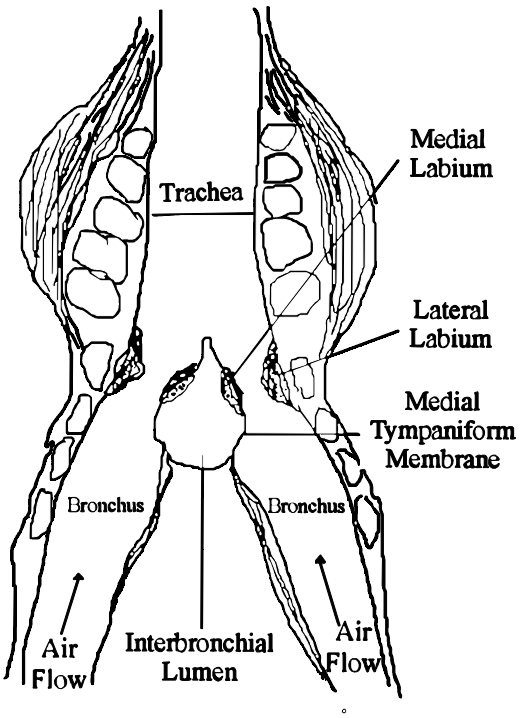

Figure 2. A "typical" songbird syrinx showing the duality of the structure allowing each side to produce sound independently. The entire syrinx is surrounded by the interclavicular air sac. Syringeal musculature and innervations from the hypoglossus together with air pressure from the interclavicular air sac and air flow through the bronchi produce sound when the medial and lateral labia adduct toward each other and vibrate. The tympaniform membranes may also play a role in sound production.

The Syrinx: Organ of Vocal Production

An abridged description of syringeal anatomy of a typical oscine passerine is necessary for what follows (Fig. 2). The syrinx is located at the convergence of the two bronchi with the trachea and is surrounded by the interclavicular air sac. Each side of the syrinx contains a medial tympaniform membrane (MTM) and a medial labium (ML) just cranial to the MTM. Opposite the ML is the lateral labium (LL). The interbronchial lumen is connected to the interclavicular air sac. The syrinx, long a mystery of anatomical complexity of membranes, muscles, and nerves, yielded little to experimentation in the early 1900s. Various authors, however, had made some progress in understanding syringeal function, and the studies of Setterwall (1901) and Rüppell (1933) contained the most insight. Setterwall deduced that sound was produced via vibrations of the medial and lateral labia, whereas Rüppell thought that passage of air past the tympaniform membranes, whose tension is controlled by syringeal muscles, was the cause of sound. Additionally, Rüppell experimentally verified that external pressure from the interclavicular air sac, which surrounds the syrinx, is essential for vocal output as well.

In 1951, Miskimen made two major contributions from her landmark experiments. First, working on the starling with its seven pairs of syringeal muscles, Miskimen systematically contracted each pair of muscles to produce rigor, and with each such ma-

nipulation passed air through the syrinx. This allowed her to observe the effect of each pair of muscles on the morphological elements of the syrinx, including the internal tympaniform membranes, and on the sounds produced. In the second emphasis of her study, she categorized 31 species into five groups depending on the number of pairs of syringeal muscles and their attachments to the cartilages of the syrinx, which determine the shape of the organ, and concluded that species with more muscles and syringeal mobility produce a greater variety of sounds.

Using recordings of bird songs, Greenwalt (1968) carried the analysis of syringeal function a large step forward by employing his knowledge of the physics of sound together with acoustical analysis equipment and mathematical calculations to deduce a theoretical model of the syrinx. This model has had considerable influence because it appeared to explain a great many of the features of bird songs, especially in the oscine passerines. One of the more intriguing findings of Greenwalt's analysis was that of "double voicing," the independent and simultaneous production of sounds from the two sides of the syrinx, a phenomenon that had been apparent to the ear of earlier workers (e.g., Saunders, 1923). Since Greenwalt's studies, many advances have been made in understanding syringeal mechanisms, and other models of the mechanism of sound production have been proposed (Casey & Gaunt, 1985; A. S. Gaunt & Gaunt, 1980; A. S. Gaunt, Gaunt, & Casey, 1982; S. L. L. Gaunt & Gaunt, 1980).

The basic vibrating membrane (MTM) model of Greenwalt came to be viewed as inadequate in several ways. Analysis of two different vibrating membrane models (Casey & Gaunt, 1985), differing in the assumed shapes taken by the MTM, suggested such models could account for some types of bird sounds, those containing "noisy" broadband sounds and partial or harmonic overtones, but not the vast majority of pure tone songs of most songbirds. A third model, called a hole-tone whistle model, relied on a nonvibrating MTM partly occluding the bronchial lumen of the syrinx and air passing through the resulting tiny opening to create vortices of air downstream. Depending on the flow rate of air, the vortices are shed in patterns that can create pure tones as well as broadband sounds, such as harmonic series (Casey & Gaunt, 1985; A. S. Gaunt et al., 1982).

A further problem with the Greenwalt model was found in the view of the syrinx as two completely independent sound sources that explain all bird sounds. That some sounds are produced by a complex coupling of the two syringeal sides was demonstrated by Nowicki and Capranica (1986a, 1986b), who examined the "dee" note of the namesake "chick-a-dee" call of the black-capped chickadee (*Poecile atricapilla*). They discovered that the "dee" note, previously thought to be a simple harmonic series produced by a single sound source, was in fact caused by an interaction of the two sides of the syrinx, a phenomenon they referred to as "cooperative coupling" of the two sound sources.

Finally, the Greenwalt model made the critical assumption that all the properties of the sound resulting from the vibrating MTM were generated at the source. Thus, his model was thought to explain the various modulations observed in songs without invoking any other postsource effects, such as tracheal resonances caused by the size, shape, or other properties of this tube-like structure, or by the beak. Resonance is a property of the particular characteristics of a resonant chamber or tube (e.g., accounting for the modifications of human speech sounds after leaving the laryngeal source and passing into the throat, nasal, and oral chamber). Nowicki (1987) and Nowicki and Marler (1988) brought Greenwalt's assumption of no resonance into question by the clever technique of having birds sing in a helium atmosphere. Helium is less dense than the nitrogen it replaces in air to create the helium atmosphere, and for a simple tube model of the trachea the greater velocity of sound in helium would have the same effect as shortening the trachea, with nearly a 75% increase in the resonant frequency of the tube. The Greenwalt model with its no-resonance assumption predicts no change in the sound of a bird song when it sings in helium. Nowicki and Marler (1988) found that for both swamp sparrows and song sparrows singing in helium a harmonic was added to the notes of the emitted song so the perceived sound was higher pitched, a result caused by the energy contained in the higher frequency overtone. This is similar to what happens to the human voice after breathing from a helium balloon. The bird song results show that vocal tract resonances are indeed contributing to the properties of the songs.

An important finding in the Nowicki and Marler study of song was that the fundamental frequency

of any given note was not altered in the helium atmosphere, only that the harmonic was added. That the fundamental was not altered means that helium did not affect the sound source, whatever the source might be. The notes of the song in normal air were pure tones (no harmonics). In a sense, the helium atmosphere rescues higher harmonics that are otherwise lost. Thus, Nowicki and Marler argued that there is a "vocal tract filter" that constrains the sound to a single narrow band of frequencies. It appears, therefore, that the configuration of the vocal tract, under nerve–muscle control, and its other physical attributes attenuates some frequencies and allows others to pass. In the song sparrow and swamp sparrow examples, the helium/air comparison shows that under normal conditions the vocal tract tuning or filtering allows the fundamental to pass and attenuates the second harmonic.

A major review of the workings of the syrinx (Brackenbury, 1982) pointed out that virtually nothing was known about intrinsic syringeal muscle physiology, and, more problematical, no direct measurements had yet been made of any vibrating internal structures including tympaniform membranes, the tissue whose tension and movements were thought to produce the sounds in the classical Greenwalt model. Recent developments include the monitoring of thoracic air sac pressures together with recording of electromyograms (electrical signals produced when muscles contract) to reveal that neural timing signals are sent to the respiratory musculature, with consequent pulses of air passing through the syrinx to create temporal patterns of song delivery (Hartley, 1990). Miniature pressure sensors have been implanted in the bronchi with results verifying both independent and coordinated action of the two sides of the syrinx (Suthers, 1990). Additionally, Suthers (1997) also placed microbead thermistors in the syrinx to measure air flow and described in yet more detail the relationship between pulse-like respiratory air flow patterns (minibreaths) and the resulting temporal patterns of song syllable production.

Finally, the syringeal mechanism has been observed directly via endoscope to reveal that in some songbirds the sound is evidently produced by the action of the medial and lateral labia, these two structures adducting toward each other into the bronchial lumen of the particular side of the syrinx involved and vibrating with the passage of air through the slit so produced (Goller & Larsen, 1997). In the first such study, the medial tympaniform membranes were inactivated by surgical procedure, and the resulting songs produced by zebra finches (*Taeniopygia guttata*) and cardinals were "nearly normal" (Goller & Larsen, 1997). These observations would seem to support the original supposition of Setterwall and discount the interpretation of Rüppell and later supporters of the MTM theory. Improved endoscopic and recording techniques have verified the vibrational roles of the ML and LL for songbird phonation and also revealed a vibrational role for the lateral tympaniform membranes in a pigeon and a parrot, but found no support for the holetone whistle model of sound production (Larsen & Goller, 1999). Thus, at the present time virtually all types of vocalizations, including tonal sounds, appear to be explained by vibrational models of syringeal function in conjunction with vocal tract filtering of the source acoustics. However, as A. S. Gaunt and Gaunt (1985) point out, "a typical syrinx may be a myth" (p. 215); therefore, as more species are examined with the current high technology approaches we will probably see new revisions of current understanding of how the syrinx works. The songbird syrinx is clearly a complex mechanism. It transduces electrical signals originating in the central nervous system that flow to syringeal muscles, altering the configuration of the syrinx, and (via cervical, thoracic, and lumbar spinal nerves) that flow to the abdominal and thoracic respiratory muscles creating air flow through the syrinx, which finally produces an acoustic signal.

Brain Mechanisms and the Vocal Control System

As we have seen, the physiological mechanism by which song is produced by the syrinx was essentially a black box until about the mid-1900s. Similarly, the neurobiology of song learning and production were also unknown. Konishi (1965a, 1965b) and Nottebohm (1968, 1969b) carried out the critical experiments that initiated this research direction by deafening birds at various times during song ontogeny to reveal an auditory learning process and a motor learning process. Briefly put, the resulting model suggested that during auditory learning, or "instructional" learning, a memory of a training song (tape tutor or live conspecific) is acquired and stored. Later in development, sometimes not until early in the next breeding season, the subject begins to sing

poorly formed song elements (subsong then plastic song) as testosterone is produced under the influence of increasing day length. As the song utterances are produced over time, their form gradually improves and comes to resemble closely, in its final crystallized condition, the model song memorized in early life. The experimental species for these studies were the white-crowned sparrow (Konishi, 1965b) and the chaffinch (Nottebohm, 1968, 1969b). Later on (Nottebohm, 1980), it was discovered that male canaries castrated at 5–10 days of age developed subsong and plastic song as juveniles but failed to achieve crystallized adult song forms. A key finding of the earlier work (Konishi, 1965b; Nottebohm, 1968), however, was that deafening after the early tutoring instructional phase, but before the onset of singing the next spring, resulted in highly abnormal song with no resemblance to that of the tutor. Thus, in the spring singing phase, a bird is thought to experiment with its own vocal output, termed sensorimotor learning, to eventually attain a match between the auditory feedback from its own production and that of the early memory foundation known as the acquired auditory template. Surprisingly, when deafening was conducted after a bird attained its fully crystallized song form it continued to perform that song without the auditory feedback that was vital to its formation.

Subsequent puzzling over how this might be explained led to one of the most remarkable and boldest new directions in the biology of bird song in the last 100 years, and certainly a direction for which there are only meager and vague hints in the literature circa 1900 (Kalischer, 1905; Thébault, 1898). Konishi (1965b) had hypothesized that the stability of song structure in a bird deafened after song crystallization could be explained by the formation of proprioceptive memory as the stable song form was being established, and that in the absence of hearing after song crystallization the proprioceptive memory could retain the stereotyped song form. An alternative hypothesis (Konishi & Nottebohm, 1969), that the motor patterns responsible for stable song structure after deafening were generated centrally (a "motor tape" or "motor program") and required no proprioceptive feedback, was in accord with what had recently been discovered in the control of locust flight patterns (Wilson & Wyman, 1965). To test these alternatives, Nottebohm conducted a series of experiments in which he severed the tracheosyringealis branch of the right and left hypoglossus innervations of the syrinx of chaffinches. When bilateral sectioning caused respiratory difficulties for the first experimental birds, he subsequently sectioned only one side. This approach led to the discovery that most of the acoustic elements in chaffinch song were produced by the left side of the syrinx (Nottebohm, 1971, 1972a). Thus, if afferent fibers carried proprioceptive feedback information to the brain via the same tracheosyringeal nerve trunk carrying efferent fibers, the loss of such information from one side of the syrinx had no influence on the remaining song syllables produced by the other side. It would seem most likely that if the song form in deafened birds is maintained by proprioceptive feedback, it would be carried out by an integration of afferent information from both sides of the syrinx. Therefore, elimination of feedback from one side of the syrinx should have degraded all song features, which it did not. The results of these experiments ran counter to the proprioceptive feedback hypothesis and supported the motor tape hypothesis, but they also revealed lateralization of neural control of syringeal function. Because human speech is also lateralized, and known to be so at the level of the cerebrum, the finding in songbirds of left hypoglossal dominance led to a number of questions concerning central nervous system control of song production.

After creating an atlas of the canary brain (Stokes, Leonard, & Nottebohm, 1974), a research strategy involving the lesioning of brain regions, staining procedures, and preoperative and postoperative song recordings provided a description of a series of discrete clusters of nervous tissue (nuclei) and their joining projections, now known as the song control system (Nottebohm, Stokes, & Leonard, 1976). The emerging view was that once song is crystallized a motor program (motor tape) stored in the song control system organizes song production by the syrinx and can do so in the absence of auditory feedback. For several commonly used experimental species, the initial observations suggested that the brain nucleus HVC (high vocal center) sends data to nucleus RA (robust nucleus of the archistriatum), which provides output to both ICo (intercollicularis) nuclei and to the motor neurons that give rise to the tracheosyringealis branch of the hypoglossus nerve innervating the syrinx.

Following on these seminal discoveries, a great deal has been added to the story of neurological con-

trol of bird song learning and production. The original observation of a lack of effect on song structure when deafening occurred in adult male white-crowned sparrows and chaffinches has been clarified by studies on zebra finches, which show that auditory feedback is indeed needed to maintain song structure in deafened adults. Fragmentary evidence of song degradation in male zebra finches deafened as adults (>10 months old) was noted by Price (1979). More complete analyses by Nordeen and Nordeen (1992) revealed that after deafening the birds did not maintain preoperative song quality over the long term, and by 16 weeks postoperative the zebra finches retained only 36% of the syllables sung prior to surgery. Lombardino and Nottebohm (2000) systematically varied age at deafening and found, for example, that birds deafened at age 2 years or older retained good quality song structures for nearly a full year after the operation, but degradation eventually set in. From these studies of zebra finches, it appears that maintenance of normal song quality does indeed require auditory feedback, although the more singing practice a bird has prior to blocking auditory feedback the longer postoperative song quality stays high. Reflecting back on the earlier deafening experiments of Nottebohm and Konishi, it seems likely that those male white-crowned sparrows and chaffinches were older birds and may have had a great deal of singing experience prior to deafening, which is why no loss of song quality was noticed during the postoperative observation period (Nottebohm, personal communication).

Once the early descriptions of song control centers and motor pathways of song production were completed, a number of research directions were pursued. The role of androgens on target receptors in the song control nuclei was investigated early on (Arnold, Nottebohm, & Pfaff, 1976; Zigmond, Nottebohm, & Pfaff, 1973), sexual dimorphism in the song control system was described, corresponding to behavioral dimorphism in song production (Nottebohm & Arnold, 1976), and a correlation was found between the size of certain nuclei of the song control system and the size of a male's repertoire of songs (DeVoogd, Krebs, Healy, & Purvis, 1993; Nottebohm, Kasparian, & Pandazis, 1981). Of special interest in the developing saga was that in certain of the song control nuclei new nerve growth, and presumably synapse formation, was under hormonal influence (DeVoogd & Nottebohm, 1981). This result was integrated with discoveries of annual size changes in song control nuclei and the correlated behavioral phenomenon of acquiring new song repertoires as adults (Nottebohm, 1981; Nottebohm & Nottebohm, 1978).

Because of potential biomedical clinical contributions, the findings related to the production of new neurons, and replacement of neurons, in a brain nucleus of an adult bird attracted special attention. In a seminal discovery, Goldman and Nottebohm (1983) treated adult female canaries with testosterone implants and injection of tritiated thymidine. The labeled thymidine was incorporated into DNA during cell division, thus marking the daughter cells for autoradiographic analysis of brain tissues. Previous work had shown that testosterone treatment of female canaries caused a doubling in size of nucleus HVC and development of male-type songs (Nottebohm, 1980). Thus, the thymidine treatment was concerned with the question of whether the enlargement of HVC indicated genesis of new neurons there. Indeed, Goldman and Nottebohm discovered that birth of new neurons occurs in a brain region overlying HVC and these cells then migrate into HVC. Following studies then showed that the new neurons are incorporated into functional circuits (Patton & Nottebohm, 1984) and revealed fascinating details of the mechanisms of migration and path finding by the newborn neurons (Alvarez-Buylla & Nottebohm, 1988).

A succinct summary of this early phase of the discovery of neurogenesis in the adult brain (Nottebohm, 1989) pointed out the significance of these discoveries. At the time, the prevailing view of nervous system development in warm-blooded vertebrates was that the complement of nerve cells in the brain was determined early in life with no further production in adulthood. Thus, loss of nervous tissue from injury or disease was permanent. The bird brain discoveries therefore held promise that basic research in mechanisms of neurogenesis in the song control system might one day lead to clinical methodology for repair of damaged human brain tissue. But more basic to bird song research itself, functional neurogenesis and birth/death turnover of neurons in the song system of the brain bolstered the hypothetical explanation for the ongoing learning of new songs and song components in fully adult birds of some species, such as the canary, that exhibit this capacity.

From a year-long study of neuron death and replacement in the canary HVC (Kirn, O'Loughlin, Kasparian, & Nottebohm, 1994) it appears that such turnover of nerve cells occurs year round but with peaks of turnover at the same time changes in song syllables occur. The temporal pattern of recruitment of new neurons in HVC is testosterone dependent, probably operating via a neurotrophic factor (Rasika, Alvarez-Buylla, & Nottebohm, 1999). Evidently, the majority of newborn (replaceable) neurons in HVC extend axons to the RA nucleus, providing connection in the motor pathway of song production leading finally to the syrinx (Alvarez-Buylla, Theelen, & Nottebohm, 1988). Other HVC neurons send projections to a different nucleus in the song system (Area X), and these neurons are generated only in very early life and not replaced in adulthood (Kirn, Fishman, Sasportas, Alvarez-Buylla, & Nottebohm, 1999). When RA-projecting (replaceable) neurons of HVC are selectively destroyed in zebra finches, the song structure deteriorates but then recovers as neurogenesis replaces the dead neurons. Such song degradation did not occur when the unreplaceable Area-X-projecting neurons of HVC were destroyed (Scharff, Kirn, Grossman, Macklis, & Nottebohm, 2000). The general finding of a learned behavior recovering its form 3 months after the induced death and subsequent replacement of HVC neurons justifies the excitement attendant to this line of research. Restoration of learned behavior patterns by inducing neuron production and replacement clearly leads one to think about biomedical applications.

New findings continue to accumulate in this attractive area of neuroethology. As mentioned earlier, recording of thoracic air sac pressures, electromyograms of respiratory muscles, pressure sensors in the bronchi, and endoscopic observation have provided important data on what information is sent from the song control system to operate the syrinx and the passage of air though it (Hartley, 1990; Suthers, 1990). Various strategies of lesioning in the song control system, with electrically recording and/or stimulating nerve cells at different times in song ontogeny, and in combination with deafening, have revealed a more elaborate view of the song control system, now numbering upwards of a dozen or more components. Nervous control of the syrinx is only one aspect of a song control system, for clearly the respiratory system and postural and jaw control must also be orchestrated (Wild, 1997). Now known are the neural sites of origin for singing activity, how auditory information accesses the song control system, and many of the contributions and interactions of the system components (Brainard & Doupe, 2000; Margoliash, 1997; Nottebohm, 1991).

Molecular biology techniques have recently provided something of a shortcut approach to obtaining information about the workings of the song control system. One technique is to monitor the expression of a transcriptional regulator (ZENK: Zif-268, Egr-1, NGFI-A, Krox-24) in the song system (Jarvis & Nottebohm, 1997). Depolarizing neurons send a chemical message to the cell nucleus causing the synthesis of ZENK messenger RNA, and therefore detection of ZENK expression reveals neurons that are activated by audition or production of songs. Thus, monitoring the ongoing behavior of a subject involved in vocal interaction, whether singing, listening, or both, and either in free-living or captive birds, is the first step in the procedure (Jarvis, Schwabl, Ribeiro, & Mello, 1997). About 30 min following the behavioral event of interest, the bird is killed and in situ hybridization of brain sections with a radioactively labeled probe allows quantification of the extent to which the immediate early gene ZENK is expressed in nerve cells in different components of the song system. Different song control nuclei are activated depending on whether the subject is singing or simply hearing another bird sing, and these patterns of ZENK activation have been examined in various situations and species, including songbirds, parrots, and hummingbirds (Jarvis & Mello, 2000; Jarvis, Ribeiro, DaSilva, Venturas, Vielliard, & Mello, 2000; Jarvis, Scharff, Grossman, Ramos, & Nottebohm, 1998; Mello & Clayton, 1994).

Induced ZENK activity resulting from auditory input provided leverage allowing major advances in deducing the neural pathways and regions by which information gains access to the song control system. Whereas the system components for acquiring and producing songs (the motor pathway) drew most early attention, the brain circuitry involved in auditory perception and long-term storage of vocalizations is only recently described. Incoming signals via the cochlea were known to arrive in the telencephalon area referred to as Field L (Kelley & Nottebohm, 1979), but definitive evidence for a connection from Field L to song control centers was lacking. The ZENK assay identified new process-

ing centers of vocal signals whose neural connections to the vocal control system (HVC) were then revealed by chemical tracer techniques (Vates, Broome, Mello, & Nottebohm, 1996). Further studies also revealed that auditory signals reaching the Field L complex are probably transmitted to the RA nucleus as well (Mello, Vates, Okuhata, & Nottebohm, 1998).

In addition to these neuroanatomical investigations that map out the components and connections involved in song perception and production, electrophysiological studies of single neurons at various locations in the song system aim to determine the cellular basis of processing incoming signals and motor production of outgoing signals. There are a great many questions to be addressed by these in vivo intracellular recording probes of the circuitry of the song system. An early breakthrough study by Margoliash (1983) showed that single cells in HVC of the white-crowned sparrow respond maximally to the bird's own song. This was a significant result because neurons strongly selective and specialized to respond to the bird's own song could be involved in song learning. During the sensory learning phase, a tutor song model is acquired and later, in the process of sensorimotor matching of vocal output to the stored model, neurons selective to the bird's own song could act as a template by differential firing rates dependent on degree of matching to model (Doupe & Konishi, 1991). Song-selective responses in single neurons in other song nuclei, how the signals propagate among the song centers, signal attenuation and modification, and differences in firing rates are foci of current studies (Janata & Margoliash, 1999; Mooney, 2000; Rosen & Mooney, 2000).

Other recent advances in the neurophysiology of song learning have been quite novel in approach and revealing in substance. Findings of Dave and Margoliash (2000) show that when a zebra finch sings, neurons in the RA nucleus fire in bursts of premotor activity. Each type of burst maps to a particular kind of note that is produced by neural motor activity following the burst. Important as that is, things got more interesting when the researchers discovered that neural patterns of response in RA occurring when the bird is asleep but being played its own song are similar to those evident during actual song production. Moreover, during undisturbed sleep, spontaneous neural firing produces bursts of impulses similar to the premotor patterns observed during singing. Thus, it appears that the zebra finch song control system is silently rehearsing its melodies while the bird sleeps.

Additional neurophysiological approaches are also being pursued. Brain slice preparations, for example, are used to examine the electrophysiological and pharmacological properties of neurons and synapses in the song system. In these preparations (e.g., Mooney & Konishi, 1991), a bird is decapitated and the brain removed and placed in a cold chemical medium to keep the tissues alive while several slices are made through the song control centers of interest. A slice can then be placed in a recording chamber where electrodes are inserted in single cells to stimulate and record neural activity. Thus, for example, study of the inputs to song nucleus RA from two other song centers (HVC, L-MAN) revealed that the axons from these two different sources apparently formed synapses on the same RA neurons, but their excitatory effects were regulated by different receptors (Kubota & Saito, 1991; Mooney & Konishi, 1991). In these brain slice preparations, it is possible to examine the role played by various neurotransmitters and receptor systems by use of specific blocking antagonists in conjunction with electrical stimulation and recording. Such treatments reveal the basic mechanisms of nerve transmission within and between components of the system (Mooney, 1992). The RA nucleus has been a focus in this line of investigation (Spiro, Dalva, & Mooney, 1999) because of its apparently central role in the initiation of nerve signals that influence both vocalization and respiratory patterns during singing (Suthers, 1997; Yu & Margoliash, 1996). It is abundantly apparent from this brief overview that striking advances are rapidly accumulating in the understanding of brain mechanisms of song production and perception, and that all the tools of modern neuroscience are being brought to the task.

The techniques of comparative biology are also contributing to advances in this field or research. It is difficult to think of any other area in neuroscience where workers have benefited so clearly from adopting an evolutionary perspective to advance their research programs as in the neurobiology of bird song. Such a neuroethological perspective allows one to reach past model species, such as the zebra finch and canary, to take advantage of the wide range of evolved systems of song learning and singing be-

havior represented among the many species of birds. Such variation often provides special leverage to attack some questions that are not easily addressed in the model species. Nowhere is the usefulness of a broad comparative approach better advocated and illustrated than in two recent reviews (Brenowitz, 1997; Brenowitz & Kroodsma, 1996). They point out, for example, that although only one parrot species has been examined, it looks like the neural vocal control system differs in a number of ways from that of songbirds. Taking advantage of the comparative method in bird song neuroscience may have happened in any case, but it may not be coincidence that the pioneers in this research field were ethologists first, and their academic offspring and grandchildren seem often to have been imbued with a similar intellectual tradition of the comparative method.

While reductionistic-minded researchers were busy explaining syringeal function and the neurobiology of song learning and production, other directions derived from the basic phenomenon of song learning were being explored with similar intensity. One of these directions in bird song biology, suggested by Newton's (1896) observations of the existence of song dialects, is the considerable interest in patterns of geographic variation in culturally acquired vocalizations, including song dialects. Such vocal variation is, as in human dialect and language populations, the single most apparent consequence of vocal learning.

Population Consequences of Song Learning

Several issues arise as a result of a population learning its vocal signals from conspecific models and converging on a common pattern. Ethologists have taken human speech as a heuristic model to generate questions about the evolution of vocal learning and address hypotheses about the possible population and social consequences of vocal learning. Vocal learning in humans has allowed the emergence of a highly flexible communication system, open and adaptable to new situations, and it was logical for researchers to look for similar patterns in bird vocalizations.

Geographic variation in the song features of populations of a species was described by von Pernau in observations prior to 1720. In discussing regional variations in songs of common nightingale (*Luscinia megarhynchos*), for whose song it was observed that "fanciers also prefer a Surry bird to those of Middlesex." Barrington (1773) noted, "These differences in the song of birds of the same species cannot perhaps be compared to anything more apposite, than the varieties of provincial dialects" (p. 280). In 1896, Newton raised the question of whether songs of a species are the same everywhere, and answered himself: "From my own observations I am inclined to think they are not, and that there exist 'dialects,' so to speak, of the song" (p. 893). From the 1930s onward, description of geographic and microgeographic variation and dialects in songbirds became a major development. The chaffinch was a focus of attention in those early years, stimulated by the research of Promptoff (1930) on geographic song variation among Russian populations, Sick (1939) on dialect variation in the "rain call" in Germany, and Marler (1952) on song variation in Western Europe including a sample of recordings from the Azores. Other major efforts along these lines were by Saunders (1935) and by Benson (1948), who outlined geographic vocal variation in numerous African bird species. These early descriptions were not aided by the sound spectrograph, however, and that instrument, as in many other research areas, soon stimulated considerable effort to improve and document the descriptions of song dialects (Marler & Tamura, 1962, 1964).

A number of issues about song dialects have emerged from the initial descriptions. It was recognized that song dialects, like human speech dialects, are cultural markers, learned traits of conformity to local population norms. At the same time, evolutionary biologists (e.g., Mayr, 1942) attributed one method of reproductive isolation between species to that of premating mechanisms of species recognition derived from song differences. Combining these lines of reasoning, it is not surprising that given the recognized role of song in mate choice and other social behavior one would develop the hypothesis that song dialect differences among populations might also play a role in reducing genetic exchange between dialects (M. C. Baker, 1982; M. C. Baker & Marler, 1980; Marler, 1970; Marler & Tamura, 1962; Nottebohm, 1969a). A similar hypothesis about geographic variation in signals was also proposed by Crews and Williams (1977). Such a dialect effect would allow the adaptation of gene pools to local ecological conditions in much the same way that a heritable reduction in dispersal tendency might

operate, or that of habitat imprinting and the tendency of migrants to return to particular breeding areas. Indeed, these factors may often work together to provide an explanation of how song dialects form (Lemon, 1975).

Payne (1973) proposed an interpretation of cultural speciation and local genetic divergence of dialects in the brood parasitic indigo birds (*Vidua*) of Africa, but at the time lacked supporting quantitative data on genetic population structure, as well as several other important variables. Baptista (1975) also proposed the essential features of the concept of dialects as representing genetic demes from his studies of white-crowned sparrow populations resident in mostly urban areas where observations crucial to testing of the hypothesis were difficult or impossible to make. The possibility of demonstrating local adaptive peaks in population gene pools, and the attendant behavioral processes, would have to be considered in the light of how recently the dialect structured populations were established, together with the strength of local selection pressures in opposition to gene flow. This would clearly be a quantitative problem of some immensity, not the least of which is to provide a thorough description of the dialect geography. It was already known from Thorpe's (1958) chaffinch work that some species learned song patterns after dispersal, in the chaffinch around 9 months of age; therefore, if dialect effects on gene flow were to be found it would be most likely in age-limited learners, such as the white-crowned sparrow.

To explore the possible effects of dialects on dispersal, interdialect discrimination, mate preferences, and consequently on genetic structure, required a continuously distributed population with dialects but no physical barriers between them. With Baptista's help, such a situation was identified in the early 1970s in the white-crowned sparrow populations of the Point Reyes National Seashore where conditions allowed thorough mapping of the system of contiguous dialects (Fig. 3), begun in the summer of 1972, in virtually undisturbed habitat (M. C. Baker & Thompson, 1985). These circumstances resulted in an examination of genetic differentiation of dialect populations by use of the recently developed allozyme methodology (M. C. Baker, 1974, 1975; M. C. Baker, Thompson, Sherman, Cunningham, & Tomback, 1982), quantification of dispersal within and between dialects (M. C. Baker & Mewaldt, 1978), playback experiments to determine the potential for behavioral isolation from male–male response to dialect differences (Thompson & Baker, 1993; Tomback, Thompson, & Baker, 1983), and the preferences of females for natal and nonnatal dialects (M. C. Baker, Spitler-Nabors, Thompson, & Cunningham, 1987; Tomback & Baker, 1984).

For the studies of female preferences for specific song dialects, a laboratory assay was developed (M. C. Baker, Spitler-Nabors, & Bradley, 1981; King & West, 1977; Searcy & Marler, 1981) that proved to be of some usefulness in addressing a variety of questions about female choice (M. C. Baker, Bjerke, Lampe, & Espmark, 1986; M. C. Baker, Bjerke, Lampe, & Espmark, 1987; M. C. Baker, McGregor, & Krebs, 1987; M. C. Baker, Spitler-Nabors, et al., 1987; Barnard, 1990; Catchpole, Dittani, & Leisler, 1984; Searcy, 1984). The general direction of the results of the several approaches on white-crowned sparrows indicated that there were significant gene frequency differences between dialects, no morphological differences between dialect populations, no environmental gradient of any appreciable magnitude across the dialect populations, reduced dispersal between dialects, and a distinct preference by females for the dialect of their own local area. Lacking in all this program of research, however, were any estimates of the history of establishment of the dialect populations. Indeed, empirical data on dialect origins are still largely unavailable, although one or two hypotheses present fairly compelling explanations, but few time estimates for any particular cases.

Other investigations of the question of dialect consequences in the population biology of songbirds also occurred in studies of the rufous-collard sparrow (*Zonotrichia capensis*) in Argentina, for which Nottebohm (1969a) had provided the initial descriptions. This research program was taken up by Paul Handford (Handford & Nottebohm, 1976) and carried exceptional promise because populations of rufous-collared sparrows could be found spread continuously over a steep ecological gradient in mountainous regions where local adaptive peaks might be expected. In their first efforts, however, Handford and Nottebohm (1976) found no consistent relationships between either morphology or allozyme frequencies and dialects along a mountain transect, although allelic frequencies showed a clinal pattern and allozymes varied with morphology. Large

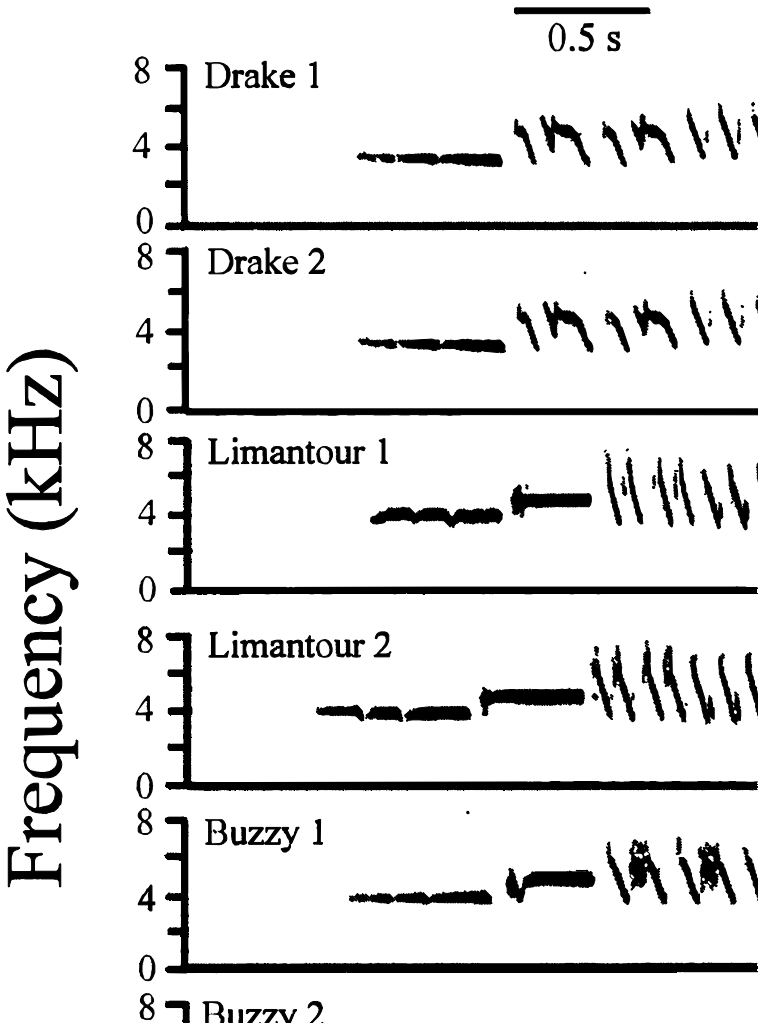

Figure 3. Sonograms of songs of three different dialects of white-crowned sparrows. The songs of two males from each dialect are illustrated. These three dialect populations are arranged geographically in a linear series, bordering on each other, in chaparral habitat along the coast in the Point Reyes National Seashore in northern California, the Drake dialect in the north.

changes in song, however, occurred consistently at transitions between vegetation zones. This suggested that the song dialect features might be adapted to the sound transmission properties of the physical and/or biotic environments. Testing this hypothesis by propagation of songs from different dialects in alternative vegetation types and measuring degradation was not attempted. Further work on this species at other sites confirmed the association between dialect change and change in vegetation type (Handford, 1988; Lougheed, Lougheed, Rae, & Handford, 1989). Apparently not considered at the

time of the first allozyme study on this species was an alternative hypothesis that the dialect populations were genetically adapted to the ecological differences among the vegetation zones, and that the allozyme data, representing essentially neutral genes, did not sample the relevant portion of the genome that would reveal adaptation.

In a follow-up allozyme and morphometric study, however, Lougheed and Handford (1992) found significant heterogeneity among dialect populations of rufous-collared sparrows for 19 of 20 morphological traits and a pattern of allozyme frequencies, analyzed by components of variance, that indicated 51% of the genetic differentiation among sample sites was attributable to dialect effects. This result was very similar to the degree of genetic differentiation (58%) found by Zink and Barrowclough (1984) in their reanalysis of the white-crowned sparrow data from Point Reyes (M. C. Baker, Baker, Cunningham, Thompson, & Tomback, 1984). This remarkable concordance of allozyme results, together with the observed morphological differentiation among dialects, would appear strong confirmation of the original hypothesis of dialect effects suggested by Marler and Tamura (1962) and Nottebohm (1969a).

Apparently, sufficient differentiation had occurred between some populations of rufous-collared sparrows that they were considered subspecific, although the authors did not substantiate the subspecies designations in their post hoc analyses, and a later paper seemed to retract the subspecies claim (Lougheed, Handford, & Baker, 1993). An interesting feature of the study of Lougheed and Handford (1992) is the morphometric result, which stands in sharp contrast to the results of previous morphological analyses of the same species. In their 1976 paper, Handford and Nottebohm examined nine external characters and found no general trends, no consistent clinal variation over the altitudinal gradient the birds occupied, no correlation with vegetation zones, and no relationship with dialects. By comparison, Handford (1985) used a set of six morphological features measured on 22 subspecies and found separation of two groups of subspecies but extensive overlap among subspecies within each of the two groups of rufous-collared sparrows. The overlap was so high that the individual subspecies could not be distinguished. In the study of Lougheed and Handford (1992), however, the 20 morphological measures showed a strong pattern of concordant variation among dialects. For 17 of the 20 morphological variables, dialect explained considerably more of the variation than did site differences within dialects. Approximately 70% of the specimens were correctly classified by dialect membership using canonical variates analysis on the 20 morphological features.

More recently Lougheed et al. (1993) examined rufous-collared sparrows using mitochondrial DNA (mtDNA) techniques on birds ($n = 42$) collected at nine sites over the transect originally studied by Handford and Nottebohm in 1976. The mtDNA analysis revealed 41 different haplotypes for the 42 birds and found no clustering of haplotypes with dialects. In this study, no song data were presented to verify dialect variation, and concern could be raised that nearly 200 birds had been collected, with unknown subsequent dispersal consequences in remaining populations, from these five sites 15 years earlier when the dialects were recorded and described. However, from their mtDNA results, the authors found two major clusters of haplotypes, but these did not correspond to two subspecies as they apparently thought they might. Because almost every individual in the sample had a unique mtDNA haplotype, it is not obvious what this study showed regarding dialects, except the possibility that ancestral populations had more than one haplotype and haplotype divergence preceded dialect formation. Nucleotide divergence in this study averaged 1.4% (maximum 3.2%). In other avian systematic studies of this and other *Zonotrichia* species (e.g., Zink, Dittmann, & Rootes, 1991), molecular clock data are often applied to estimate the time since divergence, which applied to the 1.4% figure suggests haplotype divergence about 700,000 years ago on average. How, if at all, these mtDNA data bear on the hypothesis of dialects as demes is not clear. Populations that cannot be distinguished by molecular markers, which are effectively neutral, may be significantly differentiated by natural selection at loci that reflect specialization and adaptation to local ecological conditions. In short, if neutral molecular markers reveal differences between populations this indicates a potential for adaptive divergence. The absence of molecular marker divergence, however, is unenlightening.

A cogent example is the song sparrow in which highly differentiated populations and subspecies ($n = 34$) are well known from morphological stud-

ies (Marshall, 1948; A. H. Miller, 1956), a pattern commonly interpreted as resulting from natural selection adapting populations to differing environments (Mayr, 1963; A. H. Miller, 1956). Mitochondrial DNA haplotypes, however, are literally randomly distributed across the entire North American range of the species (Zink & Dittmann, 1993). Several potential explanations for the absence of phylogeographic pattern in mtDNA yet strong morphological differentiation in the song sparrow are well-discussed by Zink and Dittmann, and they favor a view that size and plumage color evolution has been more rapid than mtDNA evolution. The song sparrow results would appear to be a useful interpretive model in appraising the rufous-collared sparrow data.

In summary, the extremely high level of haplotype diversity in mtDNA profiles and their nonconcordant distribution with respect to vegetation zones and dialect populations in rufous-collared sparrows may mean that the molecular divergence is more ancient than the dialects. The question of adaptation and dialects appears answered by the previous study showing morphological and allozymic differentiation of dialect populations. Alternatively, the morphological traits that exhibit differences among dialect populations may be ecotypic, in which case nestling transplant experiments would be informative.

Few other attempts to gather data to test the correlation of dialects and morphological or molecular genetic structure have been made. From his studies of swamp sparrows, Balaban (1988a) concluded that for two of his three population subdivisions there were correlations between syllable variation and genetic variation, although the populations were distant from one another. The original cultural speciation model of Payne (1973) was subsequently examined from the standpoint of mtDNA profiles in selected species of *Vidua* finches and their host species (Klein, Payne, & Nhlane, 1993). The authors concluded that the results were in accord with the model of cultural speciation and discounted the alternative hypothesis of cospeciation.

Key aspects of the dialect effect hypothesis for which current data are inadequate are: (a) the overall issue of gene flow versus selection cannot be avoided in any case where causation of population differentiation is under study, and in the end these opposing forces have to be estimated, (b) more information from field populations, in undisturbed habitat, on the frequency of occurrence of female preference and mate choice of same-dialect males would be useful, (c) the frequency of occurrence of young males dispersing into adjacent dialects and adopting the song features prevalent there (Rothstein & Fleischer, 1987), and finally, (d) direct observation of the formation of a regional dialect system would be informative. In regard to (c), there has ensued considerable speculation concerning the potential role of selection-based (action-based) learning in song dialect populations, and it is possible that this learning model can help explain the origin of dialect populations in some species.

To integrate selection-based learning into dialect biology, it is necessary briefly to revisit the phenomenon of song learning. Marler (1997) outlined three main models of song learning, one of which represents the interpretations developed in the early years of experimentation of tutoring and deafening [i.e., a subject memorizes a song model in early life (instructional learning) and at a later time begins to sing and match its attempts by auditory feedback (sensorimotor learning) to the original instructional song model]. Two of the additional models proposed in Marler's synthesis involve the concept of overproduction during plastic song of a larger set of song features obtained by instruction (or innately specified) in early life. This overproduction phase is followed by or concurrent with selective attrition or "winnowing out" (selection-based learning) of some of the song forms during behavioral interactions, such as counter-singing and matching songs with another male during territory establishment.

The model of selection-based learning has been advocated for a number of species, but the cases of the song sparrow and field sparrow (*Spizella pusilla*) are especially instructive. Information from a population of song sparrows indicates that a young male learns a repertoire of song types from 3-4 resident territorial males during the summer of hatching and then obtains a territory nearby. Consequently, a young male in his first breeding season will share a number of songs in his repertoire with neighbors, and in particular with the closest neighbor (Nordby, Campbell, & Beecher, 1999; Nordby, Campbell, Burt, & Beecher, 2000). Thus, song sharing is primarily among a small cluster of neighbors (Beecher, 1996). If the young bird was hatched in the same neighborhood, then the instructional learning mod-

els will be much the same as the selection-based consequences after attrition of some variants, a noticeable degree of sharing among a small number of neighbors. If the juvenile was not banded as a nestling, then its prior song model exposure is unknown. Information from a population of field sparrows indicates that when a vacant territory is filled by a new bird singing two or more song types, in a number of cases the type that resembles the song of a resident neighbor is retained and the other types either dropped or rarely used (Nelson, 1992). As in the song sparrow, only a small number of males, 2–3 on average, have similar songs as a result of this process and often the resemblance between the neighbors was found to be only an approximation. For the most part, the new birds filling territories in the field sparrow population were of unknown origin and prior learning experience.

Viewed from these case studies, such overproduction and selective retention has led to the proposal that this could explain song dialects (Nelson & Marler, 1994). This proposal can make some sense, depending on what is meant by "explain song dialects." Matching of postdispersal neighbors has to be considered together with the size of the dialect area and where the instruction phase of song model acquisition occurs. These factors were suggested earlier by Rost (1987) as important to dialect models, and in particular the size of dialect area often has been ignored in discussions of dialect biology. If, for example, we assume a system of dialects already in place and imagine a juvenile male dispersing and attempting to establish territory, selection-based learning would come into play if the juvenile has previously obtained a song form that matches a resident where the attempted territory acquisition is occurring. The critical information needed here is what song models might have been obtained during the early instructional phase of ontogeny. For a juvenile to make a successful match in a different dialect population, it would need to have experienced the new dialect features in early life. This points up several interesting problems. First, the problem of scale comes into play, because if only a small handful of males sharing a song type is considered a dialect, as might be inferred in the song sparrow and field sparrow accounts, then the action-based model is reasonable if during the instructional phase of development the youngster was exposed to all the song variety in a local area. Imagine, on the other hand, that the young bird was exposed only to variants within one dialect area and then dispersed into another dialect where none of its overproduced song types matched those of the new dialect. In this situation, the inability to match potential new neighbors might even preclude establishment there, thus inhibiting exchanges between dialects. Furthermore, if we want to label as a dialect a cluster of 2–3 or even 8–10 males with similar songs, what Mundinger (1982) would call subdialects, we need to recognize how this differs from the configuration in some other dialect species.

In terms of the white-crowned sparrow dialects at Point Reyes and those of the rufous-collared sparrow in Argentina, or a number of other species (e.g., ortolan bunting, *Emberiza hortulana*; Conrads & Conrads, 1971), the scale is very different. When dialects comprise a hundred or more territorial males spread over kilometers of range, the scale comes into play in applying the selection-based learning model and inferring population consequences. Rost (1987) estimated a dialect of marsh tits at 600 pairs occupying a 135-km^2 area. In such large dialect populations, for a successful cross-dialect dispersal and song matching via selection-based learning episode, a young bird would somehow have to acquire the new dialect features during instructional learning in early life. Given known birth to breeding dispersal distances in many songbirds, and the early movements of fledglings, the instructional song models often will be constrained to within dialect variation. Only if in the instructional phase the learner is exposed to an alternative dialect can selection-based convergence to a different dialect occur. Indeed, such may be the case of fledglings hatched in the vicinity of a song dialect border, yet even here we need to know the rate of cross-dialect dispersal and determine any inhibiting effects of dialect borders, variables that seldom have been measured.

Clusters of convergent song features (song neighborhoods or subdialects) have been described within dialects of white-crowned sparrows (Cunningham, Baker, & Boardman, 1987) and rufous-collared sparrows (Nottebohm, 1969a), and this type of pattern may be explained by a selection-based learning model. Clearly the variables needing description for a full evaluation of the role of selection-based learning in dialect biology are quantitative data on dispersal, documentation of learning models experienced during the instructional phase, documentation

of overproduction and winnowing, and detailed description of the geographic arrangement of the dialect populations involved. Whether we are considering a small number of birds in a restricted song neighborhood, or a dialect comprising many hundreds of birds over areas of several square kilometers, or more extensive regiolects (regional dialects or song institutions) of even greater geographic extent and numbers of birds (Martens, 1996), it is important to make distinctions among these different scales in discussions of geographic song variation, as was cogently argued nearly 20 years ago (Mundinger, 1982). In addition, depending on the scale, differing models of dialect origin come into play (Martens, 1996; Thielcke, 1973; Thielcke & Wüstenberg, 1985).

A related issue involves the primary data on overproduction of song types during plastic song. The phenomenon is not easily verified in every case, nor has it been established in many species. Overproduction is judged from the appearance of the acoustic units recorded during plastic song, when these units are not highly stereotyped, by definition. Thus, it is necessary to make a judgment on which of those plastic units of sound can be identified in crystallized song and which are deleted. This difficult process is not always straightforward. The most convincing cases come from the laboratory simulations of overproduction and selection-based learning, because all the inputs and outputs can be thoroughly documented (e.g., Marler & Peters, 1982b; Nelson & Marler, 1994). Some field studies of the phenomenon are less than convincing, providing little documentation and relying heavily on anecdotes (DeWolfe, Baptista, & Petrinovich, 1989). We are in the early days of exploring selection-based learning and careful studies on a variety of species would be quite valuable.

It will not be decisive, however, to provide a few anecdotes on these processes, but instead quantitative data from natural populations are required. For one reason, this is because the hypothesis of dialect effect was not modeled as an absolute barrier resulting in complete isolation of populations. The original hypothesis, an alternative to the null hypothesis, was that dialect differences have a measurable effect on the exchange of birds between dialect populations. Thus, a study showing that selection-based learning can occur by describing one or two case histories is not sufficient. A study occurring in a population of a mixture of two different dialects is not instructive to the hypothesis because when females hear songs of two or more different dialects during early life there is no reason to expect them to prefer one song type over any other (Chilton, Lein, & Baptista, 1990; Petrinovich & Baptista, 1984). The hypothesis that a female will prefer the song of her father can be approached this way, but that was not part of the dialect effect hypothesis. Clearly, early learning constrained to the father's song type could make dialect structures even more discrete and promote higher levels of assortative mating, as Rost (1987) found, but such a constraint is not essential to the hypothesis.

Holding great promise as a possible lever to evaluate female choice in dialect systems, the induction of female song by testosterone implantation or injection was used as a method to examine assortative mating in two white-crowned sparrow subspecies. By recording the dialect type of the male of a pair and inducing song in the female mate, it is possible to see if they share the same dialect features. The song produced by a female, for those species in which females do not normally sing, is likely to be a consequence of instructional learning only, because there is no selection-based phase leading to a final song form as occurs in males. Moreover, the female instructional learning phase is likely to be limited to early tutoring experiences, at least in age-limited learners. Thus, examination of song type matching in mated pairs could be informative even though it does not tell us where the male came from.

Only three published studies present adequate information for judgment to be rendered. In the first such study (Baptista & Morton, 1982), only 2 of 10 pairs revealed a dialect match between mates, which was statistically random mating. In the second study (Petrinovich & Baptista, 1984), 15 mated pairs were recorded and the results were that in only four or five pairs did the female song dialect match that of her mate. Both these studies occurred in mixed dialect populations where both males and females probably spent their early lives in an acoustic environment containing two or more song types (Morton, 1992). In the third study (Tomback & Baker, 1984), 24 of 25 females from three different dialect populations had song dialect features that matched those of their mates. For two of the three population samples, there was no dialect mixing in the nearby vicinity of the subjects and here 15 of 15 females

were assortatively mated. In the third sample, there was some interdigitation of the two dialects, although one was in the majority, and here 9 of 10 females were assortatively mated by dialect (Fig. 4). Overall, it appears that the female song induction manipulation has considerable promise if more broadly applied in a variety of species and with appropriate care in describing the microgeography of the study dialect populations. The case of the rufous-collared sparrow would seem opportune.

Another line of investigation has revealed that assortative courtship can be culturally transmitted in brown-headed cowbirds (*Molothrus ater*) as shown by female pairing and mating behavior (Freeberg, 1996, 1998; Freeberg, Duncan, Kast, & Enstrom, 1999; West, King, & Eastzer, 1981). Differing song traditions of populations of this species appear to be potentially effective in reproductive isolation, females preferring male songs of their own area (West, King, & Freeberg, 1998) as evidenced by copulation solicitation display behavior. Taking these findings on cowbirds into the field populations where two cultural song traditions come into contact may be rewarding.

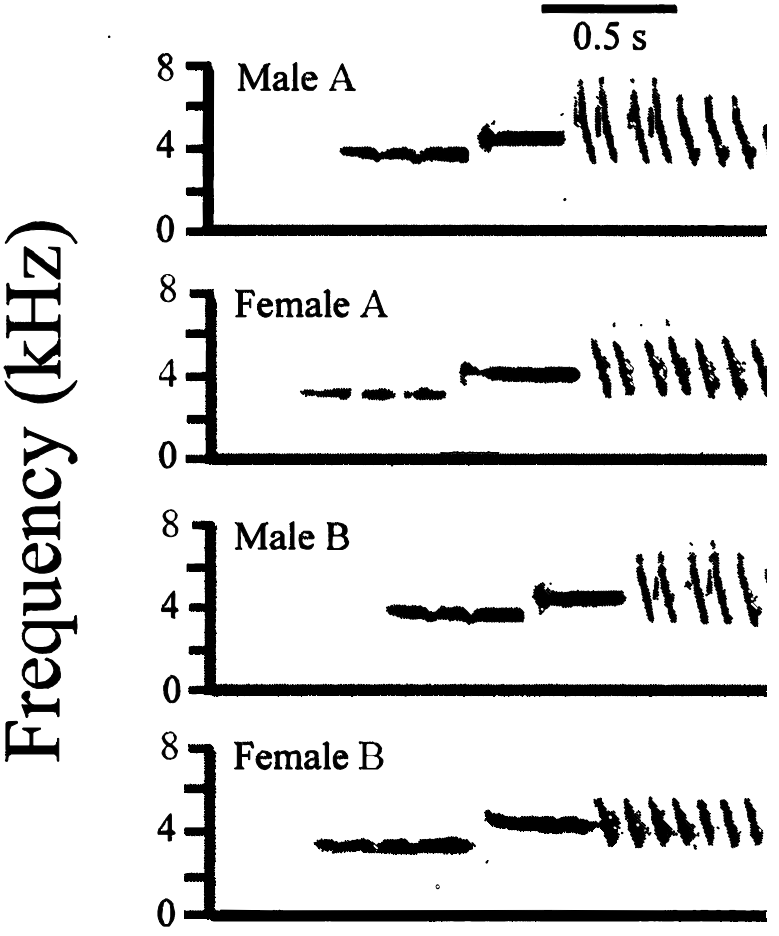

Figure 4. Sonograms of songs of two pairs of white-crowned sparrows in the Limantour dialect in Point Reyes National Seashore, northern California. Females normally do not sing but these were induced to do so with exogenous testosterone. These male–female matches illustrate that the females were assortatively mated with males from their same dialect. These two pairs of birds resided near the border of the Buzzy dialect, whose songs are illustrated in Figure 3.

Overall, the results on species for which pertinent data are available do not give a clear and consistent conclusion, or are lacking in some important information, and the value of further research seems apparent. As in many other areas of research, more work is needed to clear up a somewhat muddy picture. The question of the possibility of genetic differentiation being related to the cultural differentiation represented by song in white-crowned sparrow dialects seems unusually contentious, for reasons not readily apparent. Interested readers, however, can easily form their own opinions from the published documents (M. C. Baker, 1982; M. C. Baker & Cunningham, 1985; M. C. Baker et al., 1984; M. C. Baker & Mewaldt, 1981; M. C. Baker, Tomback, Thompson, & Cunningham, 1985; Hafner & Petersen, 1985; Petrinovich, Patterson, & Baptista, 1981; Zink & Barrowclough, 1984), and much of the earlier work on the species is summarized in Kroodsma, Baker, Baptista, and Petrinovich (1985). As mentioned previously, one area of research on song dialects that is especially sparse is on the question of dialect origin. Colonization of new habitat and dialect emergence by founder effect, perhaps in tandem with selection-based learning, is one possible model of origin, and fairly widely advocated in view of several island studies where such an effect looks likely to have occurred (A. J. Baker & Jenkins, 1987; M. C. Baker, 1996). In the summer of 2000, the many large fires in the western states of America could present the raw material for testing such a model of dialect origin as recolonization follows razing of the landscape.

Interestingly, it may be that the search for genetic differences among song dialect populations, as indicated by molecular data from allozyme or mtDNA profiles, is not as relevant as it seems at first glance. Female choice is of special significance in discussions of nonrandom mating. Female preference for local dialect songs of males is a common finding, as noted earlier for white-crowned sparrows both in the laboratory and in natural populations, but also in a number of other species [marsh tit: Rost, 1987; swamp sparrow: Balaban, 1988b; great tit (*Parus major*): M. C. Baker, McGregor, et al., 1987; yellowhammer (*Emberiza citrinella*): M. C. Baker, Bjerke, et al., 1987; corn bunting: Hegelbach, 1986; brown-headed cowbird: King, West, & Eastzer, 1980; Eastzer, King, & West, 1985]. Strong mate preferences of female birds for local dialect songs are not fundamentally different from cases in which newly differentiated populations result from sexual selection via female choice. In the case of female choice sexual selection leading to speciation, which may occur relatively quickly (Higashi, Takimoto, & Yamamura, 1999), there is no expectation of substantial genetic or morphological differentiation of the two incipient species (Kaneshiro, 1988; Lande, 1981; Meyer, 1993; Uy & Borgia, 2000; West-Eberhard, 1983). If one considers natural selection for species recognition (avoidance of gamete waste through hybridization), together with the evolution of song learning whereby a male learns from a conspecific model its species vocal features, and females likewise obtain a preference model, it is apparent that species recognition traits as well as sexually selected exaggerated vocal features (e.g., repertoire size) are both aimed at the choice of an appropriate mate (Andersson, 1994). As Searcy and Andersson (1986) put it, "Thus, preferences evolved due to reproductive isolation are a subset of sexual selection. . . ." (p. 516).

Therefore, the potential for rapid speciation caused by sexual isolation via learned vocal signals and female choice is always present and has been invoked as an explanation of the high rate of species formation in songbirds (West-Eberhard, 1983; Wyles, Kunkel, & Wilson, 1983). Gill (1995) summarized the issue as follows: "The behavioral attributes of birds, particularly their capacity for new behavior and its cultural transmission, may be extraordinary advantages. . . . Behavior, rather than the environment, can be the driving force of evolutionary change. . . ." (p. 549). From a large body of studies, there seems to be little doubt that female preferences for song characteristics exist and that they bias mating decisions (Searcy & Yasukawa, 1996). What has remained unresolved and debated is the role of social selection and cultural differences in behavior, including song, in reducing gene flow to a significant extent, be it modest population differentiation or speciation.

The hypothesis of rapid evolution in vocal learners, touched on briefly above, involves the possibility that sexual selection and vocal learning have played a causal role in promoting differentiation to the point of speciation. First noted as a hypothesis by Thielcke (1970) and Nottebohm (1972b), the idea is supported to some extent by analysis of the taxonomic diversity of songbirds and other groups of

vocal learners. The taxa in which we find vocal learning tend to be rich in numbers of species relative to taxa in which vocal learning does not occur (M. C. Baker, 1982; M. C. Baker & Marler, 1980; Nottebohm, 1972b), but there are important exceptions and thus the data are not conclusive. The hypothesis that song learning is a "key adaptation," which has led to taxonomic proliferation in songbirds, was rejected by Raikow (1986) and Baptista and Trail (1992) but supported by Vermeij (1988), Fitzpatrick (1988), and the analysis of Wyles et al. (1983). From these several discussions emerges the obvious conclusion that relevant critical data are yet too few to produce consensus. Taking a larger view of the problem, Fitzpatrick (1988) suggested that, "Suites of apparent synapomorphies such as elevated metabolic rate, relatively large brain size, advanced capacity for learning, overall behavioral plasticity, vocal learning, . . . might have pre-adapted passerine birds for rapid evolutionary radiation" (p. 73). While such a viewpoint may be more accurate in its inclusiveness, it is also much more complex than that originally proposed. Reflecting back to the origin of vocal learning, those causally unknown divergences in bird lineages, one is struck by Haldane's (1958) observation that "many of the major features of evolution were due to the fact that some groups kept possibilities open which others did not" (p. 23). Vocal learning may yet prove to have some validity as a mechanism for keeping possibilities open for new evolutionary directions (Nottebohm, 1975).

A research development that flows from the recognition of vocal dialects as cultural traits is their analysis by the mathematical methods of population genetics. Dawkins (1976) coined the term "meme," the replicating unit of cultural selection, to correspond to "gene," the replicating unit of natural selection. Mundinger (1980) applied the meme concept to song dialect evolution. Major treatises on cultural evolution (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981) have provided conceptual models that help us think about the evolutionary forces effecting stasis and change, differentiation and extinction of song memes. Application of the rich theory of population genetics to bird song memes (ergo "population memetics") is still in its infancy (Lynch, 1996), and tracking change and extinctions within and between song lineages over a significant number of generations has been carried out in very few species (Payne, 1996).

Population memetics, then, entails the study of meme flow, mutation, drift and extinctions, founder effects, bottlenecks, and meme frequency changes within and between cultural populations. In some case studies, it is possible to describe the meme pool as a set of acoustic units that are strung together in various combinations to form whole songs. This set of "syllables" or "notes" that constitutes the meme pool can be a relatively small set of "species universals" (Marler & Pickert, 1984) or analyzed over small geographic regions among local populations (M. C. Baker, Howard, & Sweet, 2000; Tracy & Baker, 1999). In such cases as these, the meme set is analogous to an alphabet of letters from which can be composed a large variety of words (songs). Some individuals in a population may share whole songs or only some of the syllables, while differing in others (M. C. Baker et al., 2000). Furthermore, it is possible to track whole song memes and their constituent syllable memes independently through time. Thus, the cultural evolutionary rates of both kinds of memes can be monitored. Such a goal emphasizes the huge importance of long-term studies. In some cases, it appears that the meme syllable pool is relatively slow to change whereas the recombination of syllables into new whole songs occurs rapidly and results in substantial turnover in song memes (M. C. Baker & Boylan, 1995; M. C. Baker et al., 2000; Payne, 1996; Payne, Thompson, Fiala, & Sweany, 1981). Syllable memes may follow rules of concatenation in the formation of songs, however. Such constraints on syntax of the song means different kinds of syllables have differing probabilities of appearing at particular loci in whole songs (Ficken & Popp, 1992). The new methods developed for quantitative comparison of sounds (Tchernichovski et al., 2000) could prove to be especially useful for defining memes or species universal song components. It seems likely that this research direction in population memetics will be pursued by persistent application of the models and analytical tools of biological evolution to bird song traditions in a variety of species. As Payne (1996) suggests, however, progress may be most noticeable from long-term studies on a variety of species that differ in life history variables such as dispersal patterns and mating systems.

Students of population memetics will need to stay current on developments in song learning research. It is not yet clear for many species what is the acous-

tic unit, or set of features that constitute a unit, that is learned during ontogeny. Is it the whole song that is encoded in the neural song control system or is it the individual syllable that is the unit of sound that is acquired? If it is the syllable, there would need to be a program that applies rules of concatenation to produce a whole song during ontogeny. Some evidence indeed suggests that syllables are fundamental units of learning (Marler & Peters, 1977) and production (Cynx, 1990; Williams & Nottebohm, 1985; Williams & Staples, 1992). Even at the early age of 2–3 weeks, well before any singing patterns develop, some birds innately recognize single syllables of their own species as readily as whole songs (Whaling, Solis, Doupe, Soha, & Marler, 1997). Although an individual bird sings a whole song, there are also indications that certain syllables may play more significant roles than others in some communicatory situations. There are particular syllables in songs of white-crowned sparrows that key female sexual responsiveness in song dialect and species discriminations (M. C. Baker, Spitler-Nabors, et al., 1987; Spitler-Nabors & Baker, 1987), and particular syllables in songs of canary (Vallet, Beme, & Kreutzer, 1998) and brown-headed cowbird (King & West, 1983) stimulate more sexual behavior in females than do other syllables.

There would seem to be a fertile ground in joining the neuroethology of bird song and field studies of population memetics. Being able to define the acoustic units stored in the brains of males and females, and finding that some of these units have more salience than others in communicative interactions, has importance for other areas of bird song research. With few exceptions (e.g., M. C. Baker, Spitler-Nabors, et al., 1987; Thompson & Baker, 1993), dialect descriptions have not been validated with playback experimentation using manipulated song stimuli to determine if the acoustic variables recognized by investigators as dialect features are actually discriminated by the birds themselves. Perhaps from neuroethological advances more sensitive assays of female preference or male aggressive response will be forthcoming. The case of the ZENK transcriptional regulator, cited earlier, brings this to mind as revealing the potential to use molecular assays of the valence of different syllables, song types, repertoire sizes, dialects, or communicatory contexts.

Bird Song as a Communication System

Progress in understanding of the functions of bird song occurred fairly slowly up until approximately 1950–1960. Prior to that, even without experimental intervention, the early phase of natural history observations allowed many inferences concerning the roles of singing behavior and other vocal behavior in the social life of birds. Altum (1868), for example, suggested that a male's song was a mating call and served to attract a female mate, was effective in territorial acquisition and defense, and carried information of species identity. E. Howard (1920) articulated in considerable detail the role of singing by males in territorial behavior and mate attraction, noting, for example, decreased singing upon pairing. He also discussed the possibility that male singing could stimulate the sexual function of the female mate, and he recognized species specificity of song patterns, despite variation, and attributed this to species recognition.

Saunders (1929) tabulated those inferred territorial and mate attraction functions and also noted that a male's song stimulated his offspring to feed and may act to teach the youngster the song of the father. There accumulated much useful information on vocal communication in general from extremely detailed and long-term ethogram descriptions of a number of species (e.g., Lack, 1939a, 1939b; Nice, 1937, 1943) in which many correlations of vocalizations, behavior and the context of signal production provided understanding of bird song functions. A considerable assist was provided this effort of intensive study of individual birds by the invention and use of colored leg bands by Burkitt (1924–1926). Armstrong (1963) summarized the state of the art in enumeration of the functions of a species song: "Difficulties throng the path of anyone who seeks to tabulate the various kinds of information conveyed by bird utterances" (p. 2). When such tabulations were carried out, the principal aim was to catalog all the sound signals of a species, song included as a category, and provide an indication of context, sex and age of the sender and receiver along with some idea of inferred function (e.g., Gompertz, 1961; Marler, 1956; Odum, 1941–42).

When Weeden and Falls (1959) performed an early and influential song playback experiment in the summer of 1955, broadcasting male songs from a loudspeaker to territorial subjects to reveal the

neighbor–stranger discrimination by male ovenbirds (*Seiurus aurocapillus*), students of bird song and its communicatory significance obtained an experimental tool that greatly stimulated research in vocal communication. Falls himself modestly credits W. W. H. Gunn with showing him the basic playback technique on American woodcock (*Scolopax minor*) in 1951 (Falls, 1992). In about the same time period, Dilger (1956) used tape-recorded song playback in combination with specimen mounts to examine species recognition by song in five species of thrushes. It had been very recently that the sonagraph development allowed the capture of marvelously detailed descriptions of variation in songs, and in conjunction with the playback technique research in birdsong communication grew very rapidly. We are still in the phase of rapid growth of knowledge derived from the combined use of sonagraph and playback in testing hypotheses about bird song function.

From a vantage point 30 years later (Kroodsma, 1986), and a newly discovered sensitivity to potential problems in experimental design, earlier playback studies such as those carried out by Weeden and Falls, and numerous others, were called into question. The reason is that from 1986 to 1990 Kroodsma applied the criticism of pseudoreplication to most playback studies that had been conducted up to then, following the lead of a paper by Hurlbert (1984) that raised the issue of pseudoreplication in ecological experiments. In Kroodsma's view, pseudoreplication arises most commonly in song playback experimentation when a general hypothesis has been stated about an effect of, for example, two or more classes of stimuli on the behavior of bird subjects. For example, consider the hypothesis that birds in a song sparrow population respond differently to song sparrow song and white-crowned sparrow song. This could be tested by using the playback technique to stimulate a sample of individuals in the song sparrow population with song sparrow song and another sample with white-crowned sparrow song, or by playing both stimuli in random order to each subject, and quantifying measures of behavioral response, such as singing or locomotor activities. Pseudoreplication is said to occur if, for example, only a single song stimulus is used to represent song sparrow songs and a single song stimulus to represent white-crowned sparrow song, but the sample size used in the statistical decision is the number of birds tested. If the original hypothesis stated that subjects in the particular song sparrow population will respond differently to the particular two individual songs used as stimuli, then there would not be pseudoreplication; however, more commonly the hypothesis is constructed for the purpose of being able to conclude something more general, in this case at least to draw a conclusion about differential behavioral effects of song sparrow songs from a particular population versus white-crowned sparrow song. Only if each subject receiving a song sparrow stimulus heard a different exemplar and each subject receiving a white-crowned sparrow stimulus heard a different exemplar would the number of bird tested be the correct sample size for statistical purposes.

The main point is that such a design would allow evaluation of variation of responses among subjects within stimulus classes in relation to variation between stimulus classes, with the number of different stimulus songs used as sample points for statistical testing. This approach allows an answer to the question of whether variation between classes significantly exceeds variation among individuals within classes. Kroodsma (1989a) discussed pseudoreplication in the context of neighbor–stranger playback experiments and admitted to his own culpability in using the same "stranger" tape on several subjects, so it may have been a quite general procedure. Pseudoreplication problems have been pointed out in a variety of song playback paradigms, including neighbor–stranger, species, dialect, and song repertoire size discriminations, but rarely has it been demonstrated that different conclusions would have been drawn from the flawed and ideal designs. Consider, for example, the hypothetical song sparrow versus white-crowned sparrow species discrimination experiment outlined above. Many workers would guess that a single song sparrow song stimulus and a single white-crowned song stimulus, providing they are representative and of good quality, would result in a conclusion that did not differ from following an ideal design, but one would need to set aside statistical correctness in accepting such a conclusion.

Others have viewed the pseudoreplication issue as one of internal and external validity of experimental procedures. Using more songs of a large number of individuals as stimuli, for example, would improve the internal validity of a playback experiment (Catchpole, 1989). Additionally, Searcy (1989)

pointed out that most of the results of playback experiments with which Kroodsma found fault would not likely be overturned by the improvements advocated. One relevant study of song sparrows tested for the effect of using one or several different songs as stimuli and found no response differences of subjects during playback, supporting the views of Searcy and Catchpole (Stoddard, Beecher, & Willis, 1988). Catchpole (2000) countered the specific criticism that results of tests of the effect of song repertoire size on female preference were invalid because of pseudoreplication. He pointed out that the findings from many studies show the same overall trend and taken together provide a powerful verification that females prefer larger repertoires. Catchpole (1989) also questioned the apparently narrow selection of studies Kroodsma chose to attack. The pseudoreplication scare probably had a chilling effect on playback studies, and it is likely that a number of papers were denied publication and grant applications rejected as a result. A considerable debate ensued in the literature (Catchpole, 1989; Kroodsma, 1989b, 1990a, 1990b; Searcy, 1989) and culminated in a "consensus" paper by a small group of playback practitioners (McGregor et al., 1992). In playback experiments, as in all other experiments in behavioral research, there is always room for improvement in both design and execution, and weaknesses can readily be found in every research publication.

Occurring about the same time as the invention of playback procedures came another development, of a more conceptual nature, in which the study of animal communication as a discipline came into theoretical fruition. This advancement, which helped ethologists formulate more precise questions and integrate their findings with communication theory, was initiated by Marler in a seminal paper in 1961. Marler systematically applied to nonhuman animals the same conceptual framework and definitions that Cherry (1957) had recently developed for human communication. In the Marler view, we understand what information is being communicated by a signal, for example a bird's song, through observing the production of the signal and the consequent response of a recipient. This view followed the logical analyses of C. S. Peirce (Peirce, 1878a, 1878b), who developed the philosophy of communication, the theory of signs, and argued that the meaning of a message is the behavior it causes. Marler emphasized the study of the physical signal units and their order of occurrence (syntactics) and their significance or function in the lives of the individuals in a communicative interaction (pragmatics). He recognized signals that occur in graded series as well as those that occur as discrete categories, and embraced the possibility of symbolic (referential) signals in nonhuman animals. The theoretical structure Marler put forth about animal communication was broadly influential and stimulated a great deal of research.

There arose shortly thereafter a somewhat alternative view of such behavioral transactions (e.g., W. J. Smith, 1963), which was concerned with the problem of a particular song signal having differing effects on a receiver depending on the context. In other words, the meaning of the message depended on circumstances. Smith also recognized only a small and discrete set of signals in most animals and no potential for symbolic communication. Although the Marler and Smith ways of looking at communication influenced workers along somewhat differing pathways initially, their views were actually complementary, and the enlarging conceptual structure of communication theory has now encompassed these and other approaches (Butlin, Guilford, & Krebs, 1993; Green & Marler, 1979; Guilford & Dawkins, 1991; Krebs & Dawkins, 1984; Owings & Morton, 1998; Snowdon, 1990). The major point is that in the middle part of the 20th century we had a productive occurrence, almost simultaneously, of three factors: the sonagraph as a descriptive tool, the playback technique as an experimental way of asking questions of the birds in their natural circumstances as well as in the laboratory, and an emerging theoretical context to help synthesize results and point to new questions.

At the turn of the new millennium, we can see that a host of good questions has been addressed with song playback experimentation, to a degree of detail and sophistication not imagined 50 years ago. From the ovenbird experiment on neighbor–stranger recognition, such discriminations have been shown in numerous other species, as have dialect recognition, individual recognition, mate recognition, parent–offspring recognition, and species and subspecies recognition (M. C. Baker, 1991; M. C. Baker & Baker, 1990; Becker, 1982; Falls, 1982; Lampe & Baker, 1994; Miller, 1979a, 1979b; Stoddard, 1996). More and more is being discovered concerning the nature of information contained in bird songs, and

the study of social behavior and its ecological variations has been revolutionized. Deducing the communicatory significance of singing behavior has involved a great deal of experimentation. Among the several possible functions of singing behavior, two have attracted the most attention: the role of song in male–male communication, and its role in male–female communication.

The role of singing in male–male interactions has been revealed by several innovative approaches. Peek (1972) surgically muted male red-winged blackbirds (*Agelaius phoeniceus*) by severing the hypoglossus innervation of the syrinx and found they were unable to retain their breeding territories. D. G. Smith (1979) studied the same species but muted territorial males by puncture of the interclavicular air sac with the result that experimental males experienced high rates of territory intrusion by other males and lost parts of their territories. McDonald (1989) also used air sac puncture to show that in a sparrow species muted males were delayed in obtaining territories and experienced problems in defending them. Apparently simple air sac puncture is not an effective muting technique in all species. Neither ducklings (Gottlieb & Vandenbergh, 1968) nor zebra finches (D. B. Miller, personal communication) were devocalized by the procedure. Surgical manipulation beyond mere puncture of the airsac, such as creating patencies in the trachea and bronchi, will mute male zebra finches, however (Pytte & Suthers, 1999).

Also revealing the territorial defense function of singing in male–male communication is the speaker-replacement procedure. In this technique, territorial males are removed and replaced with loudspeakers broadcasting songs. This clever approach, with great tits as subjects, showed that within a few hours new males seeking territories first occupied silent control territories and territories with speakers broadcasting noise but were delayed about 2 days from occupying territories with speakers playing songs (Krebs, 1977). The speaker-replacement approach was also used to address the significance of song repertoire size in territorial defense. In both great tits (Krebs, Ashcroft, & Weber, 1978) and red-winged blackbirds (Yasukawa, 1981), territories containing speakers broadcasting repertoires of multiple song types experienced slower occupation by males than did territories broadcasting single song types or no song.

A further approach to the examination of song function in male–male communication is to play songs to resident territory holders, determining how a subject alters the structure of song delivery depending upon the stimuli presented. In a number of species that sing repertoires of song types, when a subject is played a song type it has in its own repertoire it answers with the matching type (Falls, 1985; Krebs, Ashcroft, & van Orsdol, 1981). Some experiments indicate that males apparently avoid matching (Whitney, 1991), or in other ways alter the bout structure of song delivery, switch among types, or change the rate of singing (Falls, Dickinson, & Krebs, 1990; Horn & Falls, 1986). Song sparrows tend to perform song type matching early in the breeding season when territorial contests are pronounced and occupancy patterns are not yet resolved among males, but later in the season the neighboring males tend more to "repertoire match" by responding to a neighbor's song type with a song it shares with the neighbor but not the exact matching song type just received (Beecher, Campbell, Burt, Hill, & Nordby, 2000). These results on song sparrows tend to support earlier interpretations of song type matching as an escalated threat response to an opponent (Bertram, 1970; Krebs et al., 1981). Repertoire matching, on the other hand, possibly would represent a lesser degree of agonistic signaling, an acknowledgment of individual identity of established neighbors monitoring each other's locations.

The role of song in male–female communication has also attracted considerable experimentation. Pioneering studies of Lerhman (1959) showed how courtship behavior of males, including vocalizations, influences female reproductive behavior via the endocrine system. Experiments by Brockway (1965) on budgerigars (*Melopsittacus undulatus*) demonstrated that playing particular male courtship songs stimulated female reproductive physiology. Kroodsma (1976) further showed that the reproductive physiology of female canaries was more responsive to larger song repertoires than to smaller repertoires. As mentioned earlier, the sexual preferences of female songbirds, as indicated by copulation solicitation display elicited by playback of acoustic signals, have been examined in relation to several properties of male song. Preferences for dialects (M. C. Baker et al., 1986; M. C. Baker, Bjerke, et al., 1987; M. C. Baker, McGregor, et al., 1987; M. C. Baker et al., 1981; M. C. Baker, Spitler-Nabors, et

al., 1987; West et al, 1998), or for larger song repertoires (M. C. Baker, 1986; M. C. Baker et al., 1986; Catchpole et al., 1984; Catchpole, 2000; Searcy, 1984; Searcy & Marler, 1981) have been demonstrated repeatedly. This laboratory bioassay has also been used to show that females prefer the songs of their mates to neighboring males and nonneighboring males (O'Loghlen & Beecher, 1999). Testing female preferences by spatial choice methods in the laboratory has also demonstrated that females recognize their own mates by song (D. B. Miller, 1979a) and preserve a long-term memory of their father's song (D. B. Miller, 1979b). A different type of assay of female reproductive response to male singing also appears to be potentially useful for addressing a variety of questions. In this assay, fecal estrogen levels, which predict ovulation, vary with the stimulus setting. In one laboratory study, reproductive responses of female zebra finches varied with the precise context in which broadcast songs emanated from models of males (Tchernichovski, Schwabl, & Nottebohm, 1998). Field studies of male–female communication are more rare; however, Lampe and Slagsvold (1998) found that female pied flycatchers (*Ficedula hypoleuca*) prefer the song of their mate when compared with songs of neighbor males or males holding territories some distance away.

All these cited studies of male–female vocal communication deal with females responding to male songs by physiological, and, usually, nonvocal behavior such as spatial choice or sexual display postures. However, more opportunities for studies of vocal interaction exist in species in which both males and females sing either in coordinated vocal duets or independently. E. S. Morton (1996a) provides a stimulating review of the contrasting vocal communication behavior of females of tropical versus temperate zone breeding species. From limited data, it appears that the singing behavior of tropical females functions more like that of temperate zone males: primarily in territorial defense. In these tropical forms, year-round territoriality and stable song dialect neighborhoods are found in both songbirds and sub-oscine passerines. Morton mentions the baffling case of a tropical wren species in which females sing a repertoire of 4–5 song types shared as a dialect with other females but males have 30 or more song types with little or no sharing with other males. This is but one of many interesting communication systems awaiting investigation.

The communicatory significance of these tropical variations certainly deserves more attention. Experimental procedures along the lines of some of the research on temperate zone males, outlined above, could be applied to these singing females of tropical species (e.g., Levin, 1996). Whether in temperate or tropical forms, there is a persistent trend to employ vocal playback techniques on males and females to examine the complex nexus of social transactions in natural communities and to draw deductions from experiments on captive birds. The playback procedure is continually revealing new levels of detail in the sound signaling of songbirds and many questions are being probed by the use of vocal playback techniques (McGregor & Dabelsteen, 1996; Searcy, Coffman, & Raikow, 1994; Searcy, Podos, Peters, & Nowicki, 1995). In recent years, the advent of digital technology, including storage of vocal patterns combined with playback, has led to interactive procedures applied to investigations of bird song communication. Pioneered by W. J. Smith (1988), but made more immediate and truly interactive with the capability of digitized storage of sounds portable to the field (Bradbury & Vehrencamp, 1994; Dabelsteen & Pedersen, 1990, 1991), this approach allows the researcher actively to engage a subject in a conversation, the researcher transmitting a signal of choice in immediate response to that of a sending bird, matching, nonmatching, or overlapping the songs of a sender. Nowhere is this technique more clearly useful than in the area of song repertoires, their evolution and function.

Until the middle of the 20th century, little speculation occurred on the significance of song repertoires. Thorpe (1958) coined the term "song types" for the multiple songs of an individual's repertoire, whereas Armstrong (1963) advocated use of the term "song versions." In any case, interpretations of song repertoires began to accumulate. Armstrong (1963) hypothesized that they were the basis of individual recognition. Craig (1943) thought that by judicious choice of a sequence of songs a bird might display an esthetic sense. Hartshorne (1956) suggested that repertoires were deployed to avoid monotony in the listener. While these were useful ideas, the conceptualization of repertoires in the framework of evolutionary theory began in earnest in 1974 with Howard's explicit connection of repertories to the theory of sexual selection, with northern mockingbird song repertoires as the evolved exaggerated trait

under consideration. Current theories advanced to explain repertoires of more than one song type per male run along several lines: song versions may encode different kinds of information (Lein, 1978), males with larger repertoires are better able to stimulate females (Hasselquist, Bensch, & von Schantz, 1996), repertoires are advantageous in male–male contests (Bertram, 1970), and repertoires allow switching among song types to rest muscles and nerves and allow more sustained singing (Lambrechts & Dhondt, 1987). A thorough review of possible explanations for repertoires is provided by MacDougal-Shackleton (1997).

It is worth pointing out a potentially fruitful interaction between the research on birdsong neuroethology and that on song repertoires. Previous work pointed out the relationship between song repertoire size and volume of certain song control nuclei in the canary brain (Nottebohm et al., 1981). More recently, Airey, Castillo, Pollak, Casella, and DeVoogd (1999) found that the size of nuclei HVC and RA are heritable among individual male zebra finches, providing a target for sexual selection to effect repertoire size.

Up to the present time, interactive playback procedures have focused mainly on territorial song in a few species. It seems likely that interactive playback will be applied to a broader set of questions in the future and will involve a wider set of the vocal repertoire in addition to male singing. In short, we should see a more complete analysis of social behavior where vocalizations have a major role, and conducted on a more inclusive set of species whose life histories cover more variation. We are in a pioneering phase in this regard. Mass storage of vocalizations together with more complex interactive playback procedures should allow a nicely detailed analysis of bird social organization (Dabelsteen & McGregor, 1996).

It is possible, for example, to attach small wireless microphones to individuals and monitor all their vocalizations remotely (Gyger, Marler, & Pickert, 1987; McKinley, Dowell, & Schleidt, 1976). Given improvements in technology leading to increased miniaturization, a bird might be outfitted with a small microphone to pick up its vocal signals and those of conspecifics, and small speakers could be attached near the ears to transmit vocalizations selected by the researcher. Spatial positioning devices (fine scale global positioning systems) attached to all individuals in a local bird society would allow one to observe and map via computer the location of any individual, who it interacts with, and monitor vocal interaction as well as manipulate them via playback. In addition to providing information on the communicatory transactions in bird society, such detail would also answer many of the questions about the auditory learning environment during ontogeny and provide critical information on such matters as dispersal between dialects. Realistic mechanical birds should also be possible to devise and operate from a remote location, thus adding a controllable visual model to behavioral transactions with other birds. If such an invasive and manipulative approach becomes a reality, it will generate large sets of data.

In this regard, we have seen tremendous growth in methods of data analysis and the ability to perform calculations on masses of information, procedures impossible to imagine at the onset of the 20th century. Multivariate analyses have become standard practice in behavioral research and are employed routinely in bird song studies, including playback experiments and population comparisons of vocal signals (McGregor, 1992). Whenever a number of behavioral response variables are measured in a playback experiment, or when several acoustic features of songs are compared between populations, multivariate procedures are often employed to examine the data. The first explicit treatment of three- variate probability distributions was by Bravais in 1846 and generalized by Edgeworth (1892) as the multivariate normal distribution (Seal, 1967). Following this beginning, familiar names like Spearman and Pearson (factor analysis), Wilks (tests of multivariate hypotheses), Hotelling (principal components analysis and canonical correlation), Fisher (discriminant function), and Mahalanobis (distance measures) gave us most of the procedures in wide use today in bird song analyses (Kotz & Johnson, 1985). Multivariate statistical treatments of substantial data sets, however, did not become practical until computers became readily available. It seems certain that methods of data analysis will continue to improve and become more sophisticated to handle the sorts of descriptions required in future studies. One anticipated direction of development in the statistical analysis of bird song research data is in the use of permutation procedures. These are advocated as superior replacements for the conventional parametric tests (ANOVA, etc.), which are based upon least

squares regression (Mielke, 1985, 1991: Mielke & Berry, 2000). Indeed, the fundamental flaws in parametric statistical procedures pointed out by advocates of permutation methods, as well as by those in favor of Bayesian approaches (e.g., Gerhardt, 1992), may caution the very critics of playback designs who argue in favor of the analysis of variance paradigm for testing playback data.

It has been pointed out that an area of potential future growth in the examination of vocal behavior, in all its guises of function, performance, development, sex role, and neural mechanism of learning, is in the study of tropical species of birds. Unlike most temperate zone species, females in tropical species often sing, and duetting between the male and female of a pair is common, to cite just two of the interesting contrasts. Pursuit of this general theme of comparative biology may be of fundamental significance in advancing our knowledge of bird vocal behavior (Kroodsma, Vielliard, & Stiles, 1996; E. S. Morton, 1996a). It does seem clear that there is important and exciting potential in tropical studies of bird song and related social behavior because of important differences with the temperate zone species that have been the main source of our knowledge base. For comparative vocal learning, for example, one only needs to note the tiny handful of studies examining vocal communication in parrots, a group numbering some 332 species and representing a vocal learning group that evolved independently from the oscine passerines that have been targets of most work to date. A bias toward temperate species is understandable given the location of the very large number of researchers in North America and European centers, mostly university faculty members who have the opportunity to conduct studies as a result of their employment location. Although the tie to a university annual cycle is constraining (to say the least), it has allowed the accumulation of knowledge at modest expense, even in the absence of extramural funding. The extremely tight federal budget for research in animal behavior in general, at least in the United States, together with the academic-year constraint, make it less than hopeful that much can be done to exploit the tropical systems by very many researchers. Thus, the advocacy of the "extraordinary opportunities" afforded by studies in the tropical systems (Kroodsma et al., 1996) may only be a call to a lucky few.

Evolution of Song and of Vocal Learning

It is not always apparent, from the writings of ornithologists near the dawning of the 20th century, who was responsible for originating ideas and theories on the evolution of bird song. In spite of poor attribution in general, it nevertheless seems clear that almost all authors had at least read Darwin, and discussions in the literature about song evolution were either against the role of sexual selection he had proposed or in favor of it, perhaps with suggested refinements or minor complaints. The earlier disagreement between Darwin and Wallace, about the efficacy of sexual selection by female choice, found advocates chipping in on one side or the other as late as 1918. Witchell's (1896) book on the evolution of song seems to have been widely influential, and several authors accepted the ideas set forth therein that song most likely originated from call or alarm or threat notes, these having an earlier origin. For example, Witchell suggested, "We may consider the voice to have been evolved from a toneless puffing, indicative of anger, or from snorts or grunts accidentally caused" (p. 20). Later he followed a detailed description of a number of species with a summary of his view:

> but I conceive that the evidence which I have brought forward is of value as indicating the history of song of many species of birds. It shows that the songs were, at first, mere repetitions of call-notes, or possibly of defiance-cries, which have since been more rapidly uttered and varied, with the result that novel strains have been slowly developed. (p. 58)

In something of an "ontogeny recapitulates phylogeny" argument, E. Howard (1920) noted how the seasonal steps of song emergence in an individual songbird passed from single notes to more complex ones to phrases and to complete song, and he suggested that we have "every reason to suppose that it is along these lines that the evolution of the voice has proceeded" (p. 141). To rephrase that emerging view in more recent terminology, an excited repetition of call notes, for example threat notes uttered in the context of aggressive interactions between males (intrasexual selection), could lead to coevolution of territoriality along with song elaboration and ritualization (E. Howard, 1920; Saunders, 1919; Witchell, 1896).

In its effect on the evolution of song, the role of sexual selection via female choice of mate was a

more contentious idea. Concrete observations, which would allow an inference that females make comparisons and choices among potential mates differing in song properties, were nonexistent at the time the theory was first being articulated. For the hypothesized evolutionary scenario of single call notes becoming repeated call notes, which eventually became songs, some were quick to point out that for such songs to finally emerge as beautiful as they manifestly are, females as agents of sexual selection would need to possess a refined esthetic sense as well (F. H. Allen, 1919).

Not a great deal of continued speculation on the evolutionary origins of song occurred since these early efforts. Recent syntheses (e.g., Searcy & Andersson, 1986; Searcy & Yasukawa, 1996) have instead gathered together the accumulating data that demonstrate the ways mating success is influenced through sexual selection of song, both the intermale and epigamic avenues. Catchpole (2000) summarized the recent history of experimental studies of the effects of repertoires on female choice and concluded that there is clear support for the view that females of a number of species are more attracted to males with large song repertoires than to ones with smaller repertoires. Convincing strong inference studies certainly support this conclusion (e.g., Lampe & Saetre, 1995). As a theoretical construct, sexual selection has become one of the dominant themes in behavioral ecology, generating a massive amount of empirical evidence, a considerable portion of which deals with birds (Andersson, 1994).

Having established the evolutionary origin of song by an argument from natural selection, there is no reason to suppose that the different sorts of songs of various species are a random consequence. Indeed, there is every reason to expect ongoing natural selection to shape the form and properties of bird songs. Among several possibilities, one had occurred to Hudson (1892), who developed a rough idea of the correlation between vocalizations and habitats from his observations of birds of the woods and open pampas. This theme was taken up in a more serious way by E. S. Morton (1970, 1975), who proposed that different kinds of habitats had different acoustic properties. These differing transmission properties could act as a source of selection to effect song structures for maximal propagation. Morton carried out sound propagation experiments in different habitats and also described evidence that in a particular type of habitat the community of birds had song features that propagated best there.

Considerable detail and elaboration on this theme followed the initial work (e.g., Marten & Marler, 1977; Marten, Quine, & Marler, 1977) with a thorough review and updating provided by Wiley and Richards (1982). In their research, Wiley and Richards concluded that the principal effect of differing environments on sounds was in their degradation caused by reverberations and fluctuations in amplitude. Reverberation problems are of greater severity in forest habitats whereas amplitude fluctuations are greater in open habitats. Moreover, there is a concordant difference in the vocalizations of birds occupying these contrasting environments, suggesting that acoustic regimes have acted as agents of natural selection on bird song features. Wiley (1991) pursued this direction of enquiry by quantifying song features of 120 songbird species of eastern North America in relation to six types of habitats. A relationship between the temporal features of songs and habitat type was particularly strong, lending support to other studies of narrower focus.

A more general approach to explaining taxonomic differences in song was applied in the pioneering efforts of Read and Weary (1992). These authors evaluated several features that describe temporal organization and complexity of songs for 165 species of passerines and sought correlations with physiological, ecological, and behavioral variables. This comparative approach led to several interesting relationships. For example, Read and Weary estimated song complexity in two ways: the number of song types in the repertoire and the number of different syllables within song types. Song repertoire size was larger in species showing greater amounts of paternal care, such as provisioning the young, whereas syllable repertoire size was larger in species exhibiting polygyny. Both song and syllable repertoire size were also positively correlated with the migratory habit. These and other correlations between song structure and possible causal variables create a number of hypotheses that could lead to more focused studies in the future. The summary point of the research on the effects of habitat structure, physiological, ecological, and behavioral variables on the evolution of bird song attributes is that useful progress has been made on a very difficult domain of research, but we have truly just scratched the surface of try-

ing to account for the huge variety of song forms we find among bird species.

As in the evolutionary origins of song itself, speculations on the evolution of song learning have tempted relatively few authors. Nottebohm (1972b), in the first comprehensive discussion of the origins of vocal learning, noted that vocal learning in birds is a trait appearing independently in at least three groups: the oscine passerines (songbirds), parrots, and hummingbirds. He then surveyed the data available at that time and concluded that the key selective influences probably responsible for evolving song learning were (a) the advantages of positive assortative mating within a population, thus allowing gene pool divergence and local adaptation, and (b) sexual selection by female choice for increasing complexity and flexibility of male song structures, traits that might not be possible to achieve with genetically programmed song.

Following Nottebohm, one can identify a number of potential benefits of song learning as judged from contemporary utility of the resulting flexible signaling system: recognition of others, such as neighbors, strangers, mates, kin, or dialect population; social adaptation, such as in deceptive song matching to acquire a female mate (Payne, 1982); or song matching in territorial contests where matching is a more effective threat (Krebs et al., 1981). However, identifying selective factors that explain the evolutionary origin of song learning is a matter of speculation and whether any of the aforementioned benefits were involved is unknown.

Owings and Morton (1998) have provided a coherent origin model derived from Morton's early sound propagation studies mentioned above, his "ranging" theory (E. S. Morton, 1986, 1996b), studies of song degradation in natural habitats (Richards, 1981), and an hypothesis by Hansen (1979), which argued that song learning evolved as a mechanism to adjust song features for maximal undegraded propagation in the acoustic environment of the local habitat. The ranging theory hypothesizes that an assessor (individual receiving a sound signal) compares its memory of the undegraded form of the signal to the one received and the amount of degradation resulting from the comparison provides distance information to the assessor. With these ideas as background, Owings and Morton apply their assessment/management view of vocal communication by showing how song learning therefore provides for more successful assessment or management of others in social interactions. A song that is adapted to acoustic properties of the habitat retains its structure over greater distances without degradation. When a signal is better fitted to the acoustic environment, then from the manager's (sender's) perspective the assessor (receiver) has a problem in ranging the source because the received signal is relatively undegraded. As Owings and Morton put it, "Rather than being designed to inform listening males of their distance from the singer, songs hide this as much as possible" (p. 145). A mutation increasing "management" success by improving the fit of the bearer's song to the acoustic properties of the environment, thus offsetting ranging by "assessors," and the countering evolutionary improvement in assessment is the "arms race" scenario that suggests the evolutionary origin of song learning by this view.

It is not yet altogether clear that assessors must have stored in memory undegraded versions of songs being ranged. The most obvious evidence that a bird has a stored version of a song is when it sings it as part of its repertoire. It has been shown that birds do not have to produce a song version themselves to be able to range it. Thus, male Kentucky warblers (*Oporornis formosus*) each have a unique song, therefore no sharing with any other male in the population, yet readily discriminate between degraded and undegraded versions of songs of nonneighboring males (Wiley & Godard, 1996). Of course, just because a bird does not sing a song does not mean that it does not have a number of songs in memory. Studies have shown that males may retain in memory songs they themselves do not sing (Godard, 1991; McGregor & Avery, 1986), which makes it difficult to determine if ranging can be accomplished by assessing some general properties of song degradation without a memory of the undegraded version for comparison. Furthermore, for some species, individuals in a population may share one or more syllable memes even if not whole song memes and thus may have the potential for ranging by virtue of this type of sharing. Other interpretive difficulties and viewpoints are discussed by Wiley and Godard (1996) and by Owings and Morton (1998).

In terms of neurophysiological mechanisms, the evolution of song learning can be imagined by considering the steps that would need to occur from a presumed ancestral state, such as can be modeled by developmentally fixed song ontogenies as occur

in sub-oscine passerines, to those species that learn their songs. Only a fragment of relevant work thus far has occurred in sub-oscine passerines, and those few experiments have demonstrated that these species develop normal song in the absence of learning models, are refractory to laboratory tutoring (Kroodsma, 1984, 1989c), generally lack song dialects (Lanyon, 1978), and if surgically deafened prior to the onset of song they develop normal song anyway (Kroodsma & Konishi, 1991). As may have been predicted from these findings, and work on vocal learning species, although the sub-oscine brain obviously contains a mechanism to generate a song pattern, apparently it lacks the obvious discrete vocal control centers characteristic of song learning oscines (Kroodsma & Konishi, 1991).

Therefore, a hypothetical ancestral songbird would have a song pattern generator in the brain, which was refractory to auditory feedback. Several things would need to happen in the evolutionary transformation of such a sub-oscine condition to that of an oscine-like vocal learning system. Nottebohm (1972b, 1975) has outlined these changes. Perhaps the most important and obvious one would be the control of song by auditory feedback, that is, a direct linkage between the nervous tissues responsible for auditory perception and those causing vocal production. These two components would represent primordial auditory Field L and the connection to a primitive production area, like song control nucleus HVC in the oscine brain. To accompany this important modification, the ancestral song pattern generator would have to become susceptible to the influence of auditory input (i.e., become plastic).

This important step, the achievement of being able to modify a vocalization in accordance to feedback, may have had a preadaptive presence in the auditory system as a mechanism that prevents damage to the cochlea (Nottebohm, 1991). In birds, the stapedius muscle connects to the tympanum and columella, the single bone connecting the tympanum to the cochlea. As the stapedius muscle contracts, the energy of the sound signals reaching the cochlear receptor cells of the inner ear is dampened. The main function of this apparatus appears to be the attenuation of sound produced by the bird itself, because the stapedius does not contract to loud external sounds. This latter finding differs from the situation in the human ear where the stapedius contracts to loud external sounds as well as an instant prior to self-vocalization (Borg & Counter, 1989; Borg, Counter, & Rösler, 1984). Bird songs can be very loud at the source, upwards of 100 dB or more, so this stapedius adaptation serves a protective function in the contracted condition in birds, but when the stapedius is relaxed, the inner ear becomes more sensitive to faint sounds, a useful flexibility.

To bring the stapedius hypothesis into the song learning evolutionary scenario, the results of Grassi, Ottaviani, and Bambagioni (1990) are relevant. These investigators excised the stapedius muscle of young male chickens to investigate its potential role during vocal development. They found that in stapedectomized birds the acoustic energy in the "crow" vocalization shifted to higher frequency, suggesting that the stapedius muscle is involved in vocal development, possibly in modulating auditory feedback. These findings suggested to Nottebohm (1991) that the stapedius protective reflex and involvement in development could represent the early evolutionary phase of auditory-dependent vocal ontogeny in songbirds. In effect, the chicken experiment suggests that the rooster is modifying its vocal output depending on what it is hearing. In a primitive way, this is what a songbird is doing as it forms motor matching to a model song memory acquired previously.

Conclusions

Progress in understanding the biology of bird song over the past 100 years has resulted primarily from the relentless application of Darwinian thinking, characterized by a nice blend of both "how" and "why" questions. It seems doubtful that this general philosophical strategy of research will be replaced in the next 100 years.

It will probably be clear from the review itself that certain individuals stand out as having had exceptional impact on the course of bird song studies. I am convinced that one day later in the 21st century if historians of ornithology need to designate two individuals that left the largest footprints on this field of study in the years 1900–2000 they will name Peter Marler and Fernando Nottebohm. For more than 40 years, Marler has been the leading figure and of enormous influence in the field of bird song learning at the organismal level of organization. Nottebohm, a former student of Marler, in just short of the same 40-year period, has taken the song learning and production phenomenon into the neurobio-

logical realm of causation and played a leading role in a dramatic and ongoing series of discoveries, giving birth to the new research paradigm of bird song neuroethology. If any Americans receive Nobel prizes in animal behavior in the future, these two must be among our most likely candidates.

In closing this review of selected areas of bird song research developments over the past century, I pass on a quote from one of the principal synthesizers of information on bird song. Edward A. Armstrong's life (1900–1978) covered a large portion of the exciting times in the 20th century growth of bird song research. As an Anglican clergyman and lover of birds, he produced a most useful compilation of information on song biology up to 1960 (Armstrong, 1963). Subsequent to that book, Armstrong contributed a chapter in a festschrift for W. H. Thorpe published in 1969 (Hinde, 1969). Toward the end of his chapter, Armstrong offered the following sentiments, which I find compelling and moving:

> It is not only for the intrinsic interest, inspiration and beauty of bird song that we should esteem it, but also because a sense of continuity with the past is important for our spiritual health as life becomes more complex. Despite the changes in man's attitude, his response to the utterances of birds has retained so much from the past that in appreciating bird song and what has been written about it we become alive to insights and sentiments widely shared. It is an achievement of great music, visual art and literature that they alleviate our loneliness and enable us to realize that, although the centuries have brought many changes, others have stood where we stand and been inspired by universal, enduring things — not least by the songs of birds (p. 362).

Author Note

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As I surveyed the older literature and tried to portray developments in the various areas of research, it struck me how deeply went my own roots into this history and what a debt of gratitude I owe my mentors for assistance along the path to the present. My graduate (1971) Ph.D. advisor, Philip Ashmole, advocated a scholarly appreciation of the ornithological literature, having completed his doctoral research as a student of the great British ornithologist David Lack, whose volumes on bird ecology and behavior I voraciously consumed as a graduate student and profitably refer to still. Years later it was a near mystical experience for me to walk the corridors of Lack's Edward Grey Institute, the trails of Wytham Wood, home of his monumental studies of the great tit, *Parus major*, and to lecture on bird song and behavior in the very hall at Oxford University where Lack had held forth. Similarly, a few years later, I was fortunate to give a talk at Cambridge University and respond to hard questions put by Bill Thorpe, who years before had been advisor to Peter Marler. In turn, it was Marler's guidance and support that were essential and formative in my immediate postgraduate years. I am certain many will agree that more than any other single individual, Marler's contributions capture the zeitgeist of bird song research in the second half of the 20th century. Thus, my experiences during 35 years of ornithological studies have, like Armstrong noted, instilled in me a sense of continuity with the magnificent research enterprise of bird song study, but they also engendered a feeling of considerable obligation to provide some contribution to the continuing saga of bird song biology. I hope this review will be of use.

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