

HISTORICAL PERSPECTIVES

ADVANCES IN STUDIES OF AVIAN SOUND COMMUNICATION

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Abstract. Ground-breaking advances in the study of animal sound communication per se, and avian vocal behavior in particular, awaited instrumentation that enabled capture of sound signals for objective description and analyses. Once these technological advances became generally available, a groundswell of activity in vocal studies, bioacoustics, provided the "raw material" for hypothesis testing pertaining to various biological and evolutionary principles. All aspects of this field cannot be covered in one review. Thus, themes developed herein deal primarily with questions of vocal acquisition such as factors affecting song learning, the sensitive phase and stimulus filtering hypotheses pertaining to the learning process, the effect of vocal behavior on population dynamics, the effect of hormones on the song learning process and production, photoperiod and song as they are related to gonadal recrudescence, advances in the neurophysiological control of song acquisition and production, and the incidence of female song and function across taxa.

Key words: Song; song learning; vocal acquisitions; vocalizations.

All disciplines in biology begin with observation and description, and when the field matures, develop into an experimental-hypothesis testing stage (Stresemann 1947). Although the vocalizations of most birds are yet undescribed, sufficient species have been studied that experimentation and hypothesis testing have advanced. Concomitant with this maturation have been continuing technological innovations which have enabled scientists to not only capture, reproduce and thus describe these otherwise ephemeral behaviors, but also to objectively analyze the sounds that birds produce, to study the development of these sounds, to hypothesize and then design experiments to test the functions of those sounds, and to interpret these data in terms of evolutionary principles. Thus studies of sound communication behavior, or bioacoustics, can and is contributing to our growing understanding of many underlying principles of biology.

In this essay, a brief survey of recent advances in instrumentation which have facilitated the analyses of bird sounds is presented followed by a review of some of the contributions that avian bioacoustics has made to various fields of biology.

INSTRUMENTATION

Early descriptions of bird sounds were onomatopoeic (Saunders 1935), or used musical notations (one of the last being Miller 1952). Though methods for capturing sounds existed in the 1800s and early 1900s (phono discs, wire recorders, motion picture film), none were particularly well suited for field conditions. The innovation of the magnetic tape recorder by the Germans during World War II was the true breakthrough for the

field biologist, who had to wait until the instrument was declassified after the war for its introduction to the mass market. Prior to that time, important developments in microphone and parabolic reflector use had been introduced for field biologists by Kellogg, Allen and Tanner (Kellogg 1962). Associated with tape-recorders were parallel improvements in magnetic tapes and microphones. Today digital technology is proving as revolutionary in bioacoustics studies as the advent of the magnetic tape recorder both in digital sound recording and computer technology for sound synthesis, manipulation and analysis.

The special requirements of the field biologist for recording sound under less than ideal conditions are seldom the concern of commercial instrument developers. Thus, advances in conceptual issues in bioacoustics have played leap frog with instrumentation developments for the medical, military and entertainment industries. Insights into animal behavior have been coupled with advances in technologies not developed for their specific application. A prime example of this mismatch was the introduction and development of sound spectrographic (also termed sonographic) technology that has been the work-horse in bioacoustic analysis for over 40 years.

Spectrographic technology was originally designed by the Bell Laboratory prior to World War II to produce pictures of human speech that could be used by deaf persons to "read" spoken language (Potter 1945). Only one test subject ever developed a rudimentary ability to decipher spoken words from spectrograms (also termed sonograms). However, the U.S. Navy recognized the utility of the device to detect subtle dif-

ferences between individual submarines, and thus spectrographic technology was classified for the duration of the war. Several technical reports published after the war suggested the power of the instrument—especially to describe such sounds as produced by birds that were often discrete and poor in overtone structure (Potter 1945).

Spectrographic analysis provided scientists with an image of the sounds analyzed (spectrograms) and permitted quantification of sound parameters from that display. These data could then be subjected to statistical treatment (Collias 1991). The first studies of bird song using the sound spectrograph were published independently by Borror and Reese (1953), Kellogg and Stein (1953), and Collias and Joos (1953), and avian bioacoustics passed from anecdotal to objective description.

Use of the sound spectrograph machine was limited to two or four seconds of analyses at a time. This sufficed when used to analyze sounds of short duration. Analyses of long continuous songs such as those produced by Mockingbirds (*Mimus polyglottos*) and *Catharus* thrushes (Howard 1974, Raitt and Hardy 1970) were formidable tasks indeed, until the development of the continuous spectral analyzer (Hopkins et al. 1974). This technology has evolved to digital systems which allow for real-time spectrographic display and digital analysis such as the dedicated DSP Sona-graph machine, Kay Elemetrics, or computer programs for personal computers such as SIGNAL from Engineering Design and CANARY from the Cornell Laboratory of Ornithology. These advances in computer technology have enabled investigators to analyze sound and subject masses of data to statistical treatment in a timely manner. Cross-correlation programs permit investigators to compare syllables uttered by different individuals, populations and widely separated geographic areas in an objective manner (Gaunt et al. 1994). Computers also enable bioacousticians to manipulate captured natural sounds or synthesize sounds for use in tutoring (Marler and Peters 1977, Konishi 1985) and playback.

DESCRIPTIVE STUDIES

THE INDIVIDUAL SONG

Species specificity in bird sounds may be encoded in duration or rhythm (seconds), in frequency (kHz), or in tonal quality (Becker 1982). Tonal quality may be coded in the harmonic structure of the sound (Davis 1964, Marler 1969) or by singing two unrelated notes or series of notes simultaneously (Borror and Reese 1953, Greenewalt 1968).

Unlike mammals with one sound generating source, the larynx, birds have two sources for sound production from each of the two bronchi that form the vocal organ, the syrinx. Each bronchus of the syrinx may produce the same sounds of equal frequency and intensity thus doubling the loudness, or may contribute to different parts of the song. By severing the left hypoglossal nerve of the Chaffinch (*Fringilla coelebs*), Nottebohm (1971) demonstrated that the left syrinx contributes most of the notes in a song.

Close examination of spectrograms by Borror and Reese (1953, 1956) revealed that Hooded Warbler

(*Wilsonia citrina*) and Wood Thrush (*Hylocichla ustulata*) songs often consisted of notes opposite in direction of frequency modulation and thus must be produced by the two separate sound sources. Greenewalt (1968) described this two-voice phenomenon in other oscines and first developed the thesis that each side of the syrinx contributed to each "voice." European Starlings (*Sturnus vulgaris*) may actually imitate the vocalizations of two allospecifics simultaneously (Jenkins in Baptista 1990a), a most unusual example of the two-voice phenomenon. There has been much advancement of our knowledge of syringeal function and song production since Greenewalt's pioneering text, but review of this area of avian communication is beyond the scope of the present work. We refer those interested to the reviews of Gaunt and Gaunt (1985) and Gaunt (1987).

REPertoire SIZE

Hartshorne (1956; see also Kroodsma and Verner 1978) described the manner of song delivery in birds as "continuous" versus "discontinuous." Continuous singers are those birds, such as mockingbirds or skylarks (*Alauda arvensis*), that sing long songs with short intervals of silence between bursts of sound, whereas discontinuous singers are those with short songs (two to four seconds long) divided by longer intervals of silence. The intervals of silence labeled as "cadence" by Reynard (1963) may be species specific. Within a species, cadence may be used to advertise individual fitness (Payne and Payne 1977).

Thus repertoire size in bird song may be described in terms of syllable types or number of themes or both. Species may differ considerably in repertoire size even within a family. For example, among emberizid finches we find a continuum between the Chipping Sparrow (*Spizella passerina*) at one extreme who sings only one song type to the Five-striped Sparrow (*Aimophila quinquefasciata*) who may sing over 200 song types (Marler and Isaac 1960, Groschupf and Mills 1982). In between are such species as the Black-chinned Sparrow (*Spizella atrogularis*) who sings two song types (Baptista, unpublished), or Dark-eyed Juncos (*Junco hyemalis*) who sing three to seven or Song Sparrows (*Melospiza melodia*) who sing 10 or 20 (Williams and MacRoberts 1977, Mulligan 1966). Irwin (1988) has presented a thesis that in some groups, including emberizids, song complexity has been reduced during the course of evolution.

SONG SHARING

Individuals within a population may share syllables, themes, or sequences in which themes are sung. Neighboring *Colibri* hummingbirds share note types (Gaunt et al. 1994). Neighboring House Finches (*Capodacus mexicanus*) in southern California share few themes, but nearest neighbors have more syllables in common than non-neighbors and the number of syllables shared between localities sampled decreases linearly with distance (Bitterbaum and Baptista 1979). In contrast, Marsh Wrens (*Cistothorus palustris*) may have large song repertoires of over 100 song types and neighbors not only share song types but sing them in the same sequence (Verner 1975). There may be geographical variation in the amount of sharing between popula-

tions of a species (Wiens 1982, review in Bitterbaum and Baptista 1979). Even in the "classical" dialectal species, the White-crowned Sparrow, populations in Alaska do not share themes (DeWolfe et al. 1974), whereas all other populations often sing songs that are almost carbon copies of each other (Marler and Tamura 1962, Baptista 1985, DeWolfe et al. 1989).

There may be a hierarchy in the nature of sharing within a species as exemplified by the White-crowned Sparrow. Nearest neighbors may share introductory phrases, thus forming song neighborhoods (DeWolfe et al. 1989). Frequency and temporal measurements subjected to multivariate statistical treatment also revealed sharing by neighbors (Cunningham et al. 1987). Local populations may share syllables following introductory phrases (Marler and Tamura 1962, Baptista and King 1980), and populations intermediate between two dialectal areas may comprise individuals singing songs with syllables borrowed from the two neighboring populations (Baker and Thompson 1985, Jenkins 1985). Song sharing ("dialects") in migratory populations (*Zonotrichia l. pugetensis*, *Z. l. gambelii*, *Z. l. oriantha*) tend to cover larger geographical areas (tens or hundreds of kilometers) as compared to sedentary populations (a few kilometers) (Baptista 1975, 1977; Lein 1979).

At the next level, groups of populations may differ also in syntax or sequence of elements used. Thus, White-crowned Sparrow populations north of the Columbia River, Washington (*pugetensis*), sing songs containing a completely different syntactical arrangement from those south of the river with a mixed zone in between (Baptista 1977; DeWolfe and Baptista, unpubl. manuscript). Canadian and Alaskan populations of White-crowns sing songs with an entirely different syntactical arrangement from those in the Sierra Nevada or the west coast of North America (Lein 1979, Baptista and King 1980, Chilton et al. 1990).

Quite a different view of syntax in avian vocalizations is taken by Hailman and coauthors (1985, 1986, 1987). Syntactical rules are identified for the arrangement of notes in the complex call of chickadees, and the acquisition of these basic rules is compared to those hypothesized to have developed during the early stages of language evolution.

STABILITY OF SONG TYPES

Long-term studies indicate that song types of some species are stable over many years (Thielcke 1987), but in others they are not. Song changes have been documented in populations of English Chaffinches and Indigo birds (*Vidua chalybeata*) (Ince et al. 1980, Payne 1985). Jenkins and Baker (1984) have also documented changes in New Zealand Chaffinch song when compared to those of their British ancestors.

Baptista (1975) sampled a contact zone between two White-crowned Sparrow dialects in San Francisco, California, in 1970. When the area was resampled in 1990 by Baptista et al. (in prep.), they found a subset of birds singing either of two dialects and another subset of birds singing songs combining syllables from both dialectal areas. Populations of "hybrid" songs between two dialectal areas (Baker and Thompson 1985, Jenkins 1985) may be a function of time. Baptista (1990b) found a population of Chaffinches using "rain

calls" intermediate in structure between two neighboring dialect forms and a second contact zone with two rain call types occurring sympatrically with no intermediates. It was suggested that the subpopulation containing mostly "hybrid" calls was the older contact zone, a thesis supported by the data on White-crowned Sparrows (above) in which hybrid songs appeared after two decades.

Changes in song structure may be due to "withdrawal of learning," i.e., dispersing hatching-year birds settle at the peripheries of populations or on islands before requisite song-tutoring was complete, thus developing divergent song types (Thielcke 1973). Thus, insular populations of Anna's Hummingbirds (*Calypte anna*), Dark-eyed Juncos, and Brown Creepers (*Certhia americana*) sing songs similar to naive individuals raised in Kasper Hauser conditions (Mirsky 1976, Baptista and Johnson 1982, Baptista and Schuchmann 1990). Recently Gaunt and Baptista (in prep.) found that insular Trinidadian populations of Pygmy Hermit Hummingbirds (*Phaethornis longuemareus*) have less complex songs than those of mainland populations in Costa Rica.

One would expect greater song variation in species such as Creepers (*Certhia* spp.) in which social interaction is a prerequisite to song development (Thielcke 1970). In peripheral populations where habitat is often patchy, juveniles have reduced opportunities to interact with adults during song ontogeny and thus develop songs in their own direction (Thielcke 1965a).

DEVELOPMENTAL STUDIES

THE SENSITIVE PHASE

In 1768, 37 years after the death of the Baron von Perna, his experiments on song learning in Chaffinches were published (Thielcke 1988). The Baron noted that Chaffinches had two sensitive phases (i.e., "critical period" of some authors) during which they acquire song. The first phase occurs just before the juvenile molt and ends in August. The second learning phase occurs the following February and ends in April. These results were replicated by Thorpe (1958) using tape recorded songs as tutors.

Today we know that song learning in many oscines is "age limited" (Marler 1987) and that in others, such as Canaries (*Serinus canarius*) or some parrots, learning may occur throughout life (Nottebohm and Nottebohm 1978, Pepperberg 1993). Recent studies indicate that the sensitive phase is not a sharply defined time window but occurs with a gradual onset and offset (Baptista et al. 1993a, Clayton 1989).

A number of different factors are known to effect the closure of the sensitive phase. It terminates early in Chaffinches and Zebra Finches (*Taeniopygia guttata*) when learning occurs early. However, the learning phase is extended if birds are deprived of learning stimuli (Eales 1985, Thielcke 1988), and a "self termination" model for sensitive phases has been developed by ten Cate (1989:255).

In some species, e.g., the Marsh Wren, learning phases may be affected by photoperiod. Naive Marsh Wrens tutored under a regime simulating an August hatching (short day) learned new songs the following spring. No birds raised in long-day conditions (simulating a June

TABLE 1. Learned and unlearned song parameters in selected avian taxa.

Species	Syllable structure	Frequency	Rhythm	Duration	Syntax	Element number	Source
Chicken	—	—	—	—	—	—	Konishi 1963
Coturnix	—	—	—	—	—	—	Schleidt and Shalter 1973
Bobwhite	—	—	—	—	—	—	Baker and Bailey 1987
Ring Dove	—	—	—	—	—	—	Nottebohm and Nottebohm 1971
Tyrannids	—	—	—	—	—	—	Kroodsmma 1984, 1985
Creepers	—	—	+	—	+	+	Thielcke 1956b, 1970, 1971
Zebra Finch	+	—	+	—	+	—	Clayton 1989
Bengalese	+	+	+	—	+	—?	Clayton 1989
Greenfinch	+	+	—	+?	+	+?	Güttinger 1974, 1979
Northern Cardinal	±*	+	+	—	+	+	Lemon 1975
White-Crowned	+	+	+	—	+	+	Marler 1970, Petrinovich 1985
Anna Hummingbird	+	+	+	—?	+	+	Baptista and Schuchmann 1990

* Some syllables are not learned.

hatching) learned song the following year (Kroodsmma and Pickert 1980).

In White-crowned Sparrows, naive fledglings exposed to live tutors could learn beyond 50 days, whereas controls exposed to tape tutors would not (Baptista and Petrinovich 1984, 1986). Thus live tutoring extends the learning phase in this species.

NATURE VERSUS NURTURE

What is learned. The question of the interplay of environment versus genome in the shaping of behaviors has been a rich subject of debate between psychologists and ethologists (Konishi 1985, Johnston 1988, Barlow 1991). Early studies indicated a dichotomy between oscines that learned song and non-passerines whose songs were innate (Konishi and Nottebohm 1969). Since that time, learning has been documented in psittacids, trochilids and one larid (Baptista and Schuchmann 1990, Baptista 1993, Groothuis 1993, Pepperberg 1993).

Song learning is not always an all-or-none phenomenon, however, for when different species within and across groups are surveyed, one finds that nature versus nurture represents a continuum as proposed by Smith (1983). At one extreme we find columbiforms, galliforms and some tyrannids who produce normal species-specific vocalizations when raised in isolation from the egg and/or when deafened and thus deprived of audio-sensory feedback (Konishi 1963, Nottebohm and Nottebohm 1971, Baptista and Abs 1983, Baker and Bailey 1987, Kroodsmma and Konishi 1991).

At the other extreme are Anna's Hummingbird and some oscines who learn all the details of syllable structure, frequency, rhythm, duration, syntax, number of elements in the song (Table 1). In between are species for which one or more of these characteristics develop independently of learning experience (Baptista, in press).

Stimulus filtering. Von Pernau's pioneering experiments indicated that Chaffinches prefer to learn conspecific over alien song (Stresemann 1947, Thielcke 1988). Various authors have since shown that naive oscines exposed to tapes containing conspecific and allospecific sounds tend to select conspecific sounds as models to be imitated (review in Baptista, in press). Cross-fostering experiments indicated that it is easier

to reverse learning if Zebra Finches are tutored by alien Bengalese Finches (*Lonchura striata*) than if tutored by conspecifics (Clayton 1989), also indicating a preference to learn conspecific song.

Naive White-crowned Sparrows rejected taped Song Sparrow songs as models and sang abnormal (isolate) songs (Marler 1970). This reluctance to learn alien song was surmounted when White-crowned Sparrows were provided with a live Song Sparrow tutor, whereafter all experimentals learned alien song (Baptista and Petrinovich 1986). These results supported an earlier thesis that live tutors may cancel predispositions to learn conspecific song or barriers to learning allospecific vocalizations in some species (Baptista and Morton 1981).

Social factors in song learning. Although use of tape recordings as tutor stimuli enables the investigator to control number of songs played, amplitude and amount of sound degradation, all of which may affect what is learned (Petrinovich 1985, Morton et al. 1986), social interaction in the song-learning process is an additional and important factor (Nicolai 1959).

One aspect of social influence on song learning is mode of cultural transmission. Possible modes of cultural transmission include (i) vertical, or tradition from father to offspring, (ii) horizontal, or tradition between age peers, and (iii) oblique, or tradition from non-blood related adults to juveniles (Cavalli-Sforza et al. 1982). Horizontal song tradition in birds has been demonstrated only in the laboratory (review in Baptista et al. 1993a), possibly because of the difficulty in following family groups in the wild. Vertical tradition is well known in Galapagos Finches ("geospizines") (e.g., Grant 1984, Millington and Price 1985); however, the percentage of males singing their father's song under natural conditions differs from year to year (Gibbs 1990).

The interpretation of mode of transmission, vertical or horizontal, may be confounded by when and how song is sampled. Thus, Immelman (1969) and Böhner (1983) showed that Zebra Finch males sang their father's or foster father's song as adults even though they could see and hear other non-related males nearby, i.e., vertical tradition. However, Slater et al. (1988) argued oblique transmission for this species from juvenile removal experiments that demonstrated song acquisition from unrelated males after the sensitive phase as es-

established by Immelmann (1969) and Böhner (1983). This learning plasticity demonstrated in the laboratory appears, however, not to be normally realized in nature as most males of this species sang father's songs in a field study (Zann 1990, 1993).

Two modes of cultural transmission may give rise to song sharing. Sharing may result from learning from fathers but not dispersing far from the natal area (vertical tradition) or from learning songs of neighbors when settling (oblique tradition). Nice (1943) first called attention to oblique song tradition in Song Sparrows, and Kroodsmma (1974) demonstrated that Bewick's Wren (*Thryomanes bewickii*) may learn father's songs, but also learn songs from neighboring males when settling.

Even when studied under natural conditions, the initial interpretation of the mode of song transmission in a given species may be revised when the relatedness of neighboring birds is more closely examined. Cunningham et al. (1987) measured frequency and temporal parameters extracted from White-crowned Sparrow songs and subjected these to multivariate statistical treatment. In so doing they found that nearest neighbors within a dialectal area sang more similar songs than non-neighbors, and they interpreted this as vertical tradition with young birds learning from fathers and settling close to their hatching site. Contrariwise, by color-banding nestlings of the migratory montane *Z. l. oriantha* and sedentary *Z. l. nuttalli* and sampling their songs at settling sites, Baptista and Morton (1988) and Petrinovich (1988) found few males singing songs like their fathers'. Both Baptista and Morton (1988) and DeWolfe et al. (1989) found, moreover, that settling juveniles often sang more than one song type and as a result of match countersinging eventually discarded song types not used by territorial neighbors (see also Marler and Nelson 1993).

Vertical versus horizontal transmission may further be coupled in some species or populations wherein sons do not actually learn father's song, but father's song acts as a "prime." In this case, sons most often chose to match a neighbor that most closely matched the father at sites settled (White-crowned Sparrows, Lein, pers. comm.). Sons sang songs unlike their fathers' in the absence of neighbors singing the paternal theme at sites settled. Böhner (1990) has demonstrated a similar priming effect in a laboratory study of song learning in Zebra Finches.

Oblique song tradition in the Indian Hill Mynah (*Gracula religiosa*) and European Starling is along sexual lines as females learn from females and males learn from males (Bertram 1970; Hausberger, unpubl. manuscript). In Viduine Finches (*Vidua* spp., Ploceidae: Viduinae), brood parasitic species, juveniles learn courtship songs from their foster, host species belonging exclusively to the oscine family Estrildidae. However, they learn their territorial songs from conspecific adults (Nicolai 1964; Payne 1973a, 1973b). Oblique transmission is also manifested in Brown-headed Cowbirds (*Molothrus ater*) where juveniles housed with males of two subspecies selectively learned songs of males if females of their subspecies were also present in the aviary. The females gave subtle cues which influenced experimentals in their choice of a song model to copy (West and King 1985, 1988).

HORMONES AND BIRD SONG

Hormones have been used as tools in bird song studies and they have also been implicated as affecting song learning and song production in various ways. Searcy and Marler (1981) pioneered the use of implanting silastic tubes filled with estradiol to study responses of female sparrows to conspecific versus allospecific songs. Implanted females assumed a solicitation posture in response to stimulatory songs, so that strength of response could be quantified by counting number of solicitation postures to one or more test songs.

Subsequently this technique has been used to assay responses of female oscines to local, familiar versus unfamiliar dialects (Baker 1983), or response of females to song of mainland versus insular populations of uncertain taxonomic status (Clayton 1990). By implanting female Great Reed Warblers (*Acrocephalus arundinaceus*) with estradiol and playing them male songs of varying complexities, Catchpole et al. (1984) showed that females solicited more to complex songs than to simpler songs, lending support to Darwin's theory of sexual selection.

Estradiol has been implicated in being associated with song learning in domestic canaries. Güttinger et al. (1984) found two pronounced peaks in estradiol titers associated with time of change from subplastic to plastic song and from plastic to juvenile autumnal song. Marler et al. (1987) found a peak in estradiol titers from 18 to 170 days of age during the period of song acquisition and sub-song production in Swamp Sparrows (*Melospiza georgiana*). A major estradiol peak between 40 and 50 days of age occurred concomitantly with a trough in testosterone production and a hiatus in song acquisition. The exact roles of these hormones in song development is still unclear. Estradiol treatment may also "masculinize" brains of oscine females who do not have male song control centers (see below).

Testosterone has long been thought to directly affect song production. Quail chicks injected with testosterone will crow (Schleidt and Shalter 1973). Females of various species that normally do not sing will do so if treated with testosterone (Kling and Stevenson-Hinde 1977). Males treated with testosterone will sing during the period of winter quiescence (Baptista et al. 1987). Radioactive (tritiated) testosterone administered to castrated Chaffinches will concentrate in various song centers in the brain (Zigmond et al. 1973). Testis cycles tract closely the song cycles of Rufous-sided Towhees (*Pipilo erythrophthalmus*) (Davis 1958), implying that song levels and testosterone titres are correlated.

However, females of various emberizid species hold territories and sing in the fall (Arcese et al. 1988, Baptista et al. 1993b) during the period of minimal gonadal activity. Juvenile White-crowned Sparrows sing adult-like songs in the autumn and winter when trying to establish territories (De Wolfe et al. 1989). Testis sizes are minimal during this time.

Thus, although testes of many oscine species grow and regress concomitantly with the song cycle, correlation in this case is not causation. Testosterone does not affect ability to sing but apparently influences motivation to do so. Wingfield (1984) documented secretion of androgens during repeated and prolonged conflicts between Song Sparrows. He and Arcese et al.

(1988) suggest that these bursts of androgen are the causal explanation for female song. These ideas may apply to males, and are worthy of further investigation.

FUNCTIONS OF SONG

Kroodsma and Byers (1991) have commented on the validity of the traditional views of the function of male song, namely: (i) mate attraction, (ii) stimulation of the female, (iii) territoriality. We review and comment herein on some of these ideas.

MATE ATTRACTION

There is an "abundance" of indirect evidence for the mate-attraction function of bird song (Kroodsma and Byers 1991). Unpaired males or males that are experimentally or naturally widowed sing more than paired individuals. In species such as parulid warblers that sing two song types (Morse 1970), mated males shift preferences of song types used once mated. Some species, such as the European Sedge Warbler (*Acrocephalus schoenobaenus*) or California Towhee (*Pipilo crissalis*), cease singing altogether once mated (Catchpole 1973, Quaintance 1938).

Kroodsma and Byers (1991) also review the literature on experiments in devocalizing males or placing loudspeakers at nest sites to demonstrate the mate attraction function of song. They argue correctly that although these experiments demonstrate that songs can attract females, we do not know if other vocalizations could function as effectively. Szijj (1966) has conducted playback studies to demonstrate that it is a social call rather than the primary song that attracts female Meadowlarks (*Sturnella* spp.) and functions as an ethological isolating mechanism. Rothstein et al. (1988) have also shown that two vocalizations of the Brown-headed Cowbird function as song substitutes. Clearly, many such studies are needed.

A corollary of the question of mate-attraction is that of species isolation mechanisms. Various authors (e.g., Vermeij 1988, Fitzpatrick 1988) have advanced the thesis that vocal learning could lead to song divergence between adjacent populations and ultimately to speciation, and that this phenomenon explains the existence of the vast number of oscines. If this be true, then groups that learn songs should be more speciose than those that inherit song. Baptista and Trail (1992) found no significant differences in number of species between the two groups. They suggest that song is one of a hierarchy of cues, and that a female attracted by song would change to other cues such as morphology in choosing a mate once she is within visual distance of the male.

MALE SONG STIMULATING FEMALES

A review of the evidence from field observations by Kroodsma and Byers (1991) indicates that male song in many species increases with the beginning of each nesting attempt and this suggests a stimulatory function. More compelling are the experiments using taped song, indicating that these sounds alone, without visual stimuli from males, may actually stimulate gonadal growth in three domesticated species, namely, the Budgerigar (*Melopsittacus undulatus*), Canary and Ring Dove (*Streptopelia roseogrisea*).

What exactly is the role of song in stimulating hormone production? Based on her study on Ring Doves and a review of the literature, Cheng (1992) presented evidence indicating that the role of song in stimulating hormonal activity is indirect. In her review, the classical studies by Brockway (1967, 1969) are revisited. These demonstrated that gonadal recrudescence occurred when conspecific warbling calls are played to colonies of captive Budgerigars. However, she also found that devocalized males exposed to playback could not grow testis and argued that playback stimulated the male to warble, and the male's own warbles stimulate gonadal recrudescence. Cheng (1992) played nestcoos to devocalized and sham-operated female Ring Doves and found that devocalized females demonstrated a paucity of or no follicular growth. These data indicated to her that in females also, *self-stimulation* is directly responsible for hormonal production, and that self-stimulation is probably widespread among avian species.

What is the role of song at temperate latitudes where long day length is the primary stimulating agent of gonadal growth? Is song synergistic or complementary to photoperiod? To answer these questions Morton et al. (1985) raised female Gambel's White-crowned Sparrows in environmental chambers in which they were subjected to different photoperiods and exposed to song. From these experiments, song was shown to have a synergistic role in that it augments the effect of photoperiod, but it cannot affect gonadal growth below a certain photoperiod threshold.

The avian pituitary exhibits a circadian rhythmicity in its sensitivity to light stimulus in a number of avian species (Welty and Baptista 1988). Also, there is evidence that the pituitary in Budgerigars is song sensitive during the early morning, corresponding with the time of peak vocal production (Shellswell et al. 1975, Gosney and Hinde 1976, Ferrell and Baptista 1982).

Thus, the role of song in stimulating gonadal recrudescence is complex indeed. We must consider circadian sensitivity of the female to song and/or photoperiod. Additionally, we must consider the self-stimulating effect of her own song. Moreover, there are species differences in relative roles of photoperiod, sound, and nature of sound in stimulating gonads (Guyomarc'h and Guyomarc'h 1982, Millam et al. 1985, Morton et al. 1986).

FEMALE SONG

It has long been suggested that female song is abnormal and possibly a consequence of hormone imbalance (Thorpe 1961). This is likely a reflection of a Temperate Zone bias, as female singing is widespread at tropical latitudes (Farabaugh 1982).

Female song should be expected in species exhibiting reversal of roles between the sexes. For example, female advertising song has been documented in Spotted Sandpipers (*Actitis macularia*, Heidemann and Oring 1976) and serves to identify individuals. Female song is also well known among Hemipodes (Turnicidae, spectrograms in Cramp 1980, review in Johnsgard 1991).

Female singing is widespread among the Old World estrildid finches, but a survey of its distribution re-

vealed that it occurs most commonly only in one of the three tribes, namely, the Waxbills or Estrildae (Immelmann et al. 1965, 1977; Güttinger 1976). Singing may be induced in both sexes of Waxbill by separating pairs, in which case they apparently sing to seek reunion (Harrison 1962). Gahr and Güttinger (1986) analyzed songs of Red-cheeked Cordon Bleus (*Uraeginthus bengalus*) and found that although females usually used the same syllable types as males, the formers' songs tended to be shorter in duration. They suggested that in this species song also serves in mutual sexual stimulation.

At temperate latitudes female song is often encountered during the non-breeding season. Female European Robins (*Erithacus rubecula*) defend winter territories with song, as do female Townsend's Solitaires (*Myadestes townsendi*) on their wintering grounds (Hoelzel 1986, George 1987). Arcese et al. (1988) documented fall singing in female Song Sparrows as a manifestation of female/female competition. Female montane White-crowned Sparrows (*Z. l. oriantha*) may sing in late-snow years upon arrival in the breeding grounds in early summer when territories are in short supply and competition intense. However, female coastal White-crowned Sparrows (*Z. l. nuttalli*) tend to sing in the fall and winter to aid their males in preventing conspecifics of both sexes from inserting into territories. A widowed female *Z. l. nuttalli* sang until it found a new mate, indicating an advertising function (Baptista et al. 1993b).

In addition to sexual and territorial motivation, other functions have been postulated for female song. Singing in female Black-headed Grosbeaks (*Pheucticus melanocephalus*) stimulates begging from fledglings and apparently enables the female to locate her young (Ritchison 1983). Song is produced by female Northern Cardinals prior to nest-building; however, in contrast to males, females do not respond to playback. It was concluded that female song in this species is to establish pair bonds (Ritchison 1986).

BIRD SONG AND NEUROPHYSIOLOGY

Song is controlled in oscines, and possibly all birds that learn song, by brain centers that are lateralized, i.e., one hemisphere controls most of song production, and several brain nuclei have been identified (Nottebohm 1984). Female Zebra Finches who do not sing have song centers that are much reduced (Nottebohm and Arnold 1976). Gurney (1981, 1982) has demonstrated that female nestlings treated with estradiol will develop male song centers. Pohl-Apel and Sossinka (1984) found that estradiol is effective only during a time window or sensitive phase.

In a number of estrildid species, relatives of the Zebra Finch, female song is commonplace (see above). Since the female Zebra Finch possesses the potential to develop a male song system, loss of song may be a derived trait and female song the primitive condition in estrildids (Gahr and Güttinger 1986).

Western populations of Marsh Wrens possess song repertoires three times as large as those of eastern North American populations. Interestingly, the song brain centers are larger in brains of western birds (Canady et al. 1984). Nottebohm (1984) reminds us, however,

that causation and direction of this relationship has not been established.

Nottebohm (1981; see also Nottebohm et al. 1986) discovered that seasonal changes in song volume are accompanied by changes in the volumes of nuclei in the canary brain. There is also a correlation between the size of these brain nuclei and the size of the learned repertoire.

However, correlation is not necessarily causation. Vocal centers undergo annual cycles of recrudescence and remission even in species with small repertoires and age-limited learning (Arai et al. 1989, Brenowitz et al. 1991, Nottebohm 1993).

DISCUSSION

Early advances in instrumentation have enabled researchers to record and preserve avian vocalizations for later analyses. Concomitant development of spectrographic equipment enabled description and analyses. Together these techniques allowed for description of sound and investigation of questions pertaining to ontogeny and functions of vocalizations. Recent digital recording equipment and computer analysis programs expanded analyses capabilities both in statistical approaches and by permitting synthesis and greater ease of manipulation of sound for tutoring and playback experiments. These developments over the past half century have fostered the study of avian communication and facilitated its transition from purely descriptive to hypothesis testing and question generating, questions such as those regarding the interplay of nature with nurture in shaping vocalizations among many others.

One product of vocal learning is syllable or song sharing, which may be on the level of local neighborhood, larger dialectal regions, groups of dialects, or subspecies. Although geographical variation in vocalizations is expected in groups that learn vocal signals, recent literature reveals that such variation is also known in taxa not known to learn, e.g., Bobwhite Quail, European Quail, various dove species, an owl and a hawk (review in Baptista 1993, in press). These findings caution one not to assume absence of vocal sharing in taxa not known to learn, nor that neighbor sharing is a consequence of learning. Moreover, whereas early studies on vocal ontogeny focused on song learning as an all-or-none phenomenon, a survey of the literature in this review urges investigators to treat various components of song separately, including syllable structure, frequency, rhythm, duration, syntax, and element number. One or more, or all, of these may develop independently of learning experience.

We do not question the use of tape-tutoring as a tool in studying vocal development, especially since use of tape may indicate that avian species recognize conspecific vocalizations by sound alone (Konishi 1985). However, we recognize that social interaction is an additional factor that must always be considered, as these may influence time of closure of the sensitive phase, rate of song ontogeny and choice of tutor to be modelled (Baptista et al. 1993a).

We have reviewed literature indicating that some birds learn songs directly from fathers and others from non-related adults. What is the advantage of learning

directly from fathers? Zebra Finch songs are exclusively sexual in function and males may be sexually mature by three months of age (Immelmann 1982). Rains may be infrequent in the xeric habitat where they live, and individuals do not live long. Thus, a premium is placed on breeding at an early age, and Zebra Finches must have a mechanism whereby the vocal sexual signal is acquired early to prepare them for the reproductive process. The plasticity in the learning period demonstrated by Slater et al. (1988) may be an insurance against losing the father-tutor before song acquisition is completed.

What advantage is there to learning songs after dispersal? Learning from neighbors may be advantageous in that it may improve the individual's breeding success (Payne 1982, Rothstein and Fleischer 1987). Morton (1982) has presented the intriguing idea that, by storing an undegraded image of the neighbor's song, the male is able to use it as a "standard" to judge degradation of that song over distance. Fighting is energetically expensive; thus, if an individual is quickly able to judge the distance of the singing neighbor, then a decision may be made to ignore him, to threaten him by counteringing or to actually fight the singer. Playback experiments by McGregor et al. (1983) lend credence to Morton's (1982) ideas.

Sharing over a larger "dialectal" area by crowned sparrows (*Zonotrichia* spp.) has been interpreted as advantageous in that it may promote assortative mating, i.e., a female will select a male that sings her own dialect, thus increasing her chances of mating with a male possessing a genome similar to hers. This would enable them to fixate genes controlling physiological adaptations to a particular environment (Marler and Tamura 1962, Nottebohm 1969). This theory has been vigorously debated by the ornithological community (review in Loughheed and Handford 1992). Although various laboratory studies have yielded data consistent with these ideas (e.g., Baker 1983), results from field studies do not support these conclusions (Chilton et al. 1990, Loughheed and Handford 1992). Is there an advantage to singing a local dialect other than the above?

Nottebohm (1985) presented data indicating that trill rates in dialectal populations of Rufous-collared Sparrows (*Zonotrichia capensis*) are associated with specific habitat types. He and Handford (1988) have argued that these song characteristics enable these signals to travel maximally over distance in their own habitat.

Pitch/amplitude envelope in songs of Carolina Wrens (*Thryothorus ludovicianus*) and Galapagos Finches varied geographically and are associated with habitat type. Playback experiments measuring sound degradation over distance in "dialects" of these two species (Gish and Morton 1981, Bowman 1979) yielded data indicating that songs transmitted best over distance in their home habitat. The sound transmission hypothesis of the above authors, the sound degradation hypothesis of Morton (1982) and the "honest signaling" hypothesis of Rothstein and Fleischer (1987) are not necessarily contradictory, and more than one may operate concomitantly in a population. See review by Wiley and Richards (1982) for a more detailed discussion of the interplay of sound production, transmission and reception with environment.

Learning a correct song either through social bonding with a parent or because of innate preference enables a bird to acquire the correct social signal important in territoriality and advertising. Is there any selective advantage to being able to learn alien songs in species that do not regularly do so?

White-crowned Sparrows and other emberizids may learn and sing or store and not sing allospecific songs in the wild (Baptista 1990b). In playback experiments conducted in nature, subsets of White-crowned Sparrows and Song Sparrows reacted to playback of each other's songs, indicating that some individuals in the wild stored but did not sing songs of allospecifics (Catchpole and Baptista 1988, Baptista and Catchpole 1989). Perhaps in local situations where territories of two species are packed together, territorial encounters are more frequent and more intense so that a premium is placed on a bird learning, storing and/or singing allospecific song which is used in interspecific territorial encounters (review in Catchpole and Baptista 1988).

Field observations and experiments indicate that two of the functions of song are territoriality and mate attraction (Kroodsma and Byers 1991). We agree with these authors that non-song vocalizations should also be tested for these functions. For example, Brown Towhees stop singing when mated (Quaintance 1938), and the dawn chorus is filled with their monotonous monosyllabic calls which appear to serve as a song substitute (Marshall 1964). We have also seen that female Meadowlarks respond to a call rather than to a song (Szijj 1966) which is given prior to copulation.

We have reviewed some of the literature on the role of vocalizations in stimulating gonadal recrudescence and pointed out the complex nature of this phenomenon. However, most of the studies are based on domesticated species. We need more studies on wild taxa from different latitudes and different circannual light/dark cycles.

Although female song is a well-known phenomenon in tropical areas, its presence at temperate latitudes has been less well documented. This may be due to a research bias, since males are more vocal. We have reviewed a number of studies documenting female song serving a variety of functions in females of North Temperate species. We predict that there will be many more to come.

LITERATURE CITED

- ARAI, O., I. TANIGUCHI, AND N. SAITO. 1989. Correlation between the size of song control nuclei and plumage color change in Orange Bishop birds. *Neurosci. Lett.* 98:144-148.
- ARCESE, P., P. K. STODDARD, AND S. M. HIEBERT. 1988. The form and function of song in female Song Sparrows. *Condor* 90:44-50.
- BAKER, M. C. 1983. The behavioral response of female Nuttall's White-crowned Sparrows to male song of natal and alien dialects. *Behav. Ecol. Sociobiol.* 12:309-315.
- BAKER, J. A., AND E. D. BAILEY. 1987. Sources of phenotypic variation in the separation call of Northern Bobwhite (*Colinus virginianus*). *Can. J. Zool.* 65:1010-1015.

- BAKER, M. C., AND D. B. THOMPSON. 1985. Song dialects of White-crowned Sparrows: historical processes inferred from patterns of geographic variation. *Condor* 87:127-141.
- BAPTISTA, L. F. 1975. Song dialects and demes in sedentary populations of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). *Univ. of Calif. Publ. Zool.* 105:1-52.
- BAPTISTA, L. F. 1977. Geographical variation in song and song dialects of the migratory White-crowned Sparrow, *Zonotrichia leucophrys pugetensis*. *Condor* 79:356-370.
- BAPTISTA, L. F. 1985. The functional significance of song sharing in the White-crowned Sparrow. *Can. J. Zool.* 63:1741-1752.
- BAPTISTA, L. F. 1990a. Aviary in the aspens. *Pacific Discovery* 43(2):33-36.
- BAPTISTA, L. F. 1990b. Dialectal variation in the rain call of the Chaffinch. *Festschrift honoring Jürgen Nicolai, Die Vogelwarte* 35:249-256.
- BAPTISTA, L. F. 1993. El estudio de la variación geográfica usando vocalizaciones y las bibliotecas de sonidos de aves neotropicales, p. 15-30. *In* P. Escalanté-Pliego [ed.], *Proceedings of IV International Congress of Neotropical Birds* (Quito, Ecuador, 1991). Curación moderna de colecciones ornitológicas. American Ornithologists' Union, Washington, DC.
- BAPTISTA, L. F. *In press*. Nature and its nurturing in avian vocal development. *In* D. E. Kroodsma and E. H. Miller [eds.], *Ecology and evolution of acoustic communication among birds*. Cornell Univ. Press, Ithaca, NY.
- BAPTISTA, L. F., AND M. ABS. 1983. Vocalizations, p. 309-325. *In* M. Abs [ed.], *Behavior and physiology of the pigeon*. Academic Press, New York.
- BAPTISTA, L. F., D. A. BELL, AND P. W. TRAIL. 1993a. Song learning and production in the White-crowned Sparrow: parallels with sexual imprinting. *Netherlands J. Zool.* 43:17-33.
- BAPTISTA, L. F., AND C. K. CATCHPOLE. 1989. Vocal mimicry and interspecific aggression in songbirds: experiments using White-crowned Sparrow imitation of Song Sparrow song. *Behaviour* 109:247-257.
- BAPTISTA, L. F., B. B. DEWOLFE, AND L. AVERY-BEAUSOLEIL. 1987. Testosterone, aggression, and dominance in Gambel's White-crowned Sparrows. *Wilson Bull.* 99:86-91.
- BAPTISTA, L. F., AND R. B. JOHNSON. 1982. Song variation in insular and mainland California Brown Creepers. *J. Ornithol.* 123:131-144.
- BAPTISTA, L. F., AND J. R. KING. 1980. Geographical variation in song and song dialects of montane White-crowned Sparrows. *Condor* 82:267-284.
- BAPTISTA, L. F., AND M. L. MORTON. 1981. Interspecific song acquisition by a White-crowned Sparrow. *Auk* 98:383-385.
- BAPTISTA, L. F., AND M. L. MORTON. 1988. Song learning in montane White-crowned Sparrows: from whom and when. *Anim. Behav.* 36:1753-1764.
- BAPTISTA, L. F., AND L. PETRINOVICH. 1984. Social interaction, sensitive phases and the song template hypothesis in the White-crowned Sparrow. *Anim. Behav.* 32:172-181.
- BAPTISTA, L. F., AND L. PETRINOVICH. 1986. Song development in the White-crowned Sparrow: social factors and sex differences. *Anim. Behav.* 34:1359-1371.
- BAPTISTA, L. F., AND K.-L. SCHUCHMANN. 1990. Song learning in the Anna Hummingbird (*Calypte anna*). *Ethology* 84:15-26.
- BAPTISTA, L. F., AND P. W. TRAIL. 1992. The role of song in the evolution of Passerine diversity. *Syst. Biol.* 41:242-247.
- BAPTISTA, L. F., P. W. TRAIL, B. B. DEWOLFE, AND M. L. MORTON. 1993b. Singing and its functions in female White-crowned Sparrows, *Zonotrichia leucophrys*. *Anim. Behav.* 46:511-524.
- BARLOW, G. W. 1991. Nature-nurture and the debates surrounding ethology and sociobiology. *Amer. Zool.* 31:286-296.
- BECKER, P. 1982. The coding of species-specific characteristics in bird sounds, p. 214-252. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*, vol. 1. Academic Press, New York.
- BERTRAM, B. 1970. The vocal behaviour of the Indian Hill Mynah, *Gracula religiosa*. *Anim. Behav. Monogr.* 3(2):79-192.
- BITTERBAUM, E., AND L. F. BAPTISTA. 1979. Geographical variation in songs of California House Finches (*Carpodacus mexicanus*). *Auk* 96:462-474.
- BÖHNER, J. 1983. Song learning in the Zebra Finch (*Taeniopygia guttata*): selectivity in choice of a tutor and accuracy of song copies. *Anim. Behav.* 31:231-237.
- BÖHNER, J. 1990. Early acquisition of song in the Zebra Finch, (*Taeniopygia guttata*). *Anim. Behav.* 39:369-374.
- BORROR, D. J., AND C. R. REESE. 1953. The analysis of bird songs by means of a vibralyzer. *Wilson Bull.* 65:271-303.
- BORROR, D. J., AND C. R. REESE. 1956. Vocal gymnastics in Wood Thrush songs. *Ohio J. Sci.* 56:177-182.
- BOWMAN, R. I. 1979. Adaptive morphology of song dialects in Darwin's Finches. *J. Ornithol.* 120:353-389.
- BRENOWITZ, E. A., B. NALLS, J. C. WINGFIELD, AND D. E. KROODSMA. 1991. Seasonal changes in avian song nuclei without seasonal changes in song repertoire. *J. Neurosci.* 11:1367-1374.
- BROCKWAY, B. F. 1967. The influence of vocal behavior on the performer's testicular activity in Budgerigars (*Melopsittacus undulatus*). *Wilson Bull.* 79:328-334.
- BROCKWAY, B. F. 1969. Roles of Budgerigar vocalization in the integration of breeding behavior, p. 131-158. *In* R. A. Hinde [ed.], *Bird vocalizations*. Cambridge Univ. Press, London.
- CANADY, R. A., D. E. KROODSMA, AND F. NOTTEBOHM. 1984. Population differences in complexity of a learned skill are correlated with the brain space involved. *Proc. Natl. Acad. Sci. USA* 81:6232-6234.
- CATCHPOLE, C. K. 1973. The functions of advertising

- song in the Sedge Warbler (*Acrocephalus schoenobaenus*) and the Reed Warbler (*A. scirpaceus*). *Behaviour* 46:300-320.
- CATCHPOLE, C. K., AND L. F. BAPTISTA. 1988. A test of the competition hypothesis of vocal mimicry, using Song Sparrow imitation of White-crowned Sparrow song. *Behaviour* 106:119-128.
- CATCHPOLE, C. K., J. DITTANI, AND B. LEISLER. 1984. Differential responses to male song repertoires in female songbirds implanted with oestradiol. *Nature* 312:563-565.
- CAVALLI-SFORZA, L. L., M. W. FELDMAN, K. H. CHEN, AND S. M. DORNBUSCH. 1982. Theory and observation in cultural transmission. *Science* 218:19-27.
- CHENG, M. F. 1992. For whom does the female dove coo? A case for the role of vocal self-stimulation. *Anim. Behav.* 43:1035-1044.
- CHILTON, G., M. R. LEIN, AND L. F. BAPTISTA. 1990. Mate choice by female White-crowned Sparrows in a mixed-dialect population. *Behav. Ecol. Sociobiol.* 27:223-227.
- CLAYTON, N. S. 1989. Song, sex and sensitive phases in the behavioural development of birds. *Tree* 4:82-84.
- CLAYTON, N. S. 1990. Assortative mating in Zebra Finch subspecies (*Taeniopygia guttata guttata*) and (*T. g. castanotis*). *Phil. Trans. R. Soc. Lond. B* 330:351-370.
- COLLIAS, N. E. 1991. The role of American zoologists and behavioural ecologists in the development of animal sociology, 1934-1964. *Anim. Behav.* 41:613-631.
- COLLIAS, N. E., AND M. JOOS. 1953. The spectrographic analysis of sound signals of the domestic fowl. *Behaviour* 5:175-188.
- CRAMP, S. 1980. *Handbook of the birds of Europe the Middle East and North Africa*, vol. 2. Oxford Univ. Press.
- CUNNINGHAM, M. A., M. C. BAKER, AND T. J. BOARDMAN. 1987. Microgeographic song variation in the Nuttall's White-crowned Sparrow. *Condor* 88:261-275.
- DAVIS, J. 1958. Singing behavior and the gonad cycle of the Rufous-sided Towhee. *Condor* 60:308-336.
- DAVIS, L. I. 1964. Biological acoustics and the use of the sound spectrograph. *Southwestern Naturalist* 9(3):118-145.
- DEWOLFE, B. B., L. F. BAPTISTA, AND L. PETRINOVICH. 1989. Song development and territory establishment in Nuttall's White-crowned Sparrows. *Condor* 91:397-407.
- DEWOLFE, B. B., D. D. KASKA, AND L. J. PEYTON. 1974. Prominent variations in the songs of Gambel's White-crowned Sparrows. *Bird Banding* 45:224-252.
- EALLES, L. 1985. Song learning in zebra finches: some effects of song model availability on what is learnt and when. *Anim. Behav.* 33:1293-1300.
- FARABAUGH, S. 1982. Ecological and social significance of duetting, p. 85-124. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*, vol. 2. Academic Press, New York.
- FERRELL, R., AND L. F. BAPTISTA. 1982. Diurnal rhythms in the vocalizations of Budgerigars. *Condor* 84:123-124.
- FITZPATRICK, J. W. 1988. Why so many passerine birds? A response to Raikow. *Syst. Zool.* 37:72-77.
- GAHR, M., AND H.-R. GÜTTINGER. 1986. Functional aspects of singing in male and female *Uraeginthus bengalus* (Estrildidae). *Ethology* 72:123-131.
- GAUNT, A. S. 1987. Phonation, p. 71-94. *In* T. J. Seller [ed.], *Bird respiration*. CRC Press, Boca Raton, FL.
- GAUNT, A. S., AND S.L.L. GAUNT. 1985. Syringeal structure and avian phonation, p. 213-245. *In* R. F. Johnston [ed.], *Current ornithology*, vol. 2. Plenum Press, New York.
- GAUNT, S.L.L., L. F. BAPTISTA, J. E. SÁNCHEZ, AND D. HERNÁNDEZ. 1994. Song learning as evidenced from song sharing in two hummingbird species (*Colibri coruscans* and *C. thalassinus*). *Auk* 111:87-103.
- GEORGE, T. L. 1987. Behavior of territorial male and female Townsend's Solitaires (*Myadestes townsendi*) in Winter. *Am. Midl. Nat.* 118:121-127.
- GIBBS, H. L. 1990. Cultural evolution of male song types in Darwin's Medium Ground Finches (*Geospiza fortis*). *Anim. Behav.* 39:253-263.
- GISH, S. L., AND E. S. MORTON. 1981. Structural adaptations to local habitat acoustics in Carolina Wren songs. *Z. Tierpsychol.* 56:74-84.
- GOSNEY, S., AND R. A. HINDE. 1976. Changes in the sensitivity of female budgerigars to male vocalizations. *J. Zool., Lond.* 179:407-410.
- GRANT, B. R. 1984. The significance of song variation in a population of Darwin's finches. *Behaviour* 89:90-116.
- GREENEWALT, C. H. 1968. *Bird song: acoustics and physiology*. Smithsonian Institution Press, Washington, DC.
- GROOTHUIS, T.G.G. 1993. A comparison between development of bird song and development of other displays. *Netherlands J. Zool.* 43:172-193.
- GROSCHUPF, K., AND G. S. MILLS. 1982. Singing behavior of the Five-striped Sparrow. *Condor* 84:226-236.
- GURNEY, M. E. 1981. Hormonal control of cell form and number in the zebra finch song system. *J. Neurosci.* 6:658-673.
- GURNEY, M. E. 1982. Behavioural correlates of sexual differentiation in the Zebra Finch song system. *Brain Res.* 231:153-172.
- GÜTTINGER, H.-R. 1974. Gesang des Grünlings (*Chloris chloris*) Lokale Unterschiede und Entwicklung bei Schallisolation. *J. Ornithol.* 115:321-337.
- GÜTTINGER, H.-R. 1976. Zur systematischen Stellung der Gattungen *Amadina*, *Lepidopygia* und *Lonchura* (Aves, Estrildidae). *Bonn. Zool. Beitr.* 27:218-244.
- GÜTTINGER, H.-R. 1979. The integration of learnt and genetically programmed behaviour: a study of hierarchical organization in songs of canaries, greenfinches and their hybrids. *Z. Tierpsychol.* 49:285-303.
- GÜTTINGER, H.-R., E. PRÖVE, K. WEICHEL, AND A.

- PESCH. 1984. Hormonelle Korrelate zur Gesangsentwicklung der Kanarienvögel. *J. Ornithol.* 125:245-247.
- GUYOMARC'H, C., AND J. C. GUYOMARC'H. 1982. La stimulation du developpement sexuel des femelles de caille japonaise par des chants de males: mise en evidence de periodes privilegiees dans le nycthemere. *C.R. Acad. Sci.* 295:37-40.
- HAILMAN, J. P., M. S. FICKEN, AND R. W. FICKEN. 1985. The 'chick-a-dee' calls of *Parus atricapillus*: a recombinant system of animal communication compared with written English. *Semiotica* 56:191-224.
- HAILMAN, J. P., AND M. S. FICKEN. 1986. Combinatorial animal communication with computable syntax; chick-a-dee calling qualifies as 'language' by structural linguistics. *Anim. Behav.* 34:1899-1901.
- HAILMAN, J. P., M. S. FICKEN, AND R. W. FICKEN. 1987. Constraints on the structure of combinatorial "chick-a-dee" calls. *Ethology* 75:62-80.
- HANDFORD, P. 1988. Trill rate dialects in the Rufous-collared Sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Can. J. Zool.* 63:2383-2388.
- HARRISON, C.J.O. 1962. Solitary song and its inhibition in some Estrildidae. *J. Ornithol.* 4:369-373.
- HARTSHORNE, C. 1956. The monotony-threshold in singing birds. *Auk* 83:176-192.
- HEIDEMANN, M. K., AND L. W. ORING. 1976. Functional analysis of Spotted Sandpiper (*Actitis macularia*) song. *Behaviour* 56:181-193.
- HOELZEL, A. R. 1986. Song characteristics and response to playback of male and female robins *Erethacus rubecula*. *Ibis* 128:115-127.
- HOPKINS, C. D., M. ROSETTO, AND A. LUNTJEN. 1974. A continuous sound spectrum analyzer for animal sounds. *Z. Tierpsychol.* 34:313-320.
- HOWARD, R. D. 1974. The influence of sexual selection and interspecific competition on mockingbird song (*Mimus polyglottos*). *Evolution* 28:428-483.
- IMMELMANN, K. 1969. Song development in the Zebra Finch and other Estrildid finches, p. 61-74. *In* R. A. Hinde [ed.], *Bird vocalizations*. Cambridge Univ. Press, London.
- IMMELMANN, K. 1982. *Australian Finches*. Robertson Publishers, Sydney.
- IMMELMANN, K., J. STEINBACKER, AND H. E. WOLTERS. 1965. *Vogel in Käfig und Voliere, Prachtfinken*, vol. 1. Verlag Hans Limberg, Aachen, Germany.
- IMMELMANN, K., J. STEINBACKER, AND H. E. WOLTERS. 1977. *Vogel in Käfig und Voliere, Prachtfinken*, vol. 2. Verlag Hans Limberg, Aachen, Germany.
- INCE, S. A., P.J.B. SLATER, AND C. WEISMANN. 1980. Changes with time in the songs of a population of chaffinches. *Condor* 82:285-290.
- IRWIN, R. 1988. The evolutionary importance of behavioral development: the ontogeny and phylogeny of bird song. *Anim. Behav.* 36:814-824.
- JENKINS, P. 1985. Song learning, competition and dialects. *Behav. Brain Sci.* 11:108.
- JENKINS, P., AND A. J. BAKER. 1984. Mechanisms of song differentiation in introduced populations of chaffinches *Fringilla coelebs* in New Zealand. *Ibis* 126:510-524.
- JOHNSGARD, P. A. 1991. *Bustards, hemipodes, and sandgrouse*. Oxford, New York.
- JOHNSTON, T. D. 1988. Developmental explanation and the ontogeny of birdsong: nature/nurture redux. *Behav. Brain Sci.* 11:617-630.
- KELLOGG, P. P. 1962. *Bird-sound studies at Cornell*. *Living Bird* 1:37-48.
- KELLOGG, P. P., AND R. C. STEIN. 1953. Audio-spectrographic analysis of the songs of the Alder Flycatcher. *Wilson Bull.* 65:75-80.
- KLING, J. W., AND J. STEVENSON-HINDE. 1977. Development of song and reinforcing effects of song in female chaffinches. *Anim. Behav.* 25:215-220.
- KONISHI, M. 1963. The role of auditory feedback in the vocal behaviour of the domestic fowl. *Z. Tierpsychol.* 20:349-367.
- KONISHI, M. 1985. Bird song: from behavior to neuron. *Annul. Rev. Neurosci.* 8:125-170.
- KONISHI, M., AND F. NOTTEBOHM. 1969. Experimental studies in the ontogeny of avian vocalizations, p. 29-48. *In* R. A. Hinde [ed.], *Bird vocalizations*. Cambridge Univ. Press, London.
- KROODSMA, D. E. 1974. Song learning, dialects and dispersal in the Bewick's Wren. *Z. Tierpsychol.* 35:352-380.
- KROODSMA, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. *Auk* 101:13-24.
- KROODSMA, D. E. 1985. Development and use of song forms of the Eastern Phoebe. *Wilson Bull.* 97:21-29.
- KROODSMA, D. E., AND B. E. BYERS. 1991. The function(s) of bird song. *Amer. Zool.* 31:318-328.
- KROODSMA, D. E., AND M. KONISHI. 1991. A subsocial bird (Eastern Phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Anim. Behav.* 191(43):477-487.
- KROODSMA, D. E., AND R. PICKERT. 1980. Environmentally dependent sensitive periods for avian vocal learning. *Nature* 288:477-479.
- KROODSMA, D. E., AND J. VERNER. 1978. Complex singing behaviors among *Cistothorus* wrens. *Auk* 95:703-716.
- LEIN, M. R. 1979. Song pattern of the Cypress Hills population of White-crowned Sparrows. *Can. Field Nat.* 93:272-275.
- LEMON, R. E. 1975. How birds develop song dialects. *Condor* 77:385-406.
- LOUGHEED, S. C., AND P. HANDFORD. 1992. Vocal dialects and the structure of geographic variation in morphological and allozymic characters in the Rufous-collared Sparrow, *Zonotrichia capensis*. *Evolution* 46:1443-1456.
- MARLER, P. 1969. Tonal quality of bird sounds, p. 5-18. *In* R. A. Hinde [ed.], *Bird vocalizations: their relation to current problems in biology and psychology*. Cambridge Univ. Press, London.
- MARLER, P. 1970. A comparative approach to vocal learning: song development in White-crowned Sparrows. *J. Comp. Physiol. Psychol.* 71:1-25.
- MARLER, P. 1987. Sensitive periods and the role of specific and general sensory stimulation in bird-song learning, p. 99-135. *In* J. P. Rauschecker and

- P. Marler [eds.], Imprinting and cortical plasticity. John Wiley & Sons, New York.
- MARLER, P., AND D. ISAAC. 1960. Physical analysis of a simple bird song as exemplified by the Chipping Sparrow. *Condor* 62:124-135.
- MARLER, P., AND D. A. NELSON. 1993. Action-based learning: a new form of developmental plasticity in bird song. *Netherlands J. Zool.* 43:91-103.
- MARLER, P., AND S. PETERS. 1977. Selective vocal learning in a sparrow. *Science* 198:519-521.
- MARLER, P., S. PETERS, AND J. WINGFIELD. 1987. Correlations between song acquisition, song production, and plasma levels of testosterone and estradiol in sparrows. *J. Neurobiol.* 18:531-548.
- MARLER, P., AND M. TAMURA. 1962. Song 'dialects' in three populations of White-crowned Sparrows. *Condor* 64:368-377.
- MARSHALL, J. T., JR. 1964. Voice in communication and relationships among Brown Towhees. *Condor* 66:345-356.
- MCGREGOR, P. K., J. R. KREBS, AND L. M. RATCLIFFE. 1983. The reaction of Great Tits (*Parus major*) to playback of degraded and undegraded songs: the effect of familiarity with the stimulus song type. *Auk* 100:898-906.
- MILLER, L. 1952. Songs of the Western Meadowlark. *Wilson Bull.* 64:106-107.
- MILLAM, J. R., M. EL. HALAWANI, AND W. H. BURKE. 1985. Effect of cyclic sound cues on sexual development in non-photostimulated Japanese Quail. *Poultry Sci.* 64:169-175.
- MILLINGTON, S. F., AND T. D. PRICE. 1985. Song inheritance and mating patterns in Darwin's finches. *Auk* 102:342-346.
- MIRSKY, E. N. 1976. Song divergence in Hummingbird and Junco populations on Guadalupe Island. *Condor* 78:230-235.
- MORSE, D. H. 1970. Territorial and courtship songs of birds. *Nature* 226:659-661.
- MORTON, E. S. 1982. Grading, discreteness, redundancy, and motivation-structural rules, p. 183-212. *In* D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*, vol. 1. Academic Press, New York.
- MORTON, E. S., S. L. GISH, AND M. VAN DER VOORT. 1986. On the learning of degraded and undegraded songs in the Carolina Wren. *Anim. Behav.* 34:815-820.
- MORTON, M. L., M. E. PEREYRA, AND L. F. BAPTISTA. 1985. Photoperiodically induced ovarian growth in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) and its augmentation by song. *Comp. Biochem. Physiol.* 80A:93-97.
- MULLIGAN, J. A. 1966. Singing behavior and its development in the Song Sparrow, *Melospiza melodia*. *Univ. Calif. Publ. Zool.* 81:1-76.
- NICE, M. M. 1943. Studies in the life history of the Song Sparrow II. The behavior of the Song Sparrow and other passerines. *Trans. Linn. Soc. N.Y.* 6:1-238.
- NICOLAI, J. 1959. Familientradition in der Gesangsentwicklung des Gimpels (*Pyrrhula pyrrhula* L.). *J. Ornithol.* 100:39-46.
- NICOLAI, J. 1964. Brutparasitismus der Viduinae als ethologisches Problem. *Z. Tierpsychol.* 21:129-204.
- NOTTEBOHM, F. 1969. The song of the chingolo, *Zonotrichia capensis*, in Argentina: description and evaluation of a system of dialects. *Condor* 71:299-315.
- NOTTEBOHM, F. 1971. Neural lateralization of vocal control in a passerine bird. *J. Exp. Zool.* 117:229-262.
- NOTTEBOHM, F. 1981. A brain for all seasons: cyclical anatomical changes in song control nuclei of the canary brain. *Science* 214:1368-1370.
- NOTTEBOHM, F. 1984. Birdsong as a model in which to study brain processes related to learning. *Condor* 86:227-236.
- NOTTEBOHM, F. 1985. Sound transmission, signal salience and song dialects. *Behav. Brain Sci.* 8:112-113.
- NOTTEBOHM, F. 1993. The search for neural mechanisms that define the sensitive period for song learning in birds. *Netherlands J. Zool.* 43:193-234.
- NOTTEBOHM, F., AND A. P. ARNOLD. 1976. Sexual dimorphism in vocal control areas of the songbird brain. *Science* 194:211-213.
- NOTTEBOHM, F., AND M. E. NOTTEBOHM. 1971. Vocalizations and breeding behaviour of surgically deafened Ring Doves (*Streptopelia risoria*). *Anim. Behav.* 19:313-327.
- NOTTEBOHM, F., AND M. E. NOTTEBOHM. 1978. Relationship between song repertoire and age in the canary, *Serinus canarius*. *Z. Tierpsychol.* 46:298-305.
- NOTTEBOHM, F., M. E. NOTTEBOHM, AND L. CRANE. 1986. Developmental and seasonal changes in canary song and their relation to changes in the anatomy of song-control nuclei. *Behav. Neural Biol.* 46:445-471.
- PAYNE, R. B. 1973a. Behavior, mimetic songs and song dialects, and relationships of the parasitic indigobirds (*Vidua*) of Africa. *Ornithol. Monog.* 11.
- PAYNE, R. B. 1973b. Vocal mimicry of Paradise Whydahs (*Vidua*) and response of male whydahs to song of their hosts (*Pytilia*) and their mimics. *Anim. Behav.* 21:762-771.
- PAYNE, R. B. 1982. Ecological consequences of song matching: breeding success and intraspecific song mimicry in Indigo Buntings. *Ecology* 63:401-411.
- PAYNE, R. B. 1985. Behavioral continuity and change in local song populations of Village Indigobirds *Vidua chalybeata*. *Z. Tierpsychol.* 70:1-44.
- PAYNE, R. B., AND K. PAYNE. 1977. Social organization and mating success in local song populations of Village Indigobirds (*Vidua chalybeata*). *Z. Tierpsychol.* 45:113-173.
- PEPPERBERG, I. M. 1993. A review of the effects of social interaction on vocal learning in African Grey Parrots (*Psittacus erithacus*). *Netherlands J. Zool.* 43:104-124.
- PETRINOVICH, L. 1985. Factors influencing song development in the White-crowned Sparrow (*Zonotrichia leucophrys*). *J. Comp. Psychol.* 99:15-29.

- PETRINOVICH, L. 1988. Individual stability, local variability and the cultural transmission of song in White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*). *Behaviour* 107:208-240.
- PETRINOVICH, L., AND L. F. BAPTISTA. 1987. Song development in the White-crowned Sparrow: modification of learned song. *Anim. Behav.* 35: 961-974.
- POHL-APEL, G., AND R. SOSSINKA. 1984. Hormonal determination of song capacity in females of the Zebra Finch: critical phase of treatment. *Z. Tierpsychol.* 64:330-336.
- POTTER, R. K. 1945. Visible patterns of sounds. *Science* 102:463-470.
- QUAINTANCE, C. W. 1938. Content, meaning and possible origin of male song in the Brown Towhee. *Condor* 40:97-101.
- RAITT, R. J., AND J. W. HARDY. 1970. Relationships between two partly sympatric species of thrushes (*Catharus*) in Mexico. *Auk* 87:20-57.
- REYNARD, G. B. 1963. The cadence of birdsong. *Living Bird* 2:139-148.
- RITCHISON, G. 1983. Breeding biology of the Black-headed Grosbeak in northern Utah. *Western Birds* 14:159-167.
- RITCHISON, G. 1986. The singing behavior of female Northern Cardinals. *Condor* 88:156-159.
- ROTHSTEIN, S. I., AND R. C. FLEISCHER. 1987. Vocal dialects and their possible relation to honest status signalling in the Brown-headed Cowbird. *Condor* 89:1-23.
- ROTHSTEIN, S. I., D. A. YOKEL, AND R. C. FLEISCHER. 1988. The agonistic and sexual functions of vocalizations of male brown-headed cowbirds, *Molothrus ater*. *Anim. Behav.* 36:73-86.
- SAUNDERS, A. A. 1935. A guide to bird songs. Appleton-Century Co., New York.
- SCHLEIDT, W. M., AND M. D. SHALTER. 1973. Stereotype of a fixed action pattern during ontogeny in *Coturnix coturnix coturnix*. *Z. Tierpsychol.* 33:35-37.
- SEARCY, W. A., AND P. MARLER. 1981. A test for responsiveness to song structure and programming in female sparrows. *Science* 213:926-928.
- SHELLSWELL, G. B., S. G. GOSNEY, AND R. A. HINDE. 1975. Photoperiodic control of Budgerigar reproduction: circadian changes in sensitivity. *J. Zool., Lond.* 175:53-60.
- SLATER, P. J. B., L. A. EALES, AND N. S. CLAYTON. 1988. Song learning in Zebra Finches (*Taeniopygia guttata*): progress and prospects. *Adv. Study Behav.* 18:1-34.
- SMITH, S. M. 1983. The ontogeny of avian behavior, p. 85-160. In D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*, vol. 7. Academic Press, New York.
- STRESEMANN, E. 1947. Baron von Pernau, pioneer student of bird behavior. *Auk* 64:35-52.
- SZUJ, L. J. 1966. Hybridization and the nature of the isolating mechanisms in sympatric populations of meadowlarks (*Sturnella*). *Z. Tierpsychol.* 6:677-690.
- TEN CATE, C. 1989. Behavioural development: toward understanding processes, p. 243-269. In P. P. G. Bateson and P. H. Klopfer [eds.], *Perspectives in ethology*, vol. 8. Plenum, New York.
- THIELCKE, G. 1965a. Gesangsgeographische Variation des Gartenbaumläufers (*Certhia brachydactyla*) im Hinblick auf das Artbildungsproblem. *Z. Tierpsychol.* 22:542-566.
- THIELCKE, G. 1965b. Die Ontogenese der Bettellaute von Garten und Waldbaumläufer (*Certhia brachydactyla* Brehm und *C. familiaris* L.). *Zool. Anzeiger* 174:237-241.
- THIELCKE, G. 1970. Lernen von Gesang als Möglicher Schrittmacher der Evolution. *Z. Zool. Syst. Evo.* 8:309-320.
- THIELCKE, G. 1971. Versuche zur Kommunikation und Evolution der Angst-, Alarm- und Rivalenlaute des Waldbaumläufers (*Certhia familiaris*). *Z. Tierpsychol.* 28:505-516.
- THIELCKE, G. 1973. On the origin of divergence of learned signals (songs) in isolated populations. *Ibis* 115:511-516.
- THIELCKE, G. 1987. Langjährige Dialektkonstan beim Gartenbaumläufer (*Certhia brachydactyla*). *J. Ornithol.* 128:171-180.
- THIELCKE, G. 1988. Neue Befunde bestätigen Baron Pernaus (1660-1731) Angaben über Lautäusserungen des Buchfinken (*Fringilla coelebs*). *J. Ornithol.* 129:55-70.
- THORPE, W. H. 1958. The learning of song patterns by birds, with especial reference to the song of the chaffinch, *Fringilla coelebs*. *Ibis* 100:535-570.
- THORPE, W. H. 1961. *Bird song: the biology of vocal communication and expression in birds*. Cambridge Univ. Press, London.
- VERMEIJ, G. J. 1988. The evolutionary success of passerines: a question of semantics? *Syst. Zool.* 37:69-71.
- VERNER, J. 1975. Complex song repertoire of male Long-billed Marsh Wrens in eastern Washington. *Living Bird* 14:263-300.
- WELTY, J. C., AND L. F. BAPTISTA. 1988. *The life of birds*. Saunders, New York.
- WEST, M., AND A. P. KING. 1985. Social guidance of vocal learning by female cowbirds: validating its functional significance. *Z. Tierpsychol.* 70:225-335.
- WEST, M., AND A. P. KING. 1988. Female visual display affect the development of male song in the cowbird. *Nature* 334:244-246.
- WIENS, J. A. 1982. Song pattern variation in the Sage Sparrow (*Amphispiza belli*): dialects or epiphenomena? *Auk* 99:208-229.
- WILEY, R. H., AND D. G. RICHARDS. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection, p. 131-181. In D. E. Kroodsma and E. H. Miller [eds.], *Acoustic communication in birds*, vol. 1. Academic Press, New York.
- WILLIAMS, L., AND M. H. MACROBERTS. 1977. Individual variation in songs of Dark-eyed Juncos. *Condor* 79:106-112.
- WINGFIELD, J. C. 1984. Environmental and endocrine control of reproduction in the Song Sparrow *Melospiza melodia* II. Agonistic interactions as en-

- vironmental information stimulating secretion of testosterone. *Gen. Comp. Endocrinol.* 56:417-424.
- ZANN, R. 1990. Song and call learning in wild Zebra Finches in south-east Australia. *Anim. Behav.* 40: 811-828.
- ZANN, R. 1993. Variation in song structure within and among populations of Australian Zebra Finches. *Auk* 110:716-726.
- ZIGMOND, R. E., F. NOTTEBOHM, AND D. W. PFAFF. 1973. Androgen-concentrating cells in the mid-brain of songbirds. *Science* 179:1005-1007.