

# Explaining Avian Vocalizations: a Review of Song Learning and Song Communication in Male-Male Interactions

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**Abstract:** Avian vocalization has been main topics in studying animal communication. The structure and usage as well as development and function of vocalization vary enormously among species and even among populations, and thus we reviewed the general patterns of song learning and the consequences of song communication in birds at the behavioural level: first, we compared the different learning phenomena between non-songbird and songbird, and we investigated the learning process of songbird both in the field and in the lab, which are needed to fully understand vocal communication. Second, we discussed a recent trend of sexual selection hypothesis explaining the structural and functional diversity of song in songbirds with repertoire and presented how the repertoire is actually used between neighbours based on individual recognition.

**Key words:** Call, communication, repertoire, songbird, song learning, sexual selection

Communication is a process of information exchange between sender and receiver. Senders make information available through signals, and receivers interpret the information based on the signals, other stimuli, experience etc. (Smith, 1990). Receivers tend to be highly sensitive to senders' signals, while senders modify signals to obtain more beneficial responses from receivers (Johnstone, 1997). Senders should optimize the balance between the costs of time and energy spent on signalling and the benefits of signalling effects. Signals efficiently conveying information to receivers should provide accurate information on the sender's location and identity (Howard, 1974; Wiley, 1983; Endler, 1993). Thus, conspicuous and stereotyped signals provide many obvious benefits. For instance, many avian species show vocal individuality and can discriminate

between pair members, relatives, or neighbours (Wanker et al., 1998; Wiley and Wiley, 1977; Colgan, 1983; Beecher, 1988, 1989; Ydenberg et al., 1988; Studholme, 1994), which can reduce costs (e.g. time and energy) from ambiguity in the process of avian communication.

Avian vocal signals vary enormously in structure and usage among individuals among species (Miller, 1992; Catchpole and Slater, 1995). The diversity of vocalizations has been explained with various selective forces and their constraints in the process of avian communication, where vocal repertoires of birds are adapted to their social systems as well as to their habitats (Sordahl, 1979; Read and Weary, 1992; Trainer and McDonald, 1993; Sung et al., 2005). Many studies have detailed vocal structure and its possible functions (Oring, 1968; Ficken et al., 1978; Maier, 1982; Riska, 1986; Byers, 1996; Park and Park, 1996; Park and Park, 1997; Park et al., 1999; Brown and Handford, 2000; Park and Park, 2000). Such research typically relies on sonagrams and oscillograms for revealing acoustic structure, and has contributed to improve theoretical frameworks for understanding avian vocal communication.

In this study, we will review the general process and a variety of consequences of avian vocal communication at the behavioural level, especially in song learning and song communication in songbirds (Passeriformes: Oscines), and conditions necessary for recognizing individuals in birds, especially focusing on communication of male-male interactions.

## SONG LEARNING

The basic categories of vocalization, 'song' and 'call' exist (Gill, 1995). Song commonly means lengthy, complex, repeated vocal displays often performed by territorial males while call means short, sharp, and simple signals. Calls include various types in structure and function depending

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on in what situation the birds called, such as alarm calls, contact calls, warning calls, aggressive calls, flock calls, courtship calls, and so on. However, there is no strict dichotomy between song and call. Nevertheless, it helps to understand the study of avian vocal development (Thielcke, 1970). For example, the calls of eastern meadowlark are inherited while the songs are learned from other meadowlarks, as results of misdirected learning during critical learning period (Mumford, 1952; Lanyon, 1957).

The process of song learning generally requires two factors (Kroodsma and Konishi, 1991): Auditory feedback is one for normal song development because songbirds deafened prior to crystallizing his song could not produce a species-specific song. Second, special forebrain is necessary to control the normal song production like the forebrain song nuclei of songbirds. The absence of these nuclei leads to inability to learn song. It is generally admitted that the songs of songbirds are learned, while other groups of vocalizations are considered innate, not learning except for parrots and hummingbirds (Kroodsma, 1982a).

### Non- or sub-songbirds

The studies on non- or sub-songbirds showed that species-specific sounds have been produced without any chance of learning (Nottebohm and Nottebohm, 1971; Baptista and Schuchmann, 1990; Kroodsma and Konishi, 1991). Domestic fowls, cross-fostered doves from different species, and deafened young ringed turtle-doves (*Streptopelia risoria*), all non-songbirds, developed their own songs without any auditory feedback (Konishi, 1963; Lade and Thorpe, 1964; Nottebohm and Nottebohm, 1971). On the other hand, sub-songbirds including tyrant flycatchers, antbirds, ovenbirds have relatively simple songs with small size of repertoires, and geographically less variable songs. Kroodsma and Konishi (1991) reported that the eastern phoebe (sub-songbird, *Sayornis phoebe*) developed normal songs without auditory feedback and special forebrain sections contain no other cell clusters like several non-songbirds. However, numerous suspicious evidences of vocal learning exist in these avian groups, especially in sub-songbirds of about 1100 species (Kroodsma, 1982a). Thus, there will be more possible to show evidences in this group, but so far little laboratory work has been done under controls and acceptable observations in nature, such as vocal dialects from several populations. Furthermore, Baptista (1996) argued that even the birds able to learn songs or calls might genetically determine their own temporal, frequency, and tonal characteristics. Consequently, less within-individual differences or less geographic variations, if any, which is minor roles for sound learning in the non-songbirds (including sub-songbirds), will be regarded as a result of genetic control (Siegel et al., 1965; Miller, 1986; Abs and Jeismann, 1988; Bretagnolle, 1996).

### Songbirds

The study of song learning in songbirds was made not only by performing carefully controlled laboratory experiments but also by comparing objective sonagrams recorded from field works: 1) Song learning in the lab. Many researches on song learning in the lab revealed that heterospecific as well as conspecific sounds were developed from live tutor as well as taped tutor songs (Marler, 1977; Baptista and Petrinovich, 1984; Clayton, 1989). Mimicry is one of representative evidences on song learning, which occurs when individuals imitate relatively complex songs from other species. For example, the song sparrow (*Zonotrichia melodia*) easily learned Swamp sparrow (*Zonotrichia georgiana*) song components (Marler and Peters, 1977). The indigobirds (*Vidua chalybeata*) appeared to learn and imitate the songs of the foster species, the red-billed firefinch (*Lagonosticta senegala*; Payne, 1990). However, juvenile white-crowned sparrow (*Zonotrichia querula*) exposed to conspecific and heterospecific songs learned only conspecific songs (Marler, 1970). A hand-reared chestnut-sided warbler (*Dendroica pensylvanica*) failed to learn songs of yellow warbler (*Dendroica petechia*; Kroodsma, 1982a).

Laboratory experiments have provided invaluable evidence on song learning mechanism and answered questions, such as when and how birds develop songs or whether species differences exist in innate song learning programs. However, Kroodsma (1996) raised doubts on the laboratory studies because such studies were performed without any considerations on behavioural and ecological variables. Thus, he insisted to use a carefully designed comparative framework to understand the ecology and evolution of vocal development. At the same point of view, Beecher (1996) pointed out two types of problems on laboratory studies: The first is on great differences in patterns of song learning between lab and the natural context. For example, white-crowned sparrow kept learning songs after dispersal from the natal area in the wild, while being ceased in the lab at about 50 days. Second is on the inability of identifying social variables that may be critical in song learning from lab studies, such as song learning of free movement young. Thus, he argued that social and ecological variables are considered to study song learning in birds, so that the field study should precede lab study for preventing from misleading the outcome from lab study.

2) Song learning in the field. Longitudinal field studies of song learning has been restricted to a few species because of prerequisites; all or most birds within a population have to be color-banded and their song repertoire has to be fully recorded and identified (Beecher, 1996). Beecher (1996) and Beecher et al. (1998) classified the tutor-student and identified songs of song sparrow into whether the songs are shared or unique to one singer in the reference

group from field studies. Then, they found that a young bird learns songs more faithfully and precisely in the field than in the lab, and that the young bird classifies songs by type and singer identity. The result of playback experiments, in which the territorial bird replied to the neighbour's song with a different song shared with that neighbor (repertoire matching) and to the stranger's song with the same song (type matching) or with a nonshared song, supported their song learning patterns (Beecher, 1996). Furthermore, Beecher et al. (2000) showed that type matching is more common early in the breeding season and repertoire matching late in the season, which requires memorizing new neighbours' repertoire. This learning procedure between neighbours would include a process of social interaction: (1) by copying a dominant male (Payne, 1982), (2) by copying an honest song type representing high social status and mate quality (Rothstein and Fleischer, 1987), (3) by copying a male that matched one of the memorized song types stored from a hatching year or the following spring (Marler, 1990; Nelson and Marler, 1994).

In addition to longitudinal field studies, the studies of vocal geographic variations show that song learning is extensive in songbirds because geographic variation, a main product of such song learning, often forms population-specific features: geographic differentiation of songs among populations with similarity within populations. There are two main kinds of pattern in the geographic song variation. The first includes discrete variations of songs over distance, which forms well-defined boundaries with different song variants between neighbouring populations. The presence of boundaries among populations provides a mosaic or patchwork pattern, which are referred to as 'dialects' (Mundiger, 1982). Song dialects are transmitted through a continuing process of cultural evolution. Payne (1996) argued that the songs of indigo buntings (*Passerina cyanea*) could change either within an individual through an accumulation of improvisations ("error" or cultural "mutations"), or between individuals through immigration and extinction within a population. A few songs within a population were persisted for 10 years or longer. Song dialects mainly appear in species with small song repertoires: white-crowned sparrow (for example, *Zonotrichia leucophrys*: Orejuela and Morton, 1975; Baptista, 1977; Baker and Thompson, 1985), corn bunting (*Miliaria calandra*: McGregor 1980), redwing (*Turdus iliacus*: Bjerke and Bjerke, 1981), rufous-collared sparrow (*Zonotrichia capensis*, Handford, 1988), Smith's longspur (*Calcarius pictus*: Briskie, 1999), and orange-tufted sunbird (*Nectarinia osea*: Leader et al., 2000).

The second pattern involves gradual changes of song variants over distance, producing intergrading patterns of population-specific features between neighbouring populations, which form 'song clines'. Song clines have

been reported in quite a few species mainly with large repertoire size. For example, gradual decreases in the frequency of syllable sharing or syllable similarity are observed with increasing distance (eastern song sparrows, *Melospiza melodia*: Borror, 1965; western (California and northern Colorado) house finches, *Carpodacus mexicanus*: Bitterbaum and Baptista, 1979; Tracy and Baker, 1999; Lincoln's sparrow, *Melospiza lincolni*: Cicero and Benowitz-Fredericks, 2000); or gradual declines with distance in sharing song types among males (great tits, *Parus major*: Falls et al., 1982; McGregor and Krebs, 1982). However, little emphasis has been placed on clines to date, mainly because researchers' concerns were whether differences of song variants between populations were discrete or continuous. In addition, more attention has been paid to dialects rather than to clines because the process of cultural evolution can be properly applied to account for possible mechanisms and their functional significances of song dialects (Catchpole and Slater, 1995).

With such song variation over distance, sympatric populations may experience genetic differentiation by song dialects preventing the gene flow among dialect regions, contributing to reproductive isolation, which may promote sympatric speciation (Nottebohm 1969; Baker et al., 1981; Baker and Cunningham, 1985; MacDougall-Shackleton and MacDougall-Shackleton, 2001). The degree of bird's natal philopatry and the timing of song learning may cause difficulties in speciation among local populations. However, MacDougall-Shackleton and MacDougall-Shackleton (2001) showed song dialects played a role with some reduction in gene flow of the mountain white-crowned sparrow populations (*Zonotrichia leucophrys oriantha*). Compared with sympatric populations, song learning and cultural evolution may facilitate the rate of allopatric speciation by reducing the time for reproductive isolation through learning preferences (Lachlan and Servedio, 2004). In addition, the gradual intergradation of song divergence may form a reproductively isolated ring species in the greenish warbler (*Phylloscopus trochiloides*; Irwin, 2001).

## SONG COMMUNICATION

### Repertoire

Many birds use vocal repertoires for information exchange in the communication between sender and receiver. The whole set of structurally and functionally different types of vocalization is called repertoire, which is classified into song repertoire and call repertoire. While the term "call repertoire" usually applies to non-song birds delivering a variety of calls, "song repertoire" to songbirds delivering a set of different song types. In addition, contexts in which each call is used are inferred according to correlating response of the receiver, but such a context inference is rare

in song repertoire because songs are mainly used with relation to territorial advertisement and mate attraction.

The size of call repertoire shows three to 20 call types in many non-songbirds, in which highly social species, such as red junglefowl and ravens, tended to be larger than that of other non-social species (Sung, 1999). On the other hand, the size of song repertoire in songbirds ranges from one to several hundreds depending on species. For example, savannah sparrow (*Passerculus sandwichensis*) has only one basic pattern, song sparrow six to ten, rock wren (*Salpinctes obsoletus*) 85 to 90 (Kroosma, 1982b). The organization of timing and sequencing of song types is also unique to each species.

Song in most songbirds is a sexually dimorphic character mainly used by males in both male-male competition and in female attraction. As a result, song has been a primary target of sexual selection, which has been a major interest in female mate choice and male-male competition because the exaggerated number or complexity of song or syllable type are more efficient in attracting females and in excluding intruders from the territory (Searcy and Andersson, 1986; Read and Weary, 1992; Catchpole and Slater, 1995). Evidence for intersexual selection in the use of multiple song repertoires comes from several species (e.g. northern mockingbird, *Mimus polyglottus*: Howard, 1974; *Acrocephalus* warblers: Catchpole, 1980, 1986; Buchanan and Catchpole, 1997; wood warbler, *Phylloscopus sibilatrix*: Temrin, 1986; scarlet rosefinch, *Carpodacus erythrinus*: Björkund, 1990; pied flycatcher, *Ficedula hypoleuca*: Lampe and Saetre, 1995; European starling, *Sturnus vulgaris*: Mountjoy and Lemon, 1996; whitethroat warbler, *Sylvia communis*: Balsby, 2000; song sparrow, *Melospiza melodia*: Reid et al., 2004). The males with larger repertoires or more complex songs increased mating success by attracting females earlier in the season or by extra-pair copulation. Baker et al. (1986) suggested that females could receive reproductive benefits (e.g. resources or good genes) by choosing a male that has many song types because a larger repertoire may reflect male or territory quality. Captive females displayed more soliciting behaviour in response to more diverse songs (song sparrow, *Melospiza melodia*: Searcy and Marler, 1981). Searcy (1990) explained this result by suggesting that male song repertoires in birds may evolve because they are favored by habituation to specific stimuli in the neural response system. In field experiments, larger repertoires are more effective in deterring intruders (Krebs et al., 1978; Yasukawa, 1981; Mountjoy and Lemon, 1991). These studies suggest that sexual selection has played an important role in developing and using multiple song repertoires.

However, despite the general trend, through sexual selection, for large repertoire size, there has possibly been an evolutionary reduction in structural variation of songs of

the oropendolas and caciques (Price and Lanyon, 2004), common grackle, *Quiscalus quiscula* (Gray and Hagelin, 1996), and *Zonotrichia* sparrows (Irwin, 1988). In addition, captive females of white-throated sparrow (*Zonotrichia albicollis*) and field sparrow (*Spizella pusilla*), species with single-song repertoires, displayed no preference for large or small repertoires (Searcy and Marler, 1984). In other species, the effect of female preference for larger repertoire size disappeared after the factor of territory quality, which was confounded with repertoire size, was controlled in great tit (*Parus major*: Krebs et al., 1978; McGregor et al., 1981), red-winged blackbird (*Agelaius phoeniceus*: Yasukawa, 1981), and pied flycatcher (*Ficedula hypoleuca*: Alatalo et al., 1986).

### Individual recognition

Individual recognition is a process that a receiver learns to discriminate the differences between the individuals based on his own information. The ideal signals for the individual recognition are expected to be stereotyped within individuals and to be varied between individuals (Falls, 1982). On the contrary, species-specific traits require highly stereotyped and unvarying signals within and between individuals (Marler, 1960; Emlen, 1972; Kim and Park, 1993; Sung and Park, 1994; Cheon and Park, 1995). Individual recognition based on vocal signals between intimate pair, relatives, and neighbor individuals provides many advantages in their social relationships (Wiley and Wiley, 1977; Colgan, 1983; Beecher, 1988, 1989; Park and Chung, 2002; Chung et al., 2002). For example, breeding pairs can increase reproductive success by recognizing one another (mate recognition). The young chicks of gulls can avoid being attacked from the neighboring adults by recognizing their parents' calls (parent-young recognition). Furthermore, territorial neighbors can reduce unnecessary competition by recognizing neighbors' song (neighbor recognition). Neighbor recognition has been found in territorial species, while mate and parent-young recognition in the colonial species because visual contact in crowded condition may reduce the need for vocal recognition between neighbors (Falls, 1982).

### Neighbor recognition

Neighbor recognition includes neighbour-stranger discrimination (NSD) and neighbor-neighbor discrimination (NND). NSD requires only discrimination among songs of two classes, familiar and unfamiliar, whereas NND requires classification of familiar songs into as many sets as there are neighbors. Because recognition is a mental process of the discrimination between identities, researchers demonstrated individual recognition based on songs by comparing responses of birds to recordings of different individuals. For example, if the territory holder can tell the neighbor songs from stranger songs (the perceptual process of recognition),

he will respond more strongly to the songs of the more threatening birds (the behavioural process of discrimination). Closest approach to the playback speaker and number of flights are representative measurements clearly correlated to aggressive response.

Many researchers admitted that neighbor recognition by song is general phenomena among territorial species. However, there has been an issue on whether song repertoires interfere with neighbor recognition. Because as repertoire size increases, the similarity between songs of different males increases and the capacity of memorizing the whole song types decreases. Many efforts have been made to reveal the repertoire constraint hypothesis on species that have medium size of repertoire (1-25 song types/individual) or larger size.

Stoddard et al. (1991) showed that the males of song sparrow, which has a medium repertoire (nine average song types), responded more strongly to stranger song at either boundary (NSD) and neighbor song at the opposite boundary than to neighbor song at the usual boundary (NND). However, the males showed almost equally strong responses to any song from the center of his territory. The former result is interpreted as “dear enemy” effect: The tendency of territorial birds to display reduces aggression to familiar or trusted individuals, while the latter as “ceiling” effect: Neighbors and strangers are equally dangerous to the subject. Furthermore, Stoddard et al. (1992) performed a laboratory study to reveal whether memory constrains individual recognition in song sparrows; birds learned a large number of songs far enough to memorize the full song repertoire of their neighbors and learned later songs as quickly as they learned earlier songs. In addition to song sparrow, many species showed NSD and NND, or NSD: western meadowlark (*Sturnella neglecta*, 8 average repertoire size: Falls, 1985); European robin (*Erithacus rubecula*, 175 average repertoire size: Brindley, 1991); hooded warbler (*Wilsonia citrina*, 5.5 average repertoire size: Godard, 1991); American redstart (*Setophaga ruticilla*: Weary et al., 1992); yellow-throated bunting (*Emberiza elegans*, 17 average repertoire size: Sung and Park, 1993; Hwang and Park, 1996). However, the study of red-eyed Vireo (*Vireo olivaceus*, 50 average repertoire size: Godard 1991) and eastern meadowlark (*Sturnella magna*, 55 average repertoire size: Falls and d’Agincourt, 1981) failed for NSD. From these results, Stoddard (1996) suggested that song recognition among songbird neighbors is the rule for species with small and medium repertoires, but exceptions may exist among species with large repertoires.

## CONCLUSION

While songs or calls in non-songbirds are considered to be a result of genetic control, songs in songbirds are learned,

which results from various interactions between sender and receiver. A variety of consequences of song learning in songbirds play a critical role for the reproductive success and survival in their life history. To understand more thoroughly the process and the results of song learning, Kroodsma (1996) suggested to change the questions from how birds develop (i.e., on mechanisms) to why the songs develop the way they do (i.e., functions).

The study of song sparrows in which Beecher et al. (1998) suggested social and ecological hypothesis of song learning would be such an effort to overcome various problems in laboratory experiments. Beecher et al. (1998) reviewed how song sparrows construct and retain their song repertoire and how song communication and song learning are organized from longitudinal field studies. Furthermore, Beech et al. (2000) showed song sparrows tended to type-match early in the breeding season and repertoire-match late in the season. This result reflects that more uncertainty as to the identity of the singer or instability of territory boundaries between new neighbors leads to recognizing neighbors and their songs through countersing interactions. However, the study populations of song sparrows are quite stable and residents. As the authors pointed out, there will be different process and behaviours of song learning in migratory populations. For example, marsh wrens, which inhabit relatively stable communities of territorial males, develop songs via imitation, while sedge wrens, which inhabit relatively unstable communities, develop their songs largely via improvisation that in turn minimizes geographic variation (Kroodsma, 1996).

The comparative study of individual- and species-specific traits among populations is another important method to demonstrate the process and results of song learning because the traits serve information in detecting and memorizing differences in the vocal communication systems. For example, species-specific traits among populations will be expected to uncover macrogeographic variation because of a widespread isolating mechanism in birds (Marler and Tamura, 1964; Nottebohm, 1969; Armstrong, 1973). On the other hand, individual-specific traits among local dialects will be expected to reveal microgeographic variation because local populations keep contacting and learning each other.

Furthermore, one thing to be considered for understanding song learning and communication in birds is that the diversity of song has been evolved under various selective forces (i.e. intra- and intersexual selection) and their constraints (i.e. adapted song structures for local habitats: Morton, 1975; Brown and Handford, 2000; Sung, 2004). Despite the general trend for large repertoire size under sexual selection, recent evidence on evolutionary reduction in repertoire size among several groups of close species implicated the importance of opposing pressure of sexual

selection. To fully understand the functional significance of the song structure and usage, we need to investigate the process of the social song learning both in the field and in the well-designed lab experiments with consideration of ecological conditions.

## REFERENCES

- Abs M and Jeismann R (1988) Do courtship songs differ individually in the domestic pigeon (*Columba livia domestica*)? *Bioacoustics* 1: 151-157.
- Alatalo RV, Lundberg A, and Glynn C (1986) Female pied flycatchers choose territory quality and not male characteristics. *Nature* 323: 152-153.
- Armstrong EA (1973) A Study of Bird Song, 2nd Ed. Dover Publications Inc, New York, pp 343.
- Baker MC, Spitzer-Nabors KJ, and Bradley DC (1981) Early experience determines song dialect responsiveness of female sparrows. *Science* 214: 819-821.
- Baker MC and Cunningham MA (1985) The biology of bird-song dialects. *Behav Brain Sci* 8: 85-133.
- Baker MC and Thompson DB (1985) Song dialects of white-crowned sparrows: historical processes inferred from patterns of geographic variation. *Condor* 87: 127-141.
- Baker MC, Bjerke TK, Lampe H, and Espmark YO (1986) Sexual response of female great Tits to variation in size of males' song repertoires. *Am Nat* 128: 491-498.
- Balsby TJS (2000) Song activity and variability in relation to male quality and female choice in whitethroats *Sylvia communis*. *J Avian Biol* 31: 56-62.
- Baptista LF (1977) Geographic variation in song and dialects of the Puget Sound white-crowned sparrow. *Condor* 79: 356-370.
- Baptista LF (1996) Nature and its nurturing in avian vocal development. In: Kroodsma DE and Miller EH (eds), *Ecology and Evolution of Acoustic Communication in Birds*, Cornell University Press, New York, pp 39-60.
- Baptista LF and Morton ML (1981) Interspecific song acquisition by a white-crowned sparrow. *Auk* 98: 383-385.
- Baptista LF and Petrinovich L (1984) Social interactions, sensitive phases and the song template hypothesis in the white-crowned sparrow. *Anim Behav* 32: 172-181.
- Baptista LF and Schuchmann KL (1990) Song learning in the Anna hummingbird (*Calypte anna*). *Ethology* 84: 15-26.
- Beecher MD (1988) Kin recognition in birds. *Behav Genet* 18: 465-482.
- Beecher MD (1989) Signalling systems for individual recognition: an information theory approach. *Anim Behav* 38: 248-261.
- Beecher MD (1996) Bird song learning in the laboratory and the field. In: Kroodsma DE and Miller EH (eds), *Ecology and Evolution of Acoustic Communication in Birds*, Cornell University Press, New York, pp 61-78.
- Beecher MD, Stoddard PK, Campbell SL, and Horning CL (1996) Repertoire matching between neighbouring song sparrows. *Anim Behav* 51: 917-923.
- Beecher MD, Cambell SE, and Nordby JC (1998) The cognitive ecology of song communication and song learning in the song sparrow. In: Dukas R (ed), *Cognitive Ecology*, The University of Chicago Press, London, pp 175-199.
- Beecher MD, Cambell SE, Burt JM, Hill CE, and Nordby JC (2000) Song-type matching between neighbouring song sparrows. *Anim Behav* 59: 21-27.
- Beletsky LD (1983) An investigation of individual recognition by voice in female red-winged blackbirds. *Anim Behav* 31: 355-362.
- Bitterbaum E and Baptista LF (1979) Geographical variation in songs of California house finches (*Carpodacus mexicanus*). *Auk* 96: 462-474.
- Bjerke T and Bjerke TH (1981) Song dialects in the redwing. *Or Scand* 12: 40-50.
- Björkund M (1990) Mate choice is not important for female reproductive success in the common rosefinch (*Carpodacus erythrinus*). *Auk* 107: 35-44.
- Borror DJ (1965) Song variation in Maine song sparrows. *Wilson Bull* 77: 5-37.
- Bretagnolle V (1996) Acoustic communication in a group of nonpasserine birds, the petrels. In: Kroodsma DE and Miller EH (eds), *Ecology and Evolution of Acoustic Communication in Birds*, Cornell University Press, New York, pp 160-177.
- Brindley EL (1991) Response of European robins to playback of song: neighbour recognition and overlapping. *Anim Behav* 41: 503-512.
- Briskie JV (1999) Song variation and the structure of local song dialects in the polygynandrous Smith's longspur. *Can J Zool* 77: 1587-1594.
- Brown TJ and Handford P (2000) Sound design for vocalizations: quality in the woods, consistency in the fields. *Condor* 102: 81-92.
- Buchanan KL and Catchpole CK (1997) Female choice in the sedge warbler, *Acrocephalus schoenobaenus*: multiple cues from song and territory quality. *Proc Roy Soc Lond B* 364: 521-526.
- Byers BE (1996) Messages encoded in the songs of chestnut-sided warblers. *Anim Behav* 52: 691-705.
- Catchpole CK (1980) Sexual selection and the evolution of complex songs among warblers of the genus *Acrocephalus*. *Behaviour* 74: 149-166.
- Catchpole CK (1986) Song repertoire and the reproductive success in the great reed warbler *Acrocephalus arundinaceus*. *Behav Ecol Sociobiol* 19: 439-445.
- Catchpole CK (1987) Bird song, sexual selection, and female choice. *Trends Ecol Evol* 2: 94-97.
- Catchpole CK and Slater PJB (1995) *Bird Song. Biological Themes and Variations*. Cambridge University Press, Oxford.
- Cheon SM and Park SR (1995) Signal value of partial song (composed of 1 phrase unit) in great tits, *Parus major*: evidence from playback experiments. *Korean J Zool* 38: 230-237.
- Chung H, Lee HJ, and Park SR (2002) Individual recognition between siblings of the young Black-tailed gull (*Larus crassirostris*). *Korean J Ecol Sci* 1: 141-145.
- Cicero CC and Benowitz-Fredericks ZM (2000) Song types and variation in insular populations of Lincoln's sparrow (*Melospiza lincolni*), and comparisons with other *Melospiza*. *Auk* 117: 52-64.
- Clayton NS (1989) Song, sex and sensitive phases in the

- behavioural development of birds. *Trends Ecol Evol* 4: 82-84.
- Colgan P (1983) Comparative social recognition. John Wiley and Sons, New York.
- Emlen ST (1972) An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour* 41: 130-171.
- Endler JA (1993) Some general comments on the evolution and design of animal communication systems. *Phil Trans Roy Soc Lond B* 340: 215-225.
- Falls JB and d'Agincourt LG (1981) A comparison of neighbor-stranger discrimination in eastern and western meadowlarks. *Can J Zool* 59: 977-1009.
- Falls JB (1982) Individual recognition by sound in birds. In: Kroodsma DE and Miller EH (eds), *Ecology and Evolution of Acoustic Communication in Birds*, Cornell University Press, New York, pp 237-273.
- Falls JB, Krebs JR, and McGregor PK (1982) Song matching in the great tit (*Parus major*): the effect of similarity and familiarity. *Anim Behav* 30: 997-1009.
- Falls JB (1985) Song matching in western meadowlarks. *Can J Zool* 63: 2520-2524.
- Ficken MS, Ficken RW, and Witkin SR (1978). Vocal repertoire of the black-capped chickadee. *Auk* 95: 34-49.
- Gill FB (1995) Ornithology. W. H. Freeman and Company, New York.
- Godard R (1991) Long-term memory of individual neighbours in a migratory songbird. *Nature* 350: 228-229.
- Gray DA and Hagelin JH (1996) Song repertoires and sensory exploitation: reconsidering the case of the common grackle. *Anim Behav* 52: 795-800.
- Handford P (1988) Trill rate dialects in the rufous-collared sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Can J Zool* 66: 2658-2670.
- Howard RD (1974) The influence of sexual selection and interspecific competition on mockingbird song (*Mimus polyglottos*). *Evolution* 28: 428-438.
- Hwang BY and Park SR (1996) Neighbor-stranger discrimination of yellow-throated bunting (*Emberiza elegans*) and gray-headed bunting (*Emberiza fucata*) to playback of song. *Korean J Zool* 39: 89-97.
- Irwin DE, Bensch S, and Price TD (2001) Speciation in a ring. *Nature* 409: 33-337.
- Irwin RE (1988) The evolutionary importance of behavioural development: the ontogeny and phylogeny of bird song. *Anim Behav* 36: 814-824.
- Johnstone RA (1997) The evolution of animal signals. In: Krebs JR and Davies NB (eds), *Behavioural Ecology* Blackwell Science, Oxford, pp 155-178.
- Kim KW and Park SR (1993). The inter- and intra-specific comparison of stereotyped songs in sympatric gray-headed bunting (*Emberiza fucata*) and Siberian-meadow bunting (*Emberiza cioides*). *Korean J Ecol* 16: 317-327.
- Konishi M (1963) The role of auditory feedback in the vocal behaviour of the domestic fowl. *Z Tierpsychol* 20: 349-367.
- Krebs JR, Ashcroft R, and Webber MI (1978) Song repertoires and territory defence. *Nature* 271: 539-542.
- Krebs JR, Ashcroft R, and van Orsdol K (1981) Song matching in the great tit, *Parus major* L. *Anim Behav* 29: 918-923.
- Kroodsma DE (1982) Learning and the ontogeny of sound signals in birds. In: Kroodsma DE and Miller EH (eds), *Acoustic Communication in Birds*, Vol 2, Academic Press, New York, pp 1-23.
- Kroodsma DE (1982) Song repertoires: problems in their definition and use. In: Kroodsma DE and Miller EH (eds), *Acoustic Communication in Birds*, Vol 2, Academic Press, New York, pp 125-146.
- Kroodsma DE and Konishi M (1991) A subsong bird (eastern phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Anim Behav* 42: 477-487.
- Kroodsma DE (1996) Ecology of passerine song development. In: Kroodsma DE and Miller EH (eds), *Ecology and Evolution of Acoustic Communication in Birds*, Cornell University Press, New York, pp 3-19.
- Lachlan RF and Servedio MR (2004) Song learning accelerates allopatric speciation. *Evolution* 58: 2049-2063.
- Lade BI and Thorpe WH (1964) Dove songs as innately coded patterns of specific behaviour. *Nature* 202: 366-368.
- Lampe HM and GP Saetre (1995) Female pied flycatchers prefer males with larger song repertoires. *Behav Ecol Sociobiol* 262: 163-167.
- Lanyon WE (1957) The Comparative Biology of the Meadowlarks (*Sturnella*) in Wisconsin. Publication of Nuttall Ornithology Club No. 1, Cambridge.
- Leader N, Wright J, and Yom-Tov Y (2000) Microgeographic song dialects in the orange-tufted sunbird (*Nectarinia osea*). *Behaviour* 137: 1613-1627.
- MacDougall-Shackleton EA and MacDougall-Shackleton SA (2001) Cultural and genetic evolution in mountain white-crowned sparrows: song dialects are associated with population structure. *Evolution* 55: 2568-2575.
- Maier V (1982). Acoustic communication in the guinea fowl (*Numida meleagris*): structure and use of vocalizations, and the principles of message coding. *Z Tierpsychol* 59: 29-83.
- Marler P (1956) The voice of the chaffinch and its function as a language. *Ibis* 98: 231-261.
- Marler P (1960) Bird songs and mate selection. In: Lanyon WE and Tavolga WN (eds), *Animal Sounds and Communication*, Publ. 7, American Institute of Biological Sciences, Washington, pp 348-367.
- Marler P (1970) A comparative approach to vocal learning: song development in white-crowned sparrows. *J Comp Physiol Psychol* 71: 1-25.
- Marler P (1977) The structure of animal communication sounds. In: Bullock TH (ed), *Workshop on Recognition of Complex Acoustic Signals*, Abacon, Berlin, pp 17-35.
- Marler P and Tamura M (1964) Song dialects in three populations of white-crowned sparrows. *Condor* 64: 368-377.
- Marler P and Peters S (1977) Selective vocal learning in a sparrow. *Science* 198: 519-521.
- Marler P (1990) Song learning: the interface between behavior and neuroethology. *Proc Roy Soc Lond B* 329: 109-114.
- Martin EJ (1977) Songs of the fox sparrow. I. Structure of song and its comparison with other Emberizidae. *Condor* 79: 209-221.
- McGregor PK (1980) Song dialects in the corn bunting (*Emberiza calandra*). *Z Tierpsychol* 54: 285-297.
- McGregor PK, Krebs JR, and Perrins CM (1981) Song repertoires and lifetime reproductive success in the great tit (*Parus*

- major). *Am Nat* 118: 149-159.
- McGregor PK and Krebs JR (1982) Song types in a population of great tits (*Parus major*): their distribution, abundance and acquisition by individuals. *Behaviour* 79: 126-152.
- Miller EH (1986) Components of variation in nuptial calls of the least sandpiper (*Calidris minutilla*; Aves, Scolopacidae). *Syst Zool* 35: 400-413.
- Miller EH (1992) Acoustic signals of shorebirds: a survey and review of published information. Technical Report, Royal British Columbia Museum, Victoria.
- Morton ES (1975) Ecological sources of selection on avian sounds. *Am Nat* 109: 17-34.
- Mountjoy DJ and Lemon RE (1991) Song as an attractant for male and female starlings, and the influence of song complexity. *Behav Ecol and Sociobiol* 28: 97-100.
- Mumford RE (1952) Meadowlark with tow songs. *Indiana Audubon Quart* 30: 11-12.
- Mundinger PC (1982) Microgeographic and macrogeographic variation in the acquired vocalizations of birds. In: Kroodsma DE and Miller EH (eds), *Acoustic Communication in Birds*, Vol 2, Academic Press, New York, pp 147-208.
- Nelson DA and Marler P (1994) Selection-based learning in bird song development. *Proc Natl Acad Sci USA* 91: 10498-10501.
- 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 and Nottebohm ME (1971) Vocalizations and breeding behaviour of surgically deafened ring doves (*Streptopelia risoria*). *Anim Behav* 19: 313-327.
- Nottebohm F (1975) Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. *Am Nat* 109: 35-50.
- Oring LW (1968) Vocalizations of the green and solitary sandpipers. *Wilson Bull* 80: 395-420.
- Park SR and Park DS (1996) Does the bush warbler (*Cettia diphone*) defend its territory through a particular song mode or a mode sequene? *Korean J Zool* 39: 282-291.
- Park SR and Park DS (1997) Acoustic communication of the black-tailed gull (*Larus crassirostris*): the structure and behavioral context of vocalizations. *Korean J Biol Sci* 1: 565-569.
- Park SR, Han ED, and Sung HC (1999) Definition and function of two song types of the bush warbler (*Cettia diphone borealis*). *Korean J Biol Sci* 3: 149-151.
- Park SR and Park DS (2000) Song type for intrasexual interaction in the bush warbler. *Auk* 117: 228-232.
- Park SR and Chung H (2002) How do young black-tailed gulls (*Larus crassirostris*) recognize adult voice signals? *Korean J Biol Sci* 6: 221-225.
- Payne RB (1982) Ecological consequences of song matching: breeding success and intraspecific song mimicry in indigo buntings. *Ecology* 63: 401-411.
- Payne RB (1990) Song mimicry by the village indigobird (*Vidu chalybeata*) of the red-billed firefinch (*Lagonosticta senegalensis*). *Vogelwarte* 35: 321-328.
- Payne RB (1996) Song traditions in indigo buntings: origin, improvisation, dispersal, and extinction in cultural evolution. In: Kroodsma DE and Miller EH (eds), *Ecology and Evolution of Acoustic Communication in Birds*, Cornell University Press, New York, pp 198-220.
- Price JJ and Lanyon SM (2004) Patterns of song evolution and sexual selection in the oropendolas and caciques. *Behav Ecol* 15: 485-497.
- Read AF and Weary DM (1992) The evolution of bird song: comparative analyses. *Phil Trans Roy Soc Lond B* 338: 165-187.
- Reid JM, Arcese P, Cassidy ALEV, Hiebert SM, Smith JNM, Stoddard PK, Marr AB, and Keller LF (2004) Song repertoire size predicts initial mating success in male song sparrows, *Melospiza melodia*. *Anim Behav* 68: 1055-1063.
- Riska DE (1986). An analysis of vocal communication in the adult brown nodydy (*Anous stolidus*). *Auk* 103: 359-369.
- Rothstein SI and Fleischer RC (1987) Vocal dialects and their possible relation to honest status signalling in the brown-headed Cowbird. *Condor* 89: 1-23.
- Searcy WA (1990) Song repertoire and mate choice in birds. *Amer Zool* 32: 71-80.
- Sercy WA and Marler P (1981) A test for responsiveness to song structure and programming in female sparrows. *Science* 213: 926-928.
- Sercy WA and Marler P (1984) Interspecific differences in the response of female birds to song repertoires. *Z Tierpsychol* 66: 128-142.
- Searcy WA and Andersson M (1986) Sexual selection and the evolution of song. *Annu Rev Ecol Syst* 17: 507-533.
- Siegel PB, Phillips RE, and Folsom EF (1965) Genetic variations in the crow of adult chickens. *Behaviour* 24: 229-235.
- Smith WJ (1977) *The Behavior of Communicating: An Ethological Approach*. Harvard University Press, Cambridge.
- Smith WJ (1990) Communication and expectations: a social process and the cognitive operations it depends upon and influences. In: Bekoff M and Jamieson D (eds), *Interpretation and Explanation in the Study of Animal behavior*, Vol. 1, Interpretation, Intentionality and Communication. Westview Press, Colorado, pp 234-253.
- Sordahl TA (1979) Vocalizations and behavior of the willet. *Wilson Bull* 91: 551-574.
- Stoddard PK, Beecher MD, Horning CL, and Campbell SE (1991) Recognition of individual neighbors by song in the song sparrow, a bird with song repertoires. *Behav Ecol Sociobiol* 29: 211-215.
- Stoddard PK, Beecher MD, Campbell SE, and Horning CL (1992) Memory does not constrain individual recognition in a bird with song repertoires. *Behaviour* 122: 274-287.
- Stoddard PK (1996) Vocal recognition of neighbors by territorial passerines. In: Kroodsma DE and Miller EH (eds), *Ecology and Evolution of Acoustic Communication in Birds*, Cornell University Press, New York, pp 356-374.
- Studholme BJS (1994) Parent-offspring recognition in the fiordland crested penguin (*Eudyptes pachyrhynchus*). *N Z Nat Sci* 21: 27-36.
- Sung HC and Park SR (1993) Neighbor recognition by song in the yellow-throated bunting (*Emberiza elegans*). *Korean J Behav Biol* 2: 45-54.
- Sung HC and Park SR (1994) The study of species recognition on the basis of song by yellow-throated bunting (*Emberiza elegans*). *Korean J Zool* 37: 573-579.
- Sung HC (1999) *Vocal Communication and Individuality of*



- Piping Plovers (*Charadrius melodus*): Description, Quantification, and Application for Management. Ms. Thesis, Memorial University of Newfoundland, St. John's, pp 1-107.
- Sung HC (2004) Song Variation and Male Reproductive Success in the Savannah Sparrow Songs, *Passerculus sandwichensis*. Ph. D. Thesis, University of Western Ontario, London, pp 1-186.
- Sung HC, Miller EH, and Flemming SP (2005) Breeding vocalizations of piping plover (*Charadrius melodus*): repertoire organization and structure. *Can J Zool*: in press.
- Temrin H (1986) Singing behaviour in relation to polyterritorial polygyny in the wood warbler (*Phylloscopus sibilatrix*). *Anim Behav* 34: 146-157.
- Thielcke G (1970) Die sozialen Funktionen der Vogelstimmen. *Vogelwarte* 25: 204-229.
- Tracy TT and Baker MC (1999) Geographic variation in syllables of house finch songs. *Auk* 116: 666-676.
- Trainer JM and McDonald DB (1993). Vocal repertoire of the long-tailed manakin and its relation to male-male cooperation. *Condor* 95: 769-781.
- Wanker R, Apcin J, Ennerjahn BJ, and Aibel BW (1998) Discrimination of different social companions in spectacled parrotlets (*Forpus conspicillatus*): evidence for individual vocal recognition. *Behav Ecol Sociobiol* 43: 197-202.
- Weary DM, Lemon RE, and Perreault S (1992) Song repertoires do not hinder neighbor-stranger discrimination. *Behav Ecol Sociobiol* 31: 441-447.
- Wiley RH and Wiley MS (1977) Recognition of neighbors' duets by stripe-backed wrens, *Campylorhynchus nuchalis*. *Behaviour* 62: 10-34.
- Wiley RH (1983) The evolution of communication: information and manipulation. In: Halliday TR and Slater PJB (eds), *Animal Behaviour*, Vol 2, Blackwell Scientific Publications, Oxford, pp 156-189.
- Yasukawa K (1981) Song repertoires in the red-winged blackbird (*agelaius phoeniceus*): a test of the Beau Geste hypothesis. *Anim Behav* 29: 114-125.
- Ydenberg RC, Giraldeau LA, and Falls JB (1988) Neighbours, strangers, and the asymmetric war of attrition. *Anim Behav* 36: 343-347.

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