Etología, 3:113-123 (1993)

Ecological aspects of passerine song development. A personal perspective

D.E. Kroodsma

Department of Biology, University of Massachusetts, Amherst MA 01003-0027 U.S.A

ABSTRACT. *Ecological aspects of passerine song development.*- The diversity of singing behaviors and their ontogenies among passerine birds must have co-evolved with other life-history parameters, but identifying the forces involved is a challenge. Perhaps the biggest mystery is the evolution of vocal imitation itself in the ancestral oscine, and why lineages within the suboscine sister group have retained the presumably more primitive form of neural control and a non-imitative vocal ontogeny. Oscine singing behaviors and song ontogenies are extraordinarily diverse, and the comparative method provides a window on understanding both current function and evolutionary history. Studying different populations of the same species (e.g., wrens) or different song forms of the same individuals (paruline warblers and a chickadee), for example, suggests that intra- and inter-sexual forces have strongly influenced the relative variability of vocal signals.

KEY WORDS. Song, Development, Ecology, Passerine

Introduction

One of my favorite images of our small, beautiful world is of morning's first light sweeping around the globe, continuously, relentlessly, forever circling and returning to repeat the cycle. Always, somewhere, it is dawn, and always, somewhere, the birds are singing. Short songs, long songs. Simple songs, complex songs. Musical songs, harsh songs. Our earth sings like a giant player piano, with that first light evoking from each individual the extraordinary sounds that greet a new day.

Each sound is but part of each individual's effort to manage its social affairs to its own advantage, but why the tremendous diversity? The diversity seems far too great to attribute simply to a selection for species distinctiveness (see also Payne, 1983; West-Eberhard, 1983), so we are forced to ask how ecological and social circumstances within lineages have helped to design signals that differ so much. How has song, within each lineage, co-evolved with other life-history parameters, and how has the ontogeny of song been shaped to produce these successful signals?

Questions are easy, but answers are few. We have just begun to survey the variety of developmental strategies among birds, and relating the species differences to ecological circumstances is more of a dream than a reality. My approach is comparative, in that I ask questions about why different lineages (often sister groups) or even different individuals within a lineage use different signals and how song ontogeny has achieved those differences (Kroodsma, 1988a). In other words, I try to document differences in song development, and then try to make some sense of how and why those differences exist and arose. In the broad sense, I study "constraints," in both the negative and positive sense of the word (Gould, 1989); I'm interested in how developmental constraints might limit the directions in which natural selection is able to pull signals, how development is dictated by past history (and perhaps current conditions), and ultimately how these processes were and are influenced by ecological circumstances.

The oscine/suboscine split, or why (not) imitate?

Of greatest intrigue to me is why song development in the passerine sister suborders, the oscines and the suboscines, is so fundamentally different. The songbirds, of course, are the stuff of which textbooks are made. These songbirds must learn their songs from adult conspecifics, much as we learn our spoken language from adult conspecifics (Kroodsma & Baylis, 1982; Slater, 1988; Marler, 1991). The suboscines are less well-known. They are a mostly New World suborder, and include about 1000 mostly Neotropical species, such as flycatchers, antbirds, ovenbirds, woodcreepers, and the like. Unlike the songbirds, these suboscines apparently include no imitative process in their song development.

Three studies of suboscine song ontogeny have now failed to reveal any evidence of vocal imitation. In the first, I hand-reared, from about 10 days of age, alder and willow flycatchers (two sibling species, *Empidonax alnorum* and *E. traillii*) and eastern phoebes (*Sayornis phoebe*). Birds were deprived from hearing their own songs, and some were tutored with songs of another flycatcher. No interspecific learning occurred, and songs of individuals appeared normal in all respects (Kroodsma, 1984, 1985a).

In a second experiment, I attempted to influence, via both tape- and live-tutoring, the fine details of songs developed by hand-reared eastern phoebes (Kroodsma, 1989a). Again, I failed to demonstrate any form of vocal imitation, and each phoebe produced normal songs, but birds did not match any details of the tutor tape or of other phoebes in the immediate social environment.

The third experiment was intended to be the final test (Kroodsma & Konishi, 1991). Songbirds, we know, rely on their hearing during two phases of song learning. A bird must first hear and memorize the song, and later he must recall that sound, practice vocalizing it, and monitor that practice via auditory feedback, i.e., the bird listens to itself sing and improves the output to match the memory trace (Marler & Nelson, 1992). Interrupting the auditory feedback by deafening a songbird before it has crystallized its adult song destroys the ability to sing normal songs (Konishi, 1965). Our final test with a flycatcher was thus to deafen one, to see if it still developed normal songs. Again we failed to find any evidence of imitation. Eastern phoebes, in spite of being deafened at about 40 days of age (before they come into adult song), still developed normal phoebe songs. In short, the three experiments reveal that, unlike songbirds, these suboscines 1) do not need conspecific instruction after 10 days of age, 2) would not attend to details of tutor songs in the laboratory, and 3), most importantly, required no hearing to develop normal adult songs.

Why these suboscines don't learn can be addressed on both a proximate and ultimate level. Proximately, the answer seems rather simple: suboscines appear to lack the brain for the imitative task. Songbirds learn and then produce that imitated song by using an intricate neural network of brain nuclei, found primarily in the forebrain (Konishi, 1989; Gahr et al., 1993). The brains of suboscines, however, are very different, and lack these song control centers (Nottebohm, 1980; Kroodsma & Konishi, 1991). Rather, a different developmental strategy for song appears in some of these suboscines; in alder flycatchers, for example, fledglings use a call (an unstable "fee-bee-o") when they are separated from one another, and it is this (nonlearned) call that is the direct antecedent of the adult song, the crisp "fee-bee-o" so typical of this species throughout North America (Kroodsma, 1984).

In the ultimate sense, then, what happened in the evolutionary history of these two lineages? If the Passeriformes are truly a monophyletic group (Raikow, 1982), and if the suboscines and oscines are monophyletic lineages within the passerines (Sibley et al., 1988), then the songbird ancestor acquired the ability to imitate but the suboscine ancestor did not. Why, or why not? And why did that single, common ancestor of songbirds learn to imitate (the most parsimonious explanation is that vocal learning arose once among the songbirds), but none of the suboscine lineages have since then?

The origins of vocal learning among the passerines remains a mystery (Nottebohm, 1972). Although we can list the two most obvious consequences (to us, anyway) of this difference in song development, that songbirds can have larger (sometimes enormous) song repertoires and learned song dialects (Krebs & Kroodsma, 1980), we cannot infer that selection for these characteristics necessarily led to song learning. Perhaps the learning originated for some far more subtle reason, such as controlling inner ear damage during production of loud vocalizations (Nottebohm, 1991). If flycatchers were to abandon their risk-free song development, an individual's song would neither be a direct reflection of his genes nor identify him to his home population. Although some have argued that song learning among songbirds has promoted speciation (Baker & Cunningham, 1985), others have argued that the data don't strongly support that hypothesis (Baptista & Trail, 1992). To accept chance as the "force" that led to this suboscine/oscine difference is a last resort to a Darwinian biologist, but it should be one of our multiple (though untestable) hypotheses for the evolutionary origins of vocal learning among passerines.

Whatever the reasons, these nonlearned songs of flycatchers are relatively simple, repertoires are small, and geographic variation is minimal. These traits are what one would expect of a behavior that seems to be encoded securely in the genome.

Songbirds: an introduction

The songbirds, which comprise about 4/9 of all birds, are the favorite textbook examples of song learning, relationships between cultural and biological evolution, neural control of song, song dialects, the parallels between bird song and human speech, geographic variation, and much, much more. Classic studies of song development have revealed that songbirds need to hear conspecifics after 10 days of age, that they must be able to hear themselves, that they are typically influenced by tutor tapes or social partners in the laboratory, and that they learn not only what but also how to sing (West & King, 1988; Slater, 1989; Marler, 1991).

The oscine potential and the constraints on suboscines are perhaps best illustrated by the winter wren (*Troglodytes troglodytes*). Across Eurasia, male wrens sing six to seven enormously complex songs (Kreutzer, 1974; Kroodsma & Momose, 1991). In this small wren, the remarkable achievement of song learning is evident, and the contrast with the simple songs and small repertoires of flycatchers and other suboscines is striking.

The wren also illustrates how we might exploit the comparative method in trying to understand such vocal complexity. Two song populations of this wren, currently classified as belonging to the same species, occur in North America. The wrens in eastern North America typically have only one to two songs, less than half those of their European counterparts, but the wrens of western North America have 12-15 basic songs, twice as many as their European cousins, and frequent song hybrids are used to produce an immense diversity of song forms (Kroodsma, 1980). Why the differences among populations? Have ecological differences in these three regions of the Holarctic encouraged or inhibited the differences?Do we look first at sexual selection (Catchpole, 1987)? Perhaps resources are more monopolizable in some populations than others, and song is a medium by which males demonstrate or exert prowess. Or perhaps developmental time varies among populations, with juveniles of populations with small song repertoires having little time to learn their songs before departing on a migratory journey; with more time in permissive environments, selection may have encouraged the mastering of greater vocal complexity, so that now individuals from different populations differ in their ability to learn large or complex songs (Kroodsma & Canady, 1985). Or perhaps the number of competing heterospecific singers (Kroodsma, 1985b), perhaps together with the relative complexity of the physical environment through which sound must be transmitted (Wiley & Richards, 1978; Morton et al., 1986), additionally constrains or releases signals in different environments. We have many hypotheses, but no concrete answers. Welcome to the songbirds!!

Sibling lineages of the marsh wren

One species in which I have been studying vocal development in two different populations is the marsh wren (*Cistothorus palustris*). The quality of songs is different in the two populations; songs from eastern North America are more liquid and less harsh than those of western North America, and songs of the two populations have characteristically different introductory and concluding notes, too. Eastern males learn to sing about 50 songs apiece, but western males learn about three times that, or about 150. Presumably to control their larger repertoires, western males also have larger song control nuclei in their forebrains than do eastern males (Canady et al., 1984; Kroodsma & Canady, 1985; Kroodsma, 1989b).

In a laboratory experiment, we have shown that the quality of the songs is culturally transmitted, but that the ability to learn large repertoires is based on genetic differences. Western nestlings from California and eastern nestlings from New York were raised under identical settings in the laboratory. Tutored with a mixture of 50 eastern and 150 western songs, the males of the two populations learned each others' songs from the tape, but western males learned about three times as many songs as did the eastern males. The western yearlings also developed larger song control nuclei than did their eastern counterparts (Kroodsma & Canady, 1985).

So dependent are juvenile wrens on their auditory environment that their repertoires can be easily manipulated in the laboratory. If an eastern wren is tape-tutored with, say, five song types, he will develop, on average, only five types. If he hears 10, 20, 30, or 40 types, he'll likely develop about as many as he hears. Beyond 40, the males falter, and in the laboratory they reach their maximum repertoires somewhere between 40 and 50. Below five song types, however, an endogenous program seems to promote the development of repertoires larger than the male hears. Males tutored with only one type develop on average about 12 types, and those hearing no songs improvise about 20 types apiece; these improvised songs, especially for males that have heard no songs, are typically highly abnormal (Kroodsma & Pickert, 1980; Kroodsma, unpubl. data).

In the northern Great Plains of North America, these eastern and western populations co-occur. In Saskatchewan marshes, where these wrens are "interspecifically" territorial, they maintain large differences in repertoire size and they maintain, for the most part, their pure eastern or western singing traditions. Eastern style singers tend to weigh about 10% more than western males, and, not surprisingly, they maintain their genetic distinctiveness, with adjacent eastern and western style singers more similar to wrens from populations on the Atlantic and Pacific coast, respectively, than to each other. Two males, each banded as a nestling in a territory of a male singing western songs, each developed pure western repertoires, despite numerous eastern males in the neighborhood. Given the ability of these birds to learn each others' songs in the laboratory, we can conclude that social interactions in nature must guide learning and maintenance of song differences in these sympatric populations, so that young males learn to sing almost exclusively songs of their own kind. Females, too, must learn to identify males of their own kind, so that the offspring produced in these mixed populations remain true, both behaviorally and genetically, to one lineage or the other. Genetic and cultural differences that undoubtedly arose in allopatry are thus largely maintained where these two wrens meet (Albright, Braun, Winslow, and Kroodsma, unpubl. data).

For these two wren evolutionary units (they were almost certainly isolated from each other by glaciation events, and only recently have recontacted each other), several ecological factors may have placed a premium on song and more complex singing behaviors among western birds. Western males often occur on relatively small territories, within which they can acquire sizeable harems of females (Verner, 1965). Presumably songs play some role in acquiring or maintaining these resources necessary for breeding, and the apparently higher variance in male reproductive success among western birds may have led to an escalation of singing behaviors, too (Verner, 1976). Additionally, males in a larger percentage of western populations seem to be sedentary or stay on their territories longer than do eastern males; if a longer uninterrupted time for song development plays a role in developing larger, more complex song repertoires, then western males would also have the edge.

Population differences in repertoire size, sometimes associated with differences in the extent of song sharing with neighbors, may have arisen under similar circumstances among other songbird species. The rufous-sided towhee (*Pipilo erythrophthalmus*), for example, is a widespread North American species. Males in sedentary populations of Oregon and Florida (western and southeastern United States) have larger song repertoires and neighboring males possess more similar songs than do males in the migratory populations of the northeastern United States (review in Ewert & Kroodsma, in press). The red-winged blackbird (*Agelaius phoeniceus*) also occurs throughout North America; although repertoire size seems relatively constant among populations, the degree of song sharing appears higher among the more sedentary populations of California and Florida than among northeastern migratory populations (Kroodsma & James, in press). Repertoire size among North American white-crowned sparrow (*Zonotrichia leucophrys*) populations is also constant (one song type/male), but extent of sharing with neighbors in sedentary populations is greater than in migratory populations (Baptista, 1975, 1977).

Comparative approach within individual birds

Using the comparative approach to understand behavioral differences among different lineages (such as suborders, families, or conspecific populations) is useful, but I believe we can go one step better. Different learned vocalizations of the same individual can differ in the extent of geographic variation, with local dialects in one sound but not another. We are thus compelled to examine closely the function of those vocalizations and the underlying strategies of vocal development, all in an attempt to understand the ecological and social forces that led to these geographic and developmental differences.

Among songbirds, investigators have been obsessed with two consequences of song learning: repertoires of song types, with males having multiple variations of their songs, and microgeographic song variation (usually referred to as dialects), with males at one location using songs more like one another than like males at more distant locations (Krebs & Kroodsma, 1980). The puzzle, then, is why some songbirds abandon this rich oscine heritage and potential, foregoing large repertoires, geographic variation, or both, and thereby behave more as if they were suboscine flycatchers. My colleagues and I have been working with several of these species.

Unlike most songbirds, which seem to use the same multi-purpose songs in a variety of circumstances, paruline warblers in North America use different songs in different contexts (Gill & Murray, 1972; Ficken & Ficken, 1967; Lein, 1978; Morse, 1989). The chestnut-sided and blue-winged warblers (*Dendroica pensylvanica* and *Vermivora pinus*), for example, use one category of song form that is remarkably stereotyped throughout the geographic range of the species (Kroodsma, 1981). In the blue-wing, the single song form is rendered "bee-bzzzz," sounding as if the bird is inhaling on the first and exhaling on the second phrase. With the chestnut-sided warbler, however, each male typically uses three different songs from a species-wide pool of about five types; all five types can occur at a given location, but little geographic variation occurs in these basic song forms (Byers, unpubl. data).

The warblers have a second category of song form, however; used primarily in aggressive encounters (Morse, 1970), these songs vary among populations. Each chestnut-sided warbler, for example, has a small repertoire of these "B" songs, and each song form is restricted to a relatively small area, occurring on a maximum of four or five contiguous territories (though the elements within the song can have a broader distribution). The B repertoires of individuals even change from year to year, with changes usually increasing the similarity of the B repertoire to those of current or former neighbors (B. E. Byers, unpubl. data). Warblers themselves seem to recognize dialects in these aggressive songs but not in the more intersexual songs (Kroodsma et al., 1984).

These two warbler species, unlike many species of songbirds, have difficulty learning songs in tape-tutor environments in the laboratory. Blue-winged warblers, in spite of being tutored with a typical song form from each of their two song categories, developed highly abnormal songs (Kroodsma, 1988b). With the chestnut-sided warblers (Byers & Kroodsma, 1992), social experience with adult males seemed necessary for learning the geographically variable song forms, those used in an intrasexual, male-male context. The geographically invariant songs, however, used more in intersexual contexts, were learned more readily from simple tape-tutoring experiences. These data suggest that song development, at least for the chestnut-sided warbler, is somewhat compartmentalized, with intersexual songs perhaps more restricted by some form of neural selection (Marler & Nelson, 1992) and the intrasexual songs more dependent on social interaction with singing males (Pepperberg, 1985).

The intended audience for each song form must dictate, in some way, the details of song structure. The intrasexual signals used by these warblers in aggressive situations vary geographically, and the audience that shapes these vocalizations consists of males in the local neighborhood. Among songbirds, this pattern of local dialects has been documented frequently. In contrast, forces that constrain the warbler songs used in more intersexual contexts transcend local, immediate audiences, and seem to extend over broad geographic areas, yielding a geographic distribution much like that of the invariant songs of the suboscine flycatchers. Whether these song distributions are cultural evidence of a larger social cohesiveness, or whether these larger vocal geographies map onto genetically-defined evolutionary units is unknown.

If processes operating among these warblers are general and occur among other songbirds, we should find evidence for similar ontogenies and geographic distributions in other groups, too. The black-capped chickadee (*Parus atricapillus*) may provide such an example (review in Kroodsma et al., in press). This chickadee uses a single song form, the whistled "fee-bee," which seems as remarkably invariant throughout its broad geographic range in North America as does the "fee-bee-o" of the alder flycatcher. The "fee-bee" songs typically consist of two whistled components, each of which is about 0.4 sec in duration. The first whistle is slurred downward, perhaps through 200 Hz from start to end, and the second whistle then begins immediately about 400 Hz lower. A brief drop in amplitude usually (always?) occurs at the midpoint of the second whistle, thus making "fee-bee-ee" a more appropriate rendering of the song than "fee-bee." These basic features of the "fee-bee-ee" song occur over much of the North American continent. This relatively invariant song is used as the general advertising song, much like the invariant songs of the warblers.

In more aggressive contexts, however, the chickadee uses another vocalization, sometimes called a "gargle" (Ficken et al., 1987). This gargle, like the aggressive songs of the warblers, also varies microgeographically. The overall parallels with the warblers are intriguing.

As with the warblers, vocal development does not proceed smoothly in the laboratory. In nature, some force constrains the usual songbird potential and produces highly stereotyped songs, both among individuals and over time and space, but whatever this proximate force is, it is not easy to duplicate in the laboratory. We have tried several different rearing environments for the chickadees, for example, but as yet we have no chickadees singing normal "fee-bee-ee" songs. Those environments included the following: 1) tutoring two males with a sequence of normal conspecific "fee-bee-ee" songs, in a room with male and female Carolina chickadees (*Parus carolinensis*) but with no female black-caps; 2) tutoring a single male with Carolina chickadee songs, in a room with female black-caps and male and female Carolina chickadees; 3) tutoring all-male or mixed-sex groups of black-capped chickadees with the normal "fee-bee-ee" and with 3 derivatives of the normal song ("bee-ee-fee," "bee-ee-bee-ee," and "fee-fee"). In condition 3, conspecific males sang highly abnormal songs, but they did at least converge in their song forms so that males within the same groups sang similar songs. They converged, too, in their gargles, though they had not been tutored with any on the tapes. Social influences of siblings thus provided the necessary dynamics for group conformity but not for producing normal songs (Kroodsma et al., in press).

With both the warblers and the chickadee, it seems that social forces of some kind constrain the inherent songbird ability to produce a wider variety of sounds. Intersexual forces are implicated, as they are in a series of experiments with the brown-headed cowbird (*Molothrus ater*; West & King, 1988). We must next try to understand more fully what these forces are, through what evolutionary circumstances they arose, why they are more prominent in some species than others, and why they exist for some song forms within individuals and not others. Although the hypothesis that local song dialects limit gene flow in a species like the white-crowned sparrow has not been widely accepted (e.g., Hafner & Petersen, 1985), perhaps these nonlocal, geographically invariant songs do represent evolutionary units in some broader way.

Conclusions and Summary

Documenting some of the essential components of song development in the laboratory may be relatively easy, but identifying the ecological forces that have limited, enabled, or encouraged (i.e., constrained, broadly defined) particular styles of development is especially challenging. Questions abound:

1. The evolution of vocal imitation, presumably from some suboscine-like, risk-free vocal development, remains an enigma. Perhaps surveys of vocal variation and development in other suboscine groups, especially in the neotropics, will help solve this mystery.

2. Why do some songbirds, such as a winter wren, need an extraordinarily complex song, but a black-capped chickadee manages his affairs with a simple, learned song?

3. Does sexual selection explain extravagance in vocal signals? All other parameters held constant, does complexity of signals increase with variance in male reproductive success, as it seems to in the two marsh wren song populations?

4. Could the same "end" be achieved by different "means"? Songbirds have at least two ways to generate geographically invariant signals, for example: a) by restrictive imitative processes, perhaps guided by some kind of neural selection (Marler & Nelson, 1992), as illustrated by the black-capped chickadee's "fee-bee-ee" and the A songs of certain warblers (Kroodsma, 1981); and b) by extensive improvisation, in which some non-imitative internal program generates highly variable yet species-typical songs (e.g., sedge wren, *Cistothorus platensis*, Kroodsma & Verner, 1978; and perhaps the gray catbird, *Dumetella carolinensis*, Kroodsma, unpubl. data). Are these alternative means to the same end, a geographically invariant signal, or are the ends only superficially similar? Perhaps the first method can handle only a few songs (up to five in the chestnut-sided warbler), but the second can generate a hundred or more patterns.

5. If songs are multipurpose, serving, as in most songbirds, both intra- and inter-sexual functions, are the forces from the two sexes disruptive, so that one force (intrasexual) promotes variability but the other (intersexual) promotes stereotypy? Certain warblers suggest that scenario (Byers & Kroodsma, 1992), as do brown-headed cowbirds (West & King, 1988) and perhaps a chickadee (Kroodsma et al., in press). And could dispersal distances and the homogeneity of genetic backgrounds among individuals and populations influence which force has more influence on song variability?

As a Darwinian biologist, I want to believe that ecological circumstances provided the context in which the diversity of passerine singing behaviors, together with their accompanying ontogenies, evolved. I want to believe that some day we will be able to chart the multiple forces and plot, in multi-dimensional space, how these forces produced the diversity of ontogenies and singing behaviors. Our only window on this historical process is to document current function among a variety of taxa and hope that patterns emerge, patterns from which we can try to reason explicitly about how selection worked to create what we see. Clearly we've just begun our task.

Resumen

Aspectos ecológicos del desarrollo del sonido de paseriformes.

La diversidad de comportamientos canoros y sus ontogenias en paseriformes debe haber coevolucionado con otros parámetros de ciclos de vida, pero la identificación de las fuerzas involucradas es un desafio. Quizás el mayor misterio es la evolución de la imitación vocal en el oscine ancestral, y porqué los linajes dentro del grupo hermano suboscine han retenido la presumiblemente forma mas primitiva de control neural y una ontogenia vocal no imitativa. Los comportamientos de canto de los oscine y las ontogenias de sonido son extraordinariamente diversas y el método comparativo aporta una visión para entender tanto la función actual como la historia evolutiva. El estudio de diferentes poblaciones de la misma especie (por ejemplo chochines) o diferentes formas de sonido de los mismos individuos (mosquiteros parulínidos y un parido), por ejemplo, sugieren que las fuerzas intra e inter sexuales han influenciado fuertemente la variabilidad relativa de las señales vocales.

Acknowledgements

I thank Tomás Redondo and all of the gracious Spanish hosts for their invitation to attend the IEC and for their frequent help. My research is funded by the NSF (BNS-9111666). I especially thank Melissa Kroodsma for her tireless efforts in hand-rearing the baby birds.

References

Baker, M.C. & Cunningham, M.A., 1985. The biology of bird-song dialects. *Behav. Brain Sci.*, 8:85-133.

Baptista, L.F., 1975. Song dialects and demes in sedentary populations of the white-crowned sparrow *(Zonotrichia leucophrys nuttalli). Univ. Calif. Publ. Zool.,* 105:1-52.

Baptista, L.F., 1977. Geographic variation in song and dialects of the Puget Sound white-crowned sparrow. *Condor*, 79:356-370.

Baptista, L.F. & Trail, P.W., 1992. The role of song in the evolution of passerine diversity. *Syst. Biol.*, 41:242-247.

Byers, B.E. & Kroodsma, D.E., 1992. Development of two song categories by chestnut-sided warblers. *Anim. Behav.*, 44:799-810.

Canady, R.A., Kroodsma, D E. & Nottebohm, F., 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., 1987. Bird song, sexual selection and female choice. *Trends Ecol. Evol.*, 2:94-97.

Ewert, D.N. & Kroodsma, D.E., (in press). Song sharing and repertoires among migratory and resident Rufous-sided Towhees. *Condor.*

Ficken, M.S. & Ficken, R.W., 1967. Singing behaviour of blue-winged and golden-winged warblers and their hybrids. *Behaviour,* 28:149-181.

Ficken, M.S., Weise, C.M. & Reinartz, J.A., 1987. A complex vocalization of the black-capped chickadee: repertoires, dominance and dialects. *Condor*, 89:500-509.

Gahr, M., Güttinger, H-R. & Kroodsma, D.E., 1993. Estrogen receptors in the avian brain: survey reveals general distribution and forebrain areas unique to songbirds. *J. Comp. Neurology*, 327:112-122.

Gill, F.B. & Murray, B.G.,Jr., 1972. Song variation in sympatric blue-winged and golden-winged warblers. *Auk*, 89:625-643.

Gould, S.J., 1989. A developmental constraint in *Cerion*, with comments on the definition and interpretation of constraint in evolution. *Evolution*, 43:516-539.

Hafner, D.J. & Petersen, K.E., 1985. Song dialects and gene flow in the white-crowned sparrow *(Zonotrichia leucophrys nuttalli). Evolution*, 39:687-694.

Konishi, M., 1965. The role of auditory feedback in the control of vocalization in the white-crowned sparrow. *Z. Tierpsychol.*, 22:770-783.

Konishi, M., 1989. Birdsong for neurobiologists. *Neuron*, 3:541-549.

Krebs, J.R. & Kroodsma, D.E., 1980. Repertoires and geographical variation in bird song. In: *Adv. Study Behav.*, Vol. 11: 143-177 (J.S. Rosenblatt, R.A. Hinde, C. Beer & M.C. Busnel, Eds.). New York: Academic Press.

Kreutzer, M., 1974. Stereotypie et variations dans les chants de proclamation territoriale chez le Troglodyte *(Troglodytes troglodytes). Rev. Comp. Animal*, 8:270-286.

Kroodsma, D.E., 1980. Winter wren singing behavior: a pinnacle of song complexity. *Condor*, 82:356-365.

Kroodsma, D.E., 1981. Geographical variation and functions of song types in warblers (Parulidae). *Auk*, 98:743-751.

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., 1985a. Development and use of two song forms by the eastern phoebe. *Wilson Bull.*, 97:21-29.

Kroodsma, D.E., 1985b. Geographic variation in songs of the Bewick's wren: a search for correlations with avifaunal complexity. *Behav. Ecol. Sociobiol.*, 16:143-150.

Kroodsma, D.E., 1988a. Contrasting styles of song development and their consequences among the Passeriformes. In: *Evolution and Learning*: 157-184 (R.C. Bolles & M.D. Beecher, Eds.). Hillsdale, New Jersey: Erlbaum Assoc., Inc.

Kroodsma, D.E., 1988b. Song types and their use: developmental flexibility of the male blue-winged warbler. *Ethology*, 79:235-247.

Kroodsma, D.E., 1989a. Male Eastern Phoebes (Tyrannidae, Passeriformes) fail to imitate songs. *J. Comp. Psychol.*, 103:227-232.

Kroodsma, D.E., 1989b. Two North American song populations of the marsh wren reach distributional limits in the central Great Plains. *Condor*, 91:332-340.

Kroodsma, D.E., Albano, D. & Houlihan, P., (in press). Song development by Black-capped Chickadees (*Parus atricapillus*) and Carolina Chickadees (*P. carolinensis*) in mixed groups. *Auk.*

Kroodsma, D E. & Baylis, J R., 1982. Appendix: a world survey of evidence for vocal learning in birds. In *Acoustic Communication in Birds, vol.* 2: 311-337 (D.E. Kroodsma & E.H. Miller, Eds.). New York: Academic Press.

Kroodsma, D E. & Canady, R., 1985. Differences in repertoire size, singing behavior, and associated neuroanatomy among marsh wren populations have a genetic basis. *Auk*, 102:439-446.

Kroodsma, D.E. & James, F.C., (in press). Song variation among populations of the Red-winged Blackbird. *Wilson Bull.*.

Kroodsma, D. & Konishi, M., 1991. A suboscine bird (eastern phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. *Anim. Behav.*, 42:477-488.

Kroodsma, D.E., Meservey, W.R., Whitlock, A.L. & Vanderhaegen, W.M., 1984. Blue-winged warblers *(Vermivora pinus)* "recognize" dialects in type II but not type I songs. *Behav. Ecol. Sociobiol.*, 15:127-132.

Kroodsma, D.E. & Momose, H., 1991. Songs of the Japanese population of the Winter Wren (*Troglodytes troglodytes*). *Condor*, 93:424-432.

Kroodsma, D.E. & Pickert, R., 1980. Environmentally dependent sensitive periods for avian vocal learning. *Nature (London)*, 28:477-479.

Kroodsma, D.E. & Verner, J., 1978. Complex singing behaviors among *Cistothorus* wrens. *Auk*, 95:703-716.

Lein, M.R., 1978. Song variation in a population of chestnut-sided warblers *(Dendroica pensylvanica)*: its nature and suggested significance. *Can. J. Zool.*, 56:1266-1283.

Marler, P., 1991. The instinct for vocal learning:

songbirds. In *Plasticity of development*: 107-125. (S.E. Brauth, W.S. Hall & R.J. Dooling, Eds.). Cambridge, MA: MIT Press.

Marler, P. & Nelson, D., 1992. Neuroselection and song learning in birds: species universals in a culturally transmitted behavior. *Neurosci.*, 4:415-423.

Morse, D.H., 1970. Territorial and courtship songs of birds. *Nature (London)*, 226:659-661.

Morse, D.H., 1989. Song patterns of warblers at dawn and dusk. *Wilson Bull.*, 101:26-35.

Morton, E.S., Gish, S.L. & Van Der Voort, M., 1986. On the learning of degraded and undegraded songs in the Carolina wren. *Anim. Behav.*, 34:815-820.

Nottebohm, F., 1972. The origins of vocal learning. *Am. Nat.*, 106:116-140.

Nottebohm, F., 1980. Brain pathways for vocal learning in birds: a review of the first 10 years. In *Progress in Psychobiology and Physiological Psychology*, vol 9: 85-124. (J.M. S. Sprage & A.N.E. Epstein, Eds.). New York: Academic Press.

Nottebohm, F., 1991. Reassessing the mechanisms and origins of vocal learning in birds. *Trends Neurosci.*, 14:206-211.

Payne, R.B., 1983. Bird songs, sexual selection, and female mating strategies. In *Social behavior of female vertebrates:* 55-90. (S. K. Wasser, Ed.). New York: Academic Press.

Pepperberg, I.M., 1985. Social modeling theory: A possible framework for understanding avian vocal learning. *Auk*, 102:854-864.

Raikow, R.J., 1982. Monophyly of the Passeriformes: test of a phylogenetic hypothesis. *Auk*, 99:431-445.

Sibley, C.G., Ahlquist, J. E. & Monroe, B.L., Jr., 1988. A classification of the living birds of the world basedon DNA-DNA hybridization studies. *Auk*, 105:409-423

Slater, P.J.B., 1988. The nature and nurture of birdsong. *Behav. Brain Sci.*, 11:648-649.

Slater, P.J.B., 1989. Bird song learning: causes and consequences. *Ethol. Ecol. Evol.*, 1:19-46.

Verner, J., 1965. Breeding biology of the long-billed marsh wren. *Condor*, 67:6-30.

Verner, J., 1976. Complex song repertoire of male long-billed marsh wrens in eastern Washington. *Living Bird*, 14:263-300.

West, M.J. & King, A.P., 1988. Female visual displays affect the development of male song in the cowbird. *Nature*, 334:244-246.

West-Eberhard, M.J., 1983. Sexual selection, social competition, and speciation. *Quart. Rev. Biol.*, 58:155-182.

Wiley, R.H. & Richards, D.G., 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.*, 3:69-94.

(Recibido: septiembre 1993)