Social influences on vocal development

EDITED BY

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For at least 30 years, there have been close parallels between studies of bird song development and those of the development of human language. Both song and language require species-specific stimulation at a sensitive period in development and subsequent practice through subsong and plastic song in birds and babbling in infant humans, leading to the development of characteristic vocalizations for each species.

This book illustrates how social interactions during development can shape vocal learning and extend the sensitive period beyond infancy and how social companions can induce flexibility even into adulthood. Social companions in a wide range of species, including not only birds and humans but also cetaceans and nonhuman primates, play important roles in shaping vocal production, as well as the comprehension and appropriate usage of vocal communication.

Social influences on vocal development will be required reading for students and researchers interested in animal and human communication and its development.

Contents

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1 Introduction

CHARLES T. SNOWDON AND MARTINE HAUSBERGER

In the late 1960s a series of developments in linguistics, developmental psycholinguistics and animal communication led to a convergent model of vocal development in human and nonhuman species. As presented by Lenneberg (1967) and Marler (1970), the development of language and of bird song required exposure to species-specific codes during a sensitive period of development, after which subsequent learning was extremely limited. The amount of input required could be quite small, and this input could be effective regardless of social interactions. Both birds and humans needed intact hearing and an extensive time for practice (babbling for human infants, subsong and plastic song for birds) to acquire adult competence in vocal production. Subsequent to this practice crystallization occurred, and further changes in vocal structure were rare.

This paradigm has led to extremely productive research over the past 25 years, not only in the study of vocal development but also in the understanding of the neurological controls of vocal production. However, as researchers interested in the ontogeny of primate and avian vocal communication, we have become increasingly aware of the need to consider some modifications to this paradigm. Some forms of social stimulation can extend sensitive periods for song learning in birds, and songs and calls in some species can be modified throughout life, often in response to changes in social stimuli. Parrots, dolphins and great apes with exceptional training acquired codes with some similarities to human language. Yet at the same time there was little evidence of vocal plasticity in nonhuman primates, suggesting a gap in continuity of developmental processes in the evolution from birds to humans. However, at the level of pragmatics – how vocalizations are used – learning within a social environment appeared to play a critical role.

Although there was a close interaction between researchers on the ontogeny of language and of bird song 25 years ago, recently there has been little effort to cross taxonomic boundaries, and most recent volumes focus on birds, or nonhuman primates or children, with little cross-species integration.

We had several goals in the development of this book. First, we saw many parallels emerging from studies on birds, marine mammals, nonhuman primates and children, and we thought there would be considerable benefit in drawing studies on all of these species together in one volume. Second, while most of the research in the past 25 years has focused on ontogenetic factors of vocal production, understanding how organisms acquired the ability to understand and make appropriate use of vocalizations and speech seemed equally important. We sought to draw attention to the importance of considering production and pragmatics. Third, an increasing number of studies suggest that affiliative social interactions are important in shaping both vocal production and vocal usage, and we have sought to illustrate the variety of social interactions that affect development.

We have chosen contributors studying nonhuman animals who have worked in field settings or in naturalistic captive environments because, as will be seen, one may not appreciate the importance of social influences on development in more restrictive environments. Among the many scientists studying child language development we have chosen contributors who also have a strong naturalistic approach to illustrate better the parallels between human and nonhuman vocal development. We have also selected contributors with different theoretical and empirical perspectives, since our goal is to promote a productive discussion among researchers rather than to present a unified point of view.

In the second chapter *Nelson* presents a critical review of social interaction and sensitive phases, presenting evidence in support of a selective model of vocal learning, where young birds acquire the potential for producing several songs, but through territorial interactions at the time of breeding, selectively reduce the number of songs to use those that match those of territorial neighbors. Nelson is critical of those who invoke "social influences" as an explanation without specifying what aspects of social interactions influence learning.

Baptista & Gaunt review a variety of studies on both oscine and nonoscine birds, illustrating how sensitive periods for song learning can be extended through experience with social companions. They suggest that social companions can focus attention on specific songs, with the social tutor serving as both a motivator and a modeller for the young bird.

West, King & Freeberg review and revise their interpretation of research on cowbirds, obligate nest parasites where young birds do not have parental models for song learning. West *et al.* call attention to the pragmatics of communication. They report that birds with highly effective songs, will not use the songs appropriately if their social environment during development has been limited or inappropriate. Much of the complexity of vocal communication can be lost by attending only to production, and some of the most important social influences will be expressed as deficits of pragmatics rather than of production.

Payne & Payne use strong inference methods in field studies of indigo buntings and village indigo birds to argue that these birds learn new songs throughout life. Yearling birds produce song types that were rarely or never recorded in their natal territory, but which are common in the area in which they are breeding. Yearling birds acquire new songs rapidly and those birds that match songs of their territorial neighbors were more likely to retain their own territories and breed successfully.

Zann reviews the literature on song learning in zebra finches, the species that has been most extensively studied. Zann combines his own fieldwork with studies done in captivity to indicate several stages of learning. Zebra finches can memorize the songs of their fathers heard before 35 days of age, but the songs actually produced depend on subsequent experience. Both visual and vocal stimuli are important, indicating the importance of multimodal stimulation for song learning. The highly unpredictable natural environment of zebra finches in Australia coupled with the high mortality of both young and adult birds may lead to the high degree of flexibility in vocal learning found in zebra finches.

Brown & Farabaugh stress the importance of studying species of birds that live in stable year-round groups. The species they have studied, Australian magpies, American crows and budgerigars, show extensive convergence of both songs and call types, although each individual retains unique notes or syllables. They view vocal sharing or convergence as a "social badge" that signifies membership within a social group. They argue that song sharing will be found not only between territorial rivals, as noted in other chapters, but also among affiliative partners.

Hausberger continues the theme of song sharing among affiliative partners in her studies of European starlings. She demonstrates a hierarchical structure to starling songs, with some themes being species specific, others being regionally specific, other themes specific to social groups or roosts, and still others marking individual affiliations. Two different species of starling will share themes when they belong to the same colony. When social relationships among a group of starlings are experimentally altered, birds develop a new set of themes to share with new affiliative partners. She reports song sharing among females, as well as males, especially outside of the breeding season, and also suggests that vocal convergence signals group membership.

Pepperberg presents social modelling theory as a method for exceptional vocal learning. Social modelling theory emphasizes not only production but also the functional referent of a signal and is effective in exceptional learning in emphasizing attention, motivation, and comprehension. She provides an experimental study to illustrate the effectiveness of social modelling theory in vocal learning in parrots, and she analyzes the studies of language analogs in great apes to show that the most successful of these studies are those that most closely follow social modelling as a training technique.

McCowan & Reiss show that dolphins can easily learn to imitate artificial signals relating to specific objects, and then use these imitations in spontaneous play with the same objects. They also present a naturalistic study of whistle development in dolphins, arguing for a hierarchical structure similar to that suggested by Hausberger, with species-specific, group-specific and individual specific whistle structures. As with birds and human infants, there is overproduction of variants by young dolphins, with whistles becoming less variable with increasing age.

Tyack & Sayigh, though differing in their definition of the diversity of whistle types described by McCowan & Reiss, also provide evidence of social learning in dolphins. They show that signature whistles are affected by social and acoustic factors and that dolphins can acquire new whistle forms throughout life. Adult males that form coalitions acquire and use each other's signature whistles, supporting the idea that shared vocalizations serve as an affiliative badge.

Snowdon, Elowson & Roush review vocal development in marmosets and tamarins, emphasizing the need to use modern acoustic methods to determine subtle changes in call structure. They describe three phenomena that have parallels to data from birds and humans. The trill structure of pygmy marmosets is flexible and shows evidence of convergence with changes in social companions, yet individual specific features are retained. Marmosets also show extensive "babbling," with parallels to both human babbling and the subsong and plastic song of birds. Study of the ontogeny of food-associated cells in tamarins indicates that social factors can inhibit the appropriate production and usage of calls.

Seyfarth & Cheney review their research on vocal development in Old World primates and argue strongly for a greater emphasis on studying social influences on usage and responses to calls rather than on production. They note that calls used in affiliative interactions have some flexibility in development compared with alarm calls, but note that the basic pattern for vocal production in primates is either innate vocalizations or subtle modification within constraints. Evidence of modification within constraints has been increasingly common in studies published in the last decade, suggesting that new acoustic analysis methods may be important in documenting plasticity. In an important cross-fostering study, Seyfarth and Cheney demonstrate that the greatest flexibility monkeys show may be in learning how to respond appropriately to vocalizations.

Locke & Snow discuss the importance of babbling and of linguistic input in the vocal development of children. There is evidence for vocal accommodation similar to that reported in birds, dolphins, and monkeys. Adults adjust their language to levels appropriate for children, and children produce more speech-like vocalizations in social contexts. Children who hear more words learn faster. Children whose parents neglect them acquire language more slowly than do normal children or children of abusive parents. Locke & Snow note that vocal accommodation is not only possible but necessary in adults for social-group membership and for achieving intimacy with listeners.

Goldin-Meadow presents some important studies on communication in deaf children that at first appear to contradict the results of Locke & Snow. She compares communicative skills in deaf children in the USA and China (where mothers provide more important input and more elaboration than American mothers) and finds no differences in the rate of development of gestural communication in deaf children. Deaf children consistently produce more elaborate gestures and signs than hearing parents provide as input, and a community of deaf people in Nicaragua has created its own communication system. Thus, gestural languages can develop in the absence of input, and it would appear that social influences play little role in the ontogeny of communication in deaf children. Yet, if viewed from a pragmatic perspective, the elaboration of gestural communication in deaf children may be motivated by the need to communicate with someone.

Jouanjean-l'Antoëne describes a longitudinal ethological study of language development in dizygotic twins. She focuses on the different social interactions each twin has with her parents. There are preferential interactions or relationships of each twin with one parent. Parents differentially reinforced each twin. Individual differences lead to favored social interactions within families and these favored relationships play an important role in determining from whom a child will learn and the nature of what is learned.

Goodwin concludes the book with her work on the social use of language in pre-teenaged children. She finds very different types of communication style in play groups of girls versus boys, yet there is considerable flexibility. In general, girls communicate in a non hierarchical fashion, and boys have a clear hierarchical structure to their exchanges. Yet when girls supervise play of younger siblings, play "mother," challenge strangers or interact with boys, they display the same hierarchical language structure as that of boys. This flexibility of language usage is more evidence at the pragmatic level of how language is variable in response to different social companions.

Several themes emerge from these chapters. Five main themes arise.

1. Vocal learning is not only learning to produce, but also learning to use and comprehend vocalizations

Birds, like dolphins, may use their song or whistle types differentially according to social context (Hausberger, McCowan & Reiss, Tyack & Sayigh). Monkeys use different calls according to the type of predator (Seyfarth & Cheney). Young girls may modify their style of communication according to social partners (Goodwin). Vocal comprehension and usage, like vocal production must be learned. Cowbirds may develop effective songs, but do not know how to use them if they are raised in an inadequate social environment (West *et al.*). Young tamarins learn from older conspecifics how to use food calls appropriately, as vervet monkeys learn how to use alarm calls (Snowdon *et al.*, Seyfarth & Cheney). Fully referential, functional and socially interactive inputs ensure that parrots learn not only to produce but also to comprehend allospecific vocalizations (Pepperberg), while dolphins learn to associate arbitrary sounds with particular objects and then use these sounds when playing spontaneously with these objects (McCowan & Reiss).

Different processes seem to be involved for production, comprehension and usage in terms of timing (McCowan & Reiss) or degree of fixity (Seyfarth & Cheney). In children comprehension precedes vocal production as does vocal usage (Locke & Snow, Jouanjean-l'Antoëne). Interestingly, when all three aspects are being considered, there is no "gap" between birds and humans. Vocal development in mammals such as dolphins and nonhuman primates is continuous with birds and humans.

2. Social inputs influence the stages of development and may delay vocal learning

One common feature of vocal development seems to be a stage of babbling (mammals) or subsong/plastic song (birds), characterized by an overproduction and variability of structure (Nelson, McCowan & Reiss, Snowdon *et al.*, Locke & Snow). This babbling or subsong is generally thought to be a "training" phase where individuals may have the opportunity to progressively develop appropriate vocal structures by comparing their own production to a model (which may be in memory). Alex the grey parrot also displays solitary "speech" (Pepperberg), while deaf children use solitary gestures (Goldin-Meadow). Plastic song stages are particularly important in the action-based learning theory, where the animals select from an array vocalizations that are socially appropriate (Nelson). Although Nelson argues that this selective process may account for reports of delayed learning in closed-end learners, several authors in this volume defend the possibility of later learning under social influences.

However, there is also evidence of new vocal learning occurring beyond the sensitive period. Baptista & Gaunt show that the sensitive period can be extended by social tutors, Payne & Payne provide compelling evidence of learning of new songs in indigo buntings during the first breeding season and beyond. Hausberger describes the development of new song themes in starling after changes in social companions and the re-emergence of themes not heard for months or years. Pepperberg shows how parrots can acquire English words at various ages. McCowan & Reiss show that dolphins can imitate novel sounds, and Tyack & Sayigh show that dolphins can acquire new signature whistles well beyond infancy.

Several of the changes in vocal production that occur outside of a sensitive period or in response to affiliative interactions are subtle changes in vocal structure that are observable only through careful spectrographic analyses. Many of the changes reported in these chapters do not represent the acquisition of completely new vocalizations, but rather subtle modifications in structure of existing vocalizations. Thus, modern spectral analysis methods are critical to the demonstration of social influences on vocal structure. The finding of plasticity at all ages is not necessarily in conflict with the age-limited learning model proposed 25 years ago. The chapters by Nelson and Zann on birds, Snowdon *et al.* and Seyfarth & Cheney on primates, and Goldin-Meadow on deaf children indicate that there are aspects of vocal production (or gestures in the deaf children) that are fixed or modifiable only at an early age. While vocal structures do become solidified, crystallization is probably too strong a metaphor to use, since some flexibility is apparent in birds, dolphins, nonhuman primates and humans at all ages.

3. The nature of social influences is complex

Nelson notes the need to specify and to understand the mechanisms of social influences, and several chapters suggest possible mechanisms. Zann shows that multimodal stimulation appears necessary for zebra finch song-learning. Pepperberg shows experimentally how social modelling leads to exceptional learning. Seyfarth & Cheney describe the importance of social reinforcement, and Hausberger and Jouanjean-l'Antoëne illustrate how individual-specific relationships shape imitation of songs or language.

Social interactors provide an attentional focus, multimodal stimulation, and reinforcement. Each of these mechanisms might be operative in social interaction. As Nelson rightly emphasizes, there is a need for defining "social influences" that are not necessarily "social interactions." Mere proximity may provide social influence without any obvious interaction (Hausberger).

Attention appears as a common and major feature in vocal learning from the tutor as well as the learner. Children respond more to negative attention from the mother than to no attention at all (Locke & Snow). This is also part of social modelling theory (Pepperberg) and is considered a primary factor in bird song learning (Baptista & Gaunt, Zann). The learner must also be viewed as an actor in its own development (Nelson, Zann, Locke & Snow, Jouanjean-l'Antoëne) and not as a passive receiver, as has often been the case.

4. Vocal learning may be a social indicator

Birds may select particular forms of songs through aggressive affiliative interactions with other birds (Nelson, Baptista & Gaunt, West *et al.*, Payne & Payne, Zann, Brown & Farabaugh, Hausberger). Nelson, Payne & Payne, and Zann show how conflict over territory formation can lead to song sharing, but there are an impressive number of examples on the importance of affiliative interactions in vocal development (Brown & Farabaugh, Hausberger, Pepperberg for birds; McCowan & Reiss and Tyack & Sayigh for dolphins; Snowdon *et al.*, and Seyfarth & Cheney for nonhuman primates; Locke & Snow, Jouanjean-l'Antoëne and Goodwin for humans). Especially with birds, most studies have focused on vocalizations relating to territorial defense and mate selection, but the broad taxonomic range of species where vocal development is influenced by affiliative interactions suggests future research should focus more on affiliative processes.

Brown & Farabaugh suggest that in some species vocal learning has evolved to allow individuals to share vocalizations with a particular subset of conspecifics. The concept of "vocal accommodation" (Locke & Snow) may be extended to nonhuman species. Organisms adapt aspects of their vocal production to match or approach those of their social partners. This process is related to positive affect. Such vocal sharing may involve pairs of birds or nonhuman mammals or may extend to social groups or even to the processes of complex dialects that for some authors have a function of shared vocal identity.

Interestingly, in all of the species mentioned here as exhibiting vocal sharing, individuality is maintained through individual-specific vocalizations (Hausberger, McCowan & Reiss, Tyack & Sayigh). It appears important that the vocal system not only provides group identity but also allows, for individual identity, an "optimal vocal sharing" system.

5. Theoretical principles must be developed to account for the variation in the role of social influences on vocal development

There are socioecological correlates of the importance of social influences on vocal development. The species that appear to show the greatest capacity for learning new vocalizations are those with the greatest mobility, migratory birds and marine mammals, or those with the most unpredictable environments, zebra finches. High mobility and highly unpredictable environments would place selective pressures on vocal plasticity, since individuals would be likely to encounter other conspecifics with very different tutors or geographic dialects.

Animals living in year-round social groups with low mobility would be expected to have less advantage in broad plasticity of vocal structure. However, since individuals do disperse and the membership of social groups does change over time, the capacity to make subtle adjustments in vocal structure might be valuable to provide a social "badge" or indicator of group membership. Evidence for, or speculation about, vocal accommodation or a social badge has been raised with each of the taxonomic groups presented here.

Since individuals differ greatly in behavior, it seems sensible that there might be greater evidence for learning or plasticity in responding to the calls of others or in using signals appropriately than in the production of signals. Hence, it should not be surprising to find evidence of social influences on vocal pragmatics regardless of mobility or stability.

The chapters presented here collectively illustrate the importance of social influences on vocal development not only on production, but perhaps more importantly on usage and responses to vocalizations. These chapters show that there is a broad continuity in the processes of vocal development across all of the vertebrate taxa. It should no longer be necessary to focus on birds, marine mammals, nonhuman primates and humans as separate entities each requiring a different type of developmental process. It is our hope that the chapters in this book will lead to a new integrative study of vocal development in all its aspects that will involve multi-disciplinary, multi-species studies.

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2 Social interaction and sensitive phases for song learning: A critical review

DOUGLAS A. NELSON

INTRODUCTION

A major focus in the study of bird song over the past three decades has been on the involvement of learning during development. At a basic level, two models of learning mechanisms have been proposed: instructive and selective (Jerne 1967; Changeux *et al.* 1984). In an instructive model, environmental stimulation adds information not already present in the behavioral repertoire. When a young bird memorizes a novel song, it is instructed. In contrast, in a selective model, learning consists of the selection of behavior(s) from a pre-existing repertoire as a function of experience. At the time of stimulation, the animal already possesses the potential or ability to perform the behavior. Therefore, the test to distinguish between the two models is to present a novel stimulus and to record whether it is learned.

Research on song learning has been guided largely by an instructive model of learning, embodied in the sensorimotor model first proposed in Konishi's (1965) study of song development in the white-crowned sparrow (*Zonotrichia leucophrys*). The sensorimotor model includes two stages: a sensory (instructive) phase in which songs are memorized, and a sensorimotor phase in which the bird compares its own song, via auditory feedback, to the memory trace acquired earlier.

One consequence of song learning is the formation of geographic "dialects" in which males at one location sing similar songs that differ from those of the same species at other locations. If vocal plasticity in birds is mediated solely by an instructive mechanism, then song matching dialects arise when males breed in the same area where they acquired their song(s). In sedentary populations, dialects will result when males settle and breed as adults in the same area where they acquired their song. When males disperse long distances from the birthplace to breed, then the ability to acquire novel songs must persist until they settle upon a breeding territory later in life and acquire songs from their new neighbors (Kroodsma 1982). The observation that neighboring males in wild populations sing similar songs, coupled with information or assumptions about the degree of natal dispersal, is often taken as *prima facie* evidence of how long the instructive phase persists.

In recent years much experimental work has been devoted to identifying factors that influence the timing and expression of the sensory phase. In particular, a major focus has been on the social factors that may influence what and when a young bird is instructed. To borrow from Kroodsma (1978), what, when, and how a bird is instructed about song can potentially influence many other aspects of a species' biology, including mate choice, reproductive success, and population structure.

In this chapter I review some of the recent research on song learning. I argue that many of the experiments and field observations on song "learning" may actually have lumped together two different mechanisms of learning: the familiar instructive mechanism and the more recently described selective mechanism (Marler & Peters 1982a; Marler 1990; Nelson & Marler 1994). After describing how vocal plasticity may be mediated by a selective mechanism, I review recent experimental research on song learning within a framework incorporating selection. The possibility that song "learning" may be a heterogeneous process invites confusion. I use the terms "acquisition" or "memorization" to refer to the sensory phase wherein a male commits a novel song to memory, and "action-based learning" (Marler 1991), or "selective attrition" (Marler & Peters 1982a) to refer to the preferential retention of learned song(s) as a function of experience.

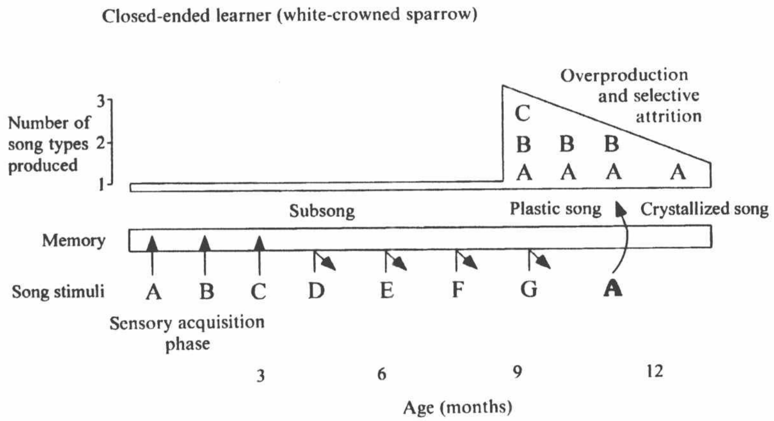

Fig. 2.1. Schematic diagram of song development in a closed-ended learner, the white-crowned sparrow (Marler 1970; Nelson & Marler 1994; Nelson *et al.* 1995). In a closed-ended learner, song stimuli are committed to memory only during a restricted interval, termed the sensitive phase. Different song stimuli (A–G) are presented at intervals throughout the first year of life. The ability to memorize song is assayed by the production of imitations. Here, song stimuli A, B, and C are memorized, while D, E, F, and G are rejected, as symbolized by the bent arrows. Males "overproduce" by imitating more (A–C) than is needed for the mature repertoire of one crystallized song type (A). Song types are gradually lost from the overproduced repertoire until the final type remains. If a stimulus that matches one type in the overproduced repertoire is presented (the bold "A" at 11 months), then song type A is crystallized. A nonmatching type presented at the same time to a different, control, bird is not memorized and reproduced (Nelson & Marler 1994). The experience-dependent plasticity of vocal behavior in males of this species at nine months of age and beyond is based on learning by selection from an overproduced repertoire, and not on learning by memorizing novel stimuli.

LEARNING BY SELECTION

A selective learning mechanism includes two stages (Changeux *et al.* 1984): (a) the production of a variety of behaviors, in this case songs or their components (notes, syllables, phrases) and their underlying neural representations and (b) the selective retention and production of a subset of this variety as a function of experience. Kroodsma (1974), Baptista (1975), and Jenkins (1977) described the second phase of the selective process, but apparently did not recognize the potential of a selective mechanism as an alternative basis of vocal plasticity operating *outside* the sensory memorization phase. Marler & Peters (1981, 1982a) clearly described the entire selective attrition process in their studies of song development in the swamp sparrow (*Melospiza georgiana*).

Song development proceeds similarly in the swamp sparrow and white-crowned sparrow (Nelson & Marler 1994; Nelson *et al.* 1995). The latter species is used to illustrate the selective attrition model in Fig. 2.1. Swamp sparrows and white-crowned sparrows are closed ended "learners" (or "memorizers" in the terminology of this chapter), in that males memorize songs only during a restricted time in the first few months of life. This is established by presenting males with a changing roster of different tutor stimuli throughout life, and then examining the birds' vocal production for specific imitations. After a storage interval of several months, during which males may "babble" in subsong (Marler & Peters 1982b; Snowdon *et al.* Chapter 12), imitations of specific tutors appear in plastic song.

During the overproduction phase of plastic song, males not only reproduce accurate imitations of their tutors, but also display "combinatorial improvisation" (Marler & Peters 1982b), in which novel songs are created by combining pieces from different tutor songs. This process is illustrated in Fig. 2.2. The overproduction of imitated song material and, in particular, the production of novel combinations (song patterns) by recombining elements

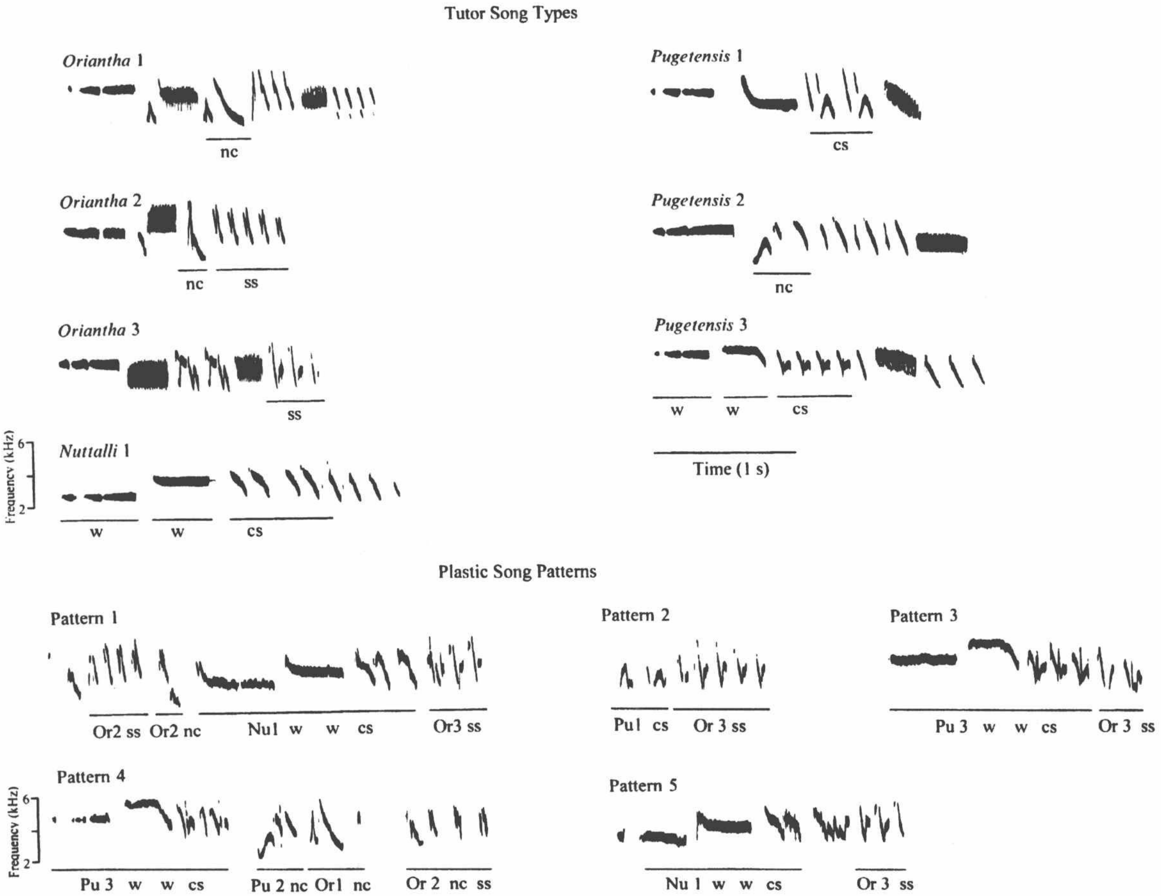

Fig. 2.2. An example of song overproduction by one male Puget Sound white-crowned sparrow in early plastic song. Males of this species sing one song type in their mature, crystallized repertoire. Shown at the top of the figure are the seven tutor song types he imitated in whole or in part. The phrases he used in generating the four song patterns on the bottom of the figure are underlined. For example, Pattern 1 consists of the simple syllables (ss) and note complex (nc) from tutor type *Oriantha* 2 (Or2), followed by the two whistles (w) and one complex syllable (cs) from tutor *Nuttalli* 1 (Nu1), and ending with three simple syllables from tutor *Oriantha* 3 (Or3). Pattern 3 was also counted as a song type, because he sang it repeatedly on at least two consecutive weeks in plastic song. Pu, *Pugetensis*. (From Nelson *et al.* 1996a.)

from different tutors provide the raw material upon which a subsequent selective stage can act. In the white-crowned sparrow, the most improvisation of novel song patterns occurs early in plastic song, followed by a gradual attrition (Fig. 2.3). Recombinatorial improvisation of song material is common to other species (northern cardinal, *Cardinalis cardinalis* (Lemon 1975); winter wren, *Troglodytes troglodytes* (Kroodsma 1981); song sparrow, *Melospiza melodia* (Marler & Peters 1987); nightingale, *Luscinia megarhynchos* (Hultsch 1990); field sparrow, *Spizella pusilla* (Nelson 1992; indigo bunting, *Passerina cyanea* (Margoliash *et al.* 1994)), as is invention, another process that will generate diversity in song (Kroodsma & Verner 1978). Both improvisation and invention are creative processes, which will introduce greater diversity into a male's vocal production.

Marler & Peters then hypothesized the next step in a selective learning mechanism. They noted that matched

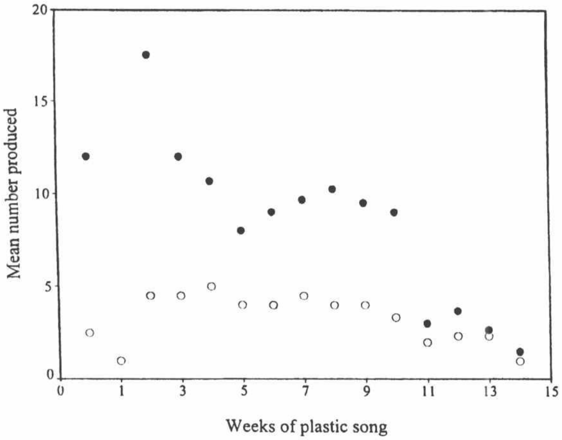

Fig. 2.3. The time course of overproduction and attrition in 11 male mountain white-crowned sparrows tutored with 32 different tutor song types between the ages of 10 and 90 days. Plotted are the mean number of different tutors imitated each week in plastic song (○) and the mean number of different song patterns produced each week (●). Plastic song week 0 began at about 270 days of age. Song patterns are unique sequences of song phrases formed by combining phrases from one or more tutors (see Fig. 2.2). Males do most of their improvisation in the first month of plastic song, followed by a decline, or attrition, in the number of different song patterns produced until they sing one stable "crystallized" song. The number of tutors imitated each week, in whole or in part, stays relatively constant throughout plastic song until just prior to crystallization. Some males crystallize a single "hybrid" song, based on two or more different tutor songs, which is why the mean number of tutors imitated in crystallized song is greater than 1.

counter-singing, the tendency of territory neighbors to exchange similar songs (Marler 1960; Kroodsma 1974; Baptista 1975; Jenkins 1977; Falls *et al.* 1982), could lead, via selective attrition of non matching song types, to local song dialects. That is, if males preferentially retained the matching song(s) from their overproduced plastic song repertoire, this would lead to song sharing among males at a locality. This is shown in Fig. 2.1, where song stimulus A is presented again at 11 months of age, when the male is already singing imitations of A and B. The male discards song type B from his overproduced repertoire and retains A as his sole crystallized song type. Marler & Peters also noted that, in other circumstances, males might selectively *delete* matching songs from their repertoire; it is not uncommon for neighboring males to have very different songs (e.g., white-eyed vireo, *Vireo griseus* (Bradley 1981); nightingale (Hultsch & Todt 1981); fox sparrow, *Passerella iliaca* (Martin 1979)). Byers & Kroodsma (1992) presented some evidence that selective rejection of matching songs from an overproduced repertoire occurs in chestnut-sided warblers (*Dendroica pennsylvanica*). It is not clear why song sharing among neighbors may be favored in some species, and non sharing in others.

Direct evidence for a selective attrition process has been obtained only recently. Field sparrows sing one "simple" song type in their crystallized repertoire (Nelson & Croner 1991), but males arriving on particular territories for the first time in spring produce two to four song types (Nelson 1992). Using a quantitative measure of song similarity, I documented that males preferentially kept the one song type in their repertoire that best matched one of their neighbors, and discarded the remaining songs. In some cases, matching of neighbors' song was quite close, in others only approximate. I return to this point later. Several lines of evidence suggested that instruction was not occurring as birds established their territories

1. Several males were found singing two or more song types as the first birds to return in their respective fields; that is, there were no adult tutors within earshot. These males did not alter their existing songs after other males arrived, but merely discarded their nonmatching song(s).
2. Discarded songs did not resemble neighbors' songs more closely than was expected at random, indicating that discarded songs were not acquired from neighbors.
3. Neighbors' songs were usually not the most similar of all songs in the local population to the retained songs. Many other similar non-neighboring songs could be found locally, suggesting that instruction was not occurring from neighbors.
4. No male ever changed his song type after the attrition phase, even if new neighbors with new songs moved in. Only one male changed his territory between years.
5. Males who did not share their song with any neighbor were not uncommon, especially in large fields containing many territories.

While this observational evidence suggested that vocal plasticity in yearlings involved selection rather than