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IMITATIONS OF WHITE-CROWNED SPARROW SONGS BY A SONG SPARROW¹

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Key words: Song Sparrows; allospecific song; White-crowned Sparrow; mimicry; song.

Although cardueline finches are known to incorporate vocalizations of many allospecific species into their advertising song (Knecht and Scheer 1968, Güttinger 1974, Remsen et al. 1982), records of emberizid finches imitating allospecific songs in the wild are rare (Baptista et al. 1981, Cooper and Murphy 1985).

The resistance to learning allospecific syllables appears to vary among species in the genus *Melospiza*. Naive Swamp Sparrows (*M. georgiana*) exposed to both taped conspecific song and song of the sympatric Song Sparrow (*M. melodia*) produced conspecific song as adults, rejecting allospecific song as learning stimuli (Marler and Peters 1977).

The song repertoire of an adult Song Sparrow consists of a number of themes. A theme is defined as "a particular set of notes always rendered in the same order and with set pitch relationships" (Nottebohm 1969:302).

Marler and Peters (1977, 1987) also exposed Song Sparrows to tapes of conspecific and alien Swamp Sparrow songs. As adults, the experimental subjects sang mostly themes containing Song Sparrow syllables, although a few themes included syllables typical of Swamp Sparrows. No themes contained exclusively allospecific syllables however, indicating that Song Sparrows possess a genetic predisposition to learn conspecific syllables.

On 11 April 1987, I tape-recorded a "mimetic" Song Sparrow on the campus of the State University of San Francisco, California, singing White-crowned Sparrow (*Zonotrichia leucophrys*) songs, Song Sparrow songs, and songs containing syllables borrowed from both species (Fig. 1). I describe herein the song repertoire

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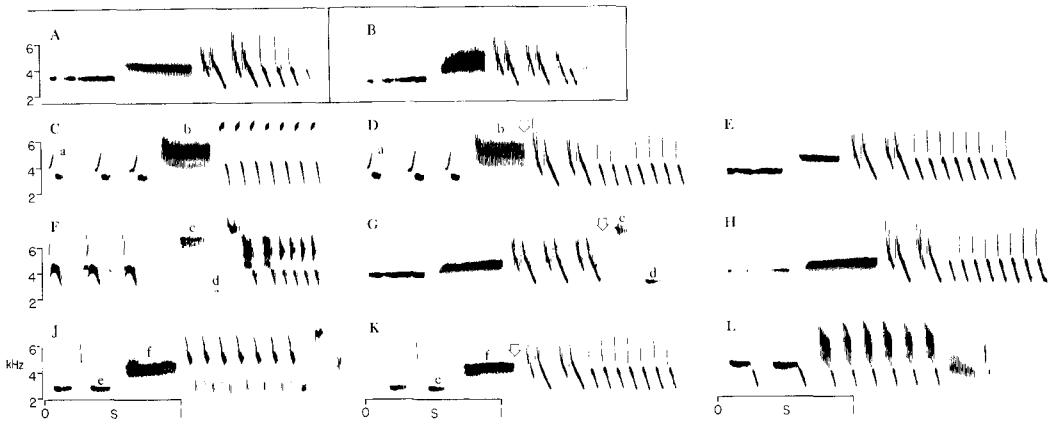


FIGURE 1. A. Song of White-crowned Sparrow typical of San Francisco city. B. Song of White-crowned Sparrow typical of Lake Merced, San Francisco. C to L: Nine song themes recorded from a Song Sparrow in San Francisco. C, F, J, and L are "pure" Song Sparrow themes. E and H are two pure White-crowned Sparrow songs. D, G, and K are three "hybrid" songs. Arrows in D and K indicate where Song Sparrow syllables cease and White-crowned Sparrow syllables commence. Arrow in G indicates where White-crowned Sparrow syllables cease and two Song Sparrow syllables commence. Syllables marked a, b, c, d, e, and f indicate Song Sparrow syllable types used in the hybrid songs.

of this Song Sparrow, and comment on the possible reasons for this unusual behavior and on the possible adaptive significance of Song Sparrows imitating alien songs in the wild.

White-crowned Sparrows from the city of San Francisco typically sing only one song type, each beginning with a whistle, followed by a buzz or vibrato, then a trill consisting of two complex (paired) syllables, followed by a series of simple syllables (Fig. 1A). Most individuals in the population sing the same theme. The number of syllables in the trill varies and ranges from five to 13 (Baptista 1975).

Ten well-studied Song Sparrows in the San Francisco Bay Area utilized song repertoires ranging from 10 to 23 themes (Mulligan 1966). Members of a local population may share syllable types, but few entire song types are shared between individuals. The same syllables may be utilized in different themes.

I recorded 63 songs from the mimetic Song Sparrow. This sample consisted of 17 Song Sparrow songs, 28 White-crowned Sparrow songs, and 16 "hybrid" songs containing syllables borrowed from songs of both species. His repertoire contained nine themes altogether. These included four Song Sparrow themes (songs C, F, J, and L in Fig. 1), two different White-crowned Sparrow themes (songs E and H), and three hybrid themes (songs D, G, and K).

Theme H in his repertoire is similar to White-crowned Sparrow song A (Fig. 1) which I recorded from a White-crowned Sparrow near the university campus. Theme E differs from theme H in that the introductory vibrato has been replaced by a whistle. Songs beginning with two whistles do occur but are in a minority in the San Francisco city region (Baptista 1975).

Theme D consists of three type a syllables followed by a type b vibrato borrowed from theme C and ends with a White-crowned Sparrow trill. Theme G begins

with a White-crowned song but ends with syllable types c and d borrowed from Song Sparrow theme F. Theme K begins with two type e syllables followed by a type f vibrato borrowed from Song Sparrow theme J, and ends once again with a White-crowned Sparrow trill.

To test the accuracy of the Song Sparrow's imitation of White-crowned Sparrow songs, I played his imitations to a White-crowned Sparrow which held a territory within hearing of the Song Sparrow. In response to playback of mimetic song the White-crowned Sparrow immediately flew towards and landed within 1.2 m of me. The White-crowned Sparrow also fluffed its body feathers so that it now looked like a round ball, a typical aggressive display of its species (photographs in Baptista 1982). This was followed by song (Fig. 1B). Mimicked theme H (Fig. 1) and true White-crowned Sparrow song A were subsequently played to naive White-crowned Sparrows in controlled experiments. The experimental subjects were equally aggressive to playback of the alien and mimetic song, suggesting that they did not distinguish between genuine conspecific song and the Song Sparrow's imitations (Catchpole and Baptista, in press). The mimetic Song Sparrow also responded to playback of White-crowned Sparrow song with aggressive displays and song.

Eberhardt and Baptista (1977) suggested that Song Sparrows competing with Wrentits (*Chamaea fasciata*) may learn a few syllables from the latter's songs. This is consistent with Marler and Peters' (1987) laboratory findings that although Song Sparrows prefer to learn conspecific song, they may incorporate a few alien syllables into their songs. This is also consistent with Cooper and Murphy's (1985) observations that in most cases of interspecific song acquisition only parts of alien songs are learned. Why then did this wild Song Sparrow learn entire alien songs in the wild?

White-crowned Sparrows exposed to tapes of both

White-crowned Sparrow song and songs of a number of alien species learned preferentially conspecific song (Marler 1970, Konishi 1985). However, White-crowned Sparrows placed in special cages, which allowed them to see and hear Song Sparrows but only hear White-crowned Sparrows, learned Song Sparrow songs and ignored conspecific song (Baptista and Petrinovich 1986). It was suggested that a live tutor is a more effective learning stimulus than a tape-recorded song (Baptista and Morton 1981) and that social interaction may cancel the innate preference to learn conspecific song (Baptista and Petrinovich 1986).

Nice (1943) followed song development of two hand-raised Song Sparrows and noted that these two individuals vied for dominance and subsequently each bird sang six identical song themes. Accuracy of copying may thus be directly related to intensity of interactions. The fact that the mimetic Song Sparrow responded to playback of White-crowned Sparrow song with aggressive displays (see above) suggests that it had experienced encounters with White-crowned Sparrows. A combination of copious exposure to White-crowned Sparrow song and aggressive encounters with the latter during its early sensitive phase could probably override the Song Sparrow's predisposition to learn conspecific song themes and result in its learning two entire allo-specific songs.

There is now a growing body of literature indicating that two bird species competing intensely may learn each other's songs which are used in aggressive encounters (Sorjonen 1986). Playback studies in areas of sympatry between two competing species of *Acrocephalus* warblers have revealed that they will respond to each other's song even if they themselves do not sing those songs (Catchpole 1978, Catchpole and Leisler 1986). These and other studies indicate that birds learn to recognize competitors by song alone.

White-crowned and Song sparrows are sympatric through much of their range in California. Marshall (1948) found the two species in equal numbers in all seaside chaparral and in wet north-facing slopes of the Richmond Hills in the San Francisco Bay area, California. His cursory observations suggested that they ignored each other and occupied "seemingly superimposed" territories (Marshall 1948:204).

However, Clive Catchpole and I have conducted extensive playback studies on Song Sparrows in San Francisco and Pacifica, California, using tapes of both conspecific and White-crowned Sparrow songs (Catchpole and Baptista, in press). In addition to the mimetic Song Sparrow (see above) we have several observations of naive Song Sparrows reacting to playback of White-crowned Sparrow songs and of Song Sparrows attacking White-crowned Sparrows venturing into their territories. These data suggest that at these localities the two species may be competing for some resource held in common although the exact nature of the resource has not been identified. Once territorial boundaries are established the two species may generally avoid or ignore each other. White-crowned Sparrow songs from a speaker placed in the middle of a Song Sparrow's territory may represent a challenge evoking an aggressive response.

Reed (1982) found that territories of the Chaffinch

(*Fringilla coelebs*) and Great Tit (*Parus major*) overlap on the mainland of Scotland but are mutually exclusive on the adjacent island of Eigg. Mainland birds responded only to playback of conspecific song. However, on Eigg both species responded to playback of both conspecific and allospecific song. There is thus a precedent to my suggestion above that interspecific territoriality may occur at some localities and not others, depending on local habitat characteristics. Competition between Song and White-crowned sparrows may be more severe at localities where optimum habitat is at a premium.

Song themes are often used by passerines in bouts of matched countersinging (Baptista 1975). A search of the campus area surrounding the locality occupied by the mimetic Song Sparrow did not produce any other conspecifics. However, two White-crowned Sparrows were within earshot of the Song Sparrow. Perhaps the singing activity of these White-crowned Sparrows stimulated the Song Sparrow to match their singing activity with mimetic songs, thus enabling the investigator to identify vocal mimicry.

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NEST COOLING AND RECESS LENGTH OF INCUBATING SPRUCE GROUSE¹

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Key words: *Spruce Grouse; Dendragapus canadensis; incubation; recess length; nest cooling.*

In birds with biparental care, foraging requirements of incubating parents can be met while maintaining relatively continuous coverage of the eggs if parents share incubation duties (e.g., gulls, kingfishers, pigeons, and woodpeckers; Skutch 1976), or if the foraging parent feeds the incubating parent (e.g., owls, parrots, some jays; Skutch 1976). However, in birds with uniparental care, the attendant parent may expose the eggs to cooling while absent from the nest on foraging recesses (e.g., pheasants, quails, and grouse; Skutch 1976). Such incubators may modify their attentiveness in response to conditions affecting the cooling of exposed eggs. Cartar and Montgomerie (1985) suggested that small-bodied incubators have a low fasting endurance and modify attentiveness by adjusting the frequency of recesses, while large-bodied incubators adjust the length of recesses.

Grouse are relatively large-bodied single-sex incubators that spend approximately 5% of each 24-hr period away from the nest foraging (e.g., Lennerstedt 1966; Pulliainen 1971, 1978; McCourt et al. 1973; Maxson

1977; Giesen and Braun 1979). We monitored the incubation rhythm of female Spruce Grouse (*Dendragapus canadensis*) in the wild to document the relationship between recess length and the cooling of exposed eggs (as measured by changes in nest-bottom temperature).

METHODS

The study was conducted during May and June in 1983 and 1984 near Gogama (47°30'N, 81°40'W), in north-eastern Ontario, Canada. The study area was a 20-year-old jack pine (*Pinus banksiana*) plantation with an understory of low woody shrubs including blueberry (*Vaccinium angustifolium*), sheep laurel (*Kalmia angustifolia*), and sweet-fern (*Comptonia peregrina*).

Nest bottom temperature was monitored in seven nests throughout incubation for a total of 2,760 hr with strip chart-thermister event recorders (Rustrak model 288). Thermisters were placed under the eggs on the surface of the needle litter comprising the floor of the nest bowl, and were anchored with 4-cm pins to avoid displacement. To ensure that they did not become buried in the needle litter, we checked the thermisters occasionally after hens departed for recesses. We present results for the period of continuous incubation (begins with clutch completion) because hens spent only short periods of time on nests during laying (Mccourt et al. 1973; Naylor et al., unpubl.).

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