

## SHORT COMMUNICATIONS

**Acquisition and recall of Gambel's Sparrow dialects by Nuttall's White-crowned Sparrows in the wild.**—Three subspecies of White-crowned Sparrow (*Zonotrichia leucophrys*) occur in the San Francisco Bay Area of California. Nuttall's Sparrow (*Z. l. nuttalli*) is a circumannual resident (Blanchard 1941, DeWolfe et al. 1989) and often encounters the migratory Puget Sound Sparrow (*Z. l. pugetensis*) which breeds from northern California to British Columbia and winters in the San Francisco Bay Area (Blanchard 1941; DeWolfe and Baptista 1995). The boreal Gambel's Sparrow (*Z. l. gambelii*) also overwinters in the San Francisco Bay Area (Blanchard and Erickson 1949:259). However, in many years of intense banding during migration, DeWolfe (pers. comm.) found that only about 1% of wintering migrant flocks consisted of *gambelii*. The rest were mostly *pugetensis*.

Since 1968, Baptista has encountered twelve territorial White-crowned Sparrows in the San Francisco Bay Area singing songs typical of Puget Sound Sparrows. Ten were positively identified as Nuttall's Sparrows (Baptista 1974, Baptista 1977, and unpubl. data). Nuttall's Sparrows may learn Gambel's Sparrows songs in the laboratory (Baptista and Petrinovich 1986), yet learning of Gambel's Sparrow songs by Nuttall's Sparrows has not been encountered in the wild. We document herein two incidences of Nuttall's Sparrows learning Gambel's Sparrow songs in the wild, and postulate how they acquired these songs.

At 08:15 on 15 May 1993, Baptista heard a song typical of a migratory Gambel's Sparrow (Fig. 1A) on the corner of Pacheco and Sunset Boulevard, San Francisco, California. On 27 May, we recorded an individual (probably the same one) singing a Gambel's Sparrow song (Fig. 1B) as well as a Nuttall's Sparrow theme at this same locality (Fig. 1D, E). This individual (henceforth referred to as G1) responded to playback with approach, aggressive trilling, song, and display, suggesting that he was defending a territory. On 18–19 June 1996, we recorded a second individual (G2) singing a song typical of wintering Gambel's Sparrows (Fig. 1C) in Golden Gate Park, San Francisco, and this bird also responded to playback, indicating that it had settled on a territory. Subsequently, both G1 and G2 were trapped, color-banded and identified to subspecies (see below).

Songs of Gambel's Sparrows are easily distinguished from those of Nuttall's Sparrows from San Francisco on the basis of syllable structure and syntax (Austen and Handford 1991; Baptista and King 1980; Chilton et al. 1990; Chilton and Lein 1996a; DeWolfe et al. 1974; Kern and King 1972). We recorded 27 renditions of Gambel's songs and eight renditions of Nuttall's songs from G1 on May 27 and examined them with a Kay Elemetrics DSP continuous Spectral Analyser. Songs of four Nuttall's Sparrow neighbors were also recorded for comparison. Six of G1's Gambel's songs ranged in duration from 2.06 to 2.20 sec ( $\bar{x}$  = 2.13 sec). The warble following G1's introductory whistle (Fig. 1B) was similar to warble number six from DeWolfe et al.'s (1974) catalogue. Other than variation in duration his songs were very stereotyped and typical of those described by DeWolfe et al. (1974) for Gambel's Sparrows.

Ten of G2's songs ranged from 2.1 to 2.34 sec ( $\bar{x}$  = 2.26 sec) in duration. The warble following the introductory whistle in G2's song (Fig. 1C) may also be assigned to type six in DeWolfe et al.'s (1974) catalog. The two buzzes that follow the warble are typical of Gambel's songs (compare with A), however, the terminal trill does not match any Gambel's song published to date. Terminal buzzes range from about 2.5 or 2.75 to 6 kHz, and this is always preceded by a syllable ranging from about 3 or 3.5 kHz to 7 or 7.5 kHz. The structure of each syllable in G2's terminal trill and the fact that they range from 3 to 7.5 kHz suggests

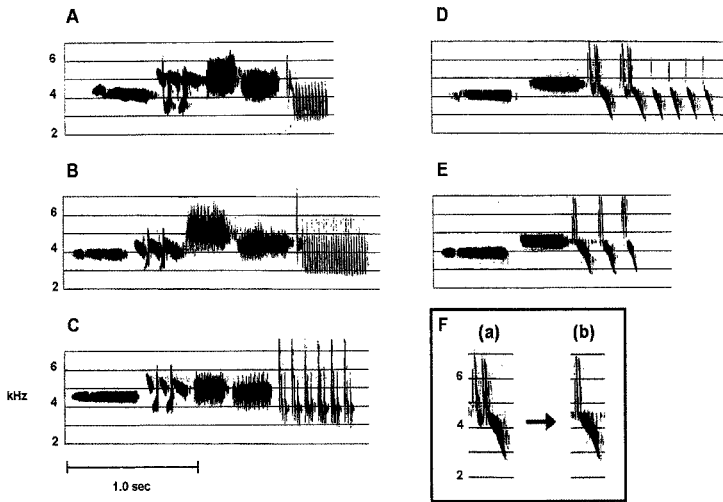


FIG. 1. (A) Gambel's Sparrow song from a visiting territorial migrant recorded on 20 December 1993. (B) Gambel's Sparrow song of bird G1. (C) Gambel's Sparrow song of bird G2. (D) Nuttall's Sparrow theme of neighbor of G1. (E) Nuttall's Sparrow theme of G1. (F) (a) Complex syllable of song D. (F) (b) Trill syllable from song E. Note that this is the second subsyllable of complex syllable (a).

that G2 improvised during song ontogeny and constructed a novel trill consisting of syllables typically preceding the terminal buzz in Gambel's Sparrow songs.

G1 sang a second theme (Fig. 1E) similar to those of local Nuttall's White-crowned Sparrows (Fig. 1D). Following two introductory whistles, G1's renditions of a Nuttall's theme (Fig. 1E) contained three syllables which were a modification of the complex syllables in its immediate neighbor's song. G1's songs contain the second subsyllable of his neighbor's complex syllable type (Fig. 1D and insert F). Similar modifications of complex syllables are commonplace in songs of female Nuttall's Sparrows (Baptista et al. 1993a), but this is only the second time we have encountered this phenomenon in male song.

There is individual variation in complex syllables contained in Nuttall's songs (Baptista 1975, Petrinovich 1988). Four other Nuttall males were recorded near G1's territory, but only his immediate neighbor (Fig. 1D) sang a song containing complex syllables most similar to his. On 6 August 1993, Baptista returned to this locality and with playback attracted G1 and a second individual believed to be his mate. The two birds foraged within a meter of each other, no aggression was observed, and both birds arrived and left together. On this day G1 sang only Nuttall's songs.

To test if the unused song could be elicited by playback, Baptista played 101 Gambel's songs to G1 on 7 August 1993. G1 responded by approach, aggressive displays, and countersinging with the tape recorder. He sang 163 Nuttall's songs and only three Gambel's songs in response to playback. The first Gambel's song was sung only after 75 Gambel's songs were played to him. His preference had shifted from singing Gambel's songs to singing Nuttall's songs. The following year, on 27 May 1994, we played 78 renditions of his Gambel's songs, and he responded with 120 Nuttall's songs and four Gambel's songs. He had been singing only Nuttall's songs prior to our playback experiments.

Migratory Gambel's Sparrows are 100% separable from sedentary Nuttall's Sparrows in morphology (Blanchard and Erickson 1949). G1 and G2 matched the local Nuttall Sparrows in all the characteristics outlined by Blanchard and Erickson (1949) and Banks (1964). We conclude from this that G1 and G2 were local Nuttall's Sparrows that had acquired their song from migratory Gambel's Sparrows. How were the alien dialects acquired?

Gambel's Sparrows typically arrive on their wintering grounds between mid-September and early October and leave in mid- to late April. Blanchard and Erickson (1949) documented much singing, pursuits, and brief fights by newly arrived Gambel's Sparrows in September. Singing is sporadic throughout much of the winter and then increases over the winter level by the second week of March, notably when birds gather in their roosting tree (DeWolfe, pers. comm.). Nuttall's Sparrows have been seen feeding young from late March to early September (DeSante and Baptista 1989). Thus, early or late-hatched Nuttall's Sparrows could encounter overwintering Gambel's Sparrows in their acoustic environment.

We found, moreover, that an over-wintering Gambel's Sparrow would respond to playback of Nuttall's song with approach to the speaker, posturing, and loud singing (Fig. 1A). This individual was captured in Golden Gate Park, and banded and reappeared at the same site the following year. This suggests that not only do over-wintering flocks occupy exclusive home ranges (Mewaldt 1964) but that these areas may be defended with song even against allosubspecific individuals. Some juvenile Nuttall's Sparrows begin staking out territories and sing full songs between mid July and late September (DeWolfe et al. 1989, Baptista and Gaunt 1997). Such juveniles may challenge and countersing with visiting Gambel's Sparrows, and thus acquire the latter's song.

If Nuttall's Sparrows are able to acquire songs from visiting migrants and songs are passed on by vocal tradition, why are there not more individuals singing alien dialects and how are local song dialects preserved? Although individuals in the wild typically sing only one song type (more rarely two or three; reviews in Baptista and King 1980; Chilton and Lein 1996b), birds in the laboratory may be tutored with as many as seven dialects, elements of which may be produced during the rehearsed song stage (Marler and Nelson 1993). Marler and Nelson (1993) suggested that through the process of matched countersinging, the songs sung by a neighbor or neighbors are evoked and retained and those not present in the repertoire of local birds fall into disuse and are eliminated. There is thus "overproduction" during the practice stage, followed by narrowing of the repertoire as a result of social interaction.

Matched countersinging in the wild has been documented for several subspecies of White-crowned Sparrows (Baptista 1975, 1977; Baptista and Morton 1988; Chilton and Lein 1996b), and Baptista and Morton (1988) have documented narrowing of repertoire at the start of the first breeding season in the montane White-crowned Sparrow (*Z. l. oriantha*).

On 27 and 29 May 1993, G1's song repertoire consisted mostly of Gambel's songs (27 vs. 8 Nuttall's songs recorded). On August 6 and 7, his repertoire consisted mostly of Nuttall's songs (163 vs 3). Matched-countersinging with his three Nuttall's neighbors had apparently shifted his preference from singing Gambel's themes to singing Nuttall's songs.

Juvenile Nuttall's Sparrows in the laboratory begin singing (the practice stage) nine months after hatching (Konishi 1965, Baptista and Petrinovich 1986, Nelson et al. 1995); however, fledgling Nuttall's Sparrows in the wild may sing subcrystallized song by 28 days of age (Baptista et al. 1993b). Song may crystallize by 90 days when juveniles first establish territories. Matched countersinging and repertoire reduction has been observed in January (DeWolfe et al. 1989). Our observations of G1 indicate, however, that whittling of repertoire size is not confined to the early part of the year but may take place as late as August or in whatever period a bird singing several songs finally settles on a territory.

Playback studies have shown that Nuttall's Sparrows respond strongly to local dialects

but hardly at all to song of the alien subspecies *pugetensis* (Petrinovich and Patterson 1981). In contrast, G2's three Nuttall neighbors responded strongly to playback of his alien Gambel's song. By associative learning, these neighbors had learned to react to his alien dialect (see Richards 1979).

To our surprise, five out of seven White-crowns holding territories out of earshot from G2 also responded to playback of his Gambel song (Cebrian, unpubl. data). These individuals held territories 0.31 to 2.1 km from G2's territory (median 2.07 km). This indicates that these aggressive individuals must have interacted with wintering Gambel's Sparrows or with G2 himself. Since wintering Gambel's Sparrows are sometimes territorial (see above), storing their songs enables Nuttall's Sparrows to identify potential competitors. Storage of alien songs by White-crowns, namely those of Song Sparrows (*Melospiza melodia*), to be used for recognition of competitors, has been documented previously (Baptista 1990, Catchpole and Baptista 1988).

It is thus likely that more Nuttall's Sparrows acquire songs of Gambel's Sparrows in the wild than are detected. However, due to matched countersinging with neighbors during settling, local dialects are selected for and rare alien dialects fall into disuse. Elimination of song from a bivalent repertoire in a White-crown's second year has been documented previously (Baptista and Morton 1988). If G1 behaved likewise, then our playback experiments indicate that such lost songs may be recalled and vocalized with stimulation by intense playback even a year later.

In summary, if there are barriers to Nuttall's Sparrows learning songs of Gambel's Sparrows in the wild, it is clear that they are not insurmountable. Under appropriate conditions, Nuttall's Sparrows can indeed learn songs of the other subspecies. Incidence of Nuttall's Sparrows learning Gambel's songs may be rare only because the latter are rare as winter visitants. Local dialects are preserved by matched countersinging and narrowing of song repertoires, and the narrowing process may take place well beyond the start of the breeding season. Moreover, a previously used song absent from the current repertoire may be evoked by matched countersinging.

*Acknowledgments.*—These studies were supported in part by NSF stipends BNS 8919453 and IBN 9306467 to LFB. DAB was supported by a Tilton Postdoctoral Fellowship from the California Academy of Sciences. We thank Peter Marler, Douglas Nelson, David Spector and two anonymous reviewers, for comments on an earlier version of the manuscript, and Kathleen Berge for typing the manuscript.

#### LITERATURE CITED

- AUSTEN, M. J. W. AND P. T. HANDFORD. 1991. Variation in the songs of breeding Gambel's White-crowned Sparrows near Churchill, Manitoba. *Condor* 93:147–152.
- BANKS, R. C. 1964. Geographic variation in the White-crowned Sparrow *Zonotrichia leucophrys*. *Univ. Calif. Publ. Zool.* 70:1–123.
- BAPTISTA, L. F. 1974. The effects of songs of wintering White-crowned Sparrows on song development in sedentary populations of the species. *Z. Tierpsychol.* 34:147–171.
- . 1975. Song dialects and demes in sedentary populations of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). *Univ. Calif. Publ. Zool.* 105:1–52.
- . 1977. Geographic variation in song and dialects of the Puget Sound White-crowned Sparrow. *Condor* 79:356–370.
- . 1990. Song learning in the White-crowned Sparrow (*Zonotrichia leucophrys*): sensitive phases and stimulus filtering revisited. Pp. 143–152 in *Current Topics Avian Biol.* Proc. Int. 100. DO-G Meeting, Bonn, Germany.
- AND S. L. L. GAUNT. 1997. The role of social interaction on vocal development in

- birds. Pp. 23–40 in *Social Influences on vocal development* (M. Hausberger and C. Snowden, eds.). Cambridge Univ. Press, London, England.
- AND J. R. KING. 1980. Geographical variation in song and song dialects of montane White-crowned Sparrows. *Condor* 82:267–284.
- AND M. L. MORTON. 1988. Song learning in montane White-crowned Sparrows: from whom and when. *Anim. Behav.* 36:1753–1764.
- AND L. PETRINOVICH. 1986. Song development in the White-crowned Sparrow: social factors and sex differences. *Anim. Behav.* 34:1359–1371.
- , P. W. TRAIL, B. B. DEWOLFE, AND M. L. MORTON. 1993a. Singing and the functions thereof in female White-crowned Sparrows, *Zonotrichia leucophrys*. *Anim. Behav.* 46: 511–524.
- , D. A. BELL, AND P. W. TRAIL. 1993b. Song learning and production in the White-crowned Sparrow: parallels with sexual imprinting. Pp. 17–33 in *Proceedings International Conference on Sexual Imprinting and Song-learning* (Haaren, Holland, 1992) (C. ten Cate and J. Kruijt, eds). Netherlands J. Zool. 43(1–2).
- BLANCHARD, B. D. 1941. The White-crowned Sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. *Univ. Calif. Publ. Zool.* 46:1–78.
- AND M. M. ERICKSON. 1949. The cycle in the Gambel Sparrow. *Univ. Calif. Publ. Zool.* 47:255–318.
- CATCHPOLE, C. K. AND L. F. BAPTISTA. 1988. A test of the competition hypothesis of vocal mimicry, using Song Sparrow imitations of White-crowned Sparrow song. *Behaviour* 106:119–128.
- CHILTON, G. AND M. R. LEIN. 1996a. Songs and sexual responses of female White-crowned Sparrows (*Zonotrichia leucophrys*) from a mixed-dialect population. *Behaviour* 133: 173–198.
- AND ———. 1996b. Song repertoires of Puget Sound White-crowned Sparrows *Zonotrichia leucophrys pugetensis*. *Journal of Avian Biology* 27:31–40.
- , ———, AND L. F. BAPTISTA. 1990. Mate choice by female White-crowned Sparrows in a mixed-dialect population. *Behav. Ecol. Sociobiol.* 27:223–227.
- DESANTE, D. AND L. F. BAPTISTA. 1989. Factors affecting the termination of breeding in Nuttall's White-crowned Sparrow. *Wilson Bull.* 101:120–124.
- DEWOLFE, B. B. AND L. F. BAPTISTA. 1995. Singing behavior, song types on their wintering grounds and the question of leap-frog migration in Puget Sound White-crowned Sparrows. *Condor* 97:376–389.
- , ———, AND L. PETRINOVICH. 1989. Song development and territory establishment in Nuttall's White-crowned Sparrows. *Condor* 91:397–407.
- , D. D. KASKA, AND L. J. PEYTON. 1974. Prominent variations in the songs of Gambel's White-crowned Sparrows. *Bird Banding* 45:224–252.
- KERN, M. D. AND J. R. KING. 1972. Testosterone-induced singing in female White-crowned Sparrows. *Condor* 74:204–209.
- KONISHI, M. 1965. The role of auditory feedback in the control of vocalization in the White-crowned Sparrow. *Z. Tierpsychol.* 22:770–783.
- MARLER, P. AND D. A. NELSON. 1993. Action-based learning: a new form of developmental plasticity in bird song. *Netherlands J. Zool.* 43:91–103.
- MEWALDT, L. R. 1964. Effects of bird removal on a winter population of sparrows. *Bird Banding* 35:184–195.
- NELSON, D. A., P. MARLER, AND A. PALLERONI. 1995. A comparative approach to vocal learning: intraspecific variation in the learning process. *Anim. Behav.* 50:83–97.
- PETRINOVICH, L. 1988. Individual stability, local variability and the cultural transmission of

song in White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*). Behaviour 107:208–240.

— AND T. L. PATTERSON. 1981. The response of White-crowned Sparrows to songs of different dialects and subspecies. Z. Tierpsychol. 57:1–14.

RICHARDS, D. G. 1979. Recognition of neighbors by associative learning in Rufous-sided Towhees. Auk 96:688–693.

LUIS F. BAPTISTA, ANDREA JESSE, DOUGLAS A. BELL, AND CHRISTIAN CEBRIAN, *Dept. of Ornithology and Mammalogy, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118. Received 25 Sept. 1996, accepted 1 April 1997.*

*Wilson Bull.*, 109(3), 1997, pp. 521–526

**Status of Neotropical migrants in three forest fragments in Illinois.**—Species that breed in temperate North America but migrate to the tropics in the nonbreeding season (hereafter “Neotropical migrants”) have become a focal point of ornithological research and management (e.g., Hagan and Johnston 1992, Martin and Finch 1995). This concern and interest results from the finding that some Neotropical migrants have shown clear and unambiguous declines throughout their ranges (e.g., Cerulean Warbler [*Dendroica cerulea*], Robbins et al. 1992), and most species have shown pronounced declines in isolated woodlots (Askins et al. 1990) and/or some geographic regions (James et al. 1996). Regardless of how widespread declines are, high levels of nest parasitism by cowbirds and increased levels of nest predation on these species are phenomena worthy of research and management concern.

Reproductive success of many Neotropical migrants varies dramatically across their ranges in response to the degree of forest fragmentation (Robinson et al. 1995). Generally, the greater the fragmentation and the lower the proportion of forest in the landscape, the lower the reproductive success (Robinson et al. 1995). This pattern suggests that source-sink models of population structure may be very applicable to forest-nesting neotropical migrants (Brawn and Robinson 1996). The contiguous “cornbelt” region of Illinois, Indiana, Ohio, Missouri, and adjacent states may represent one of the largest reproductive sinks for these species (Brawn and Robinson 1996). We tested the generality of this idea by using mist nets to monitor reproductive success in three woodlots in east-central Illinois, including two of the largest forest fragments in this region.

**Study area and methods.**—We selected three forest fragments that appeared to be the best available habitat in east-central Illinois for area-sensitive, forest-nesting neotropical migrants. Two sites, Fox Ridge State Park (454 ha) in Coles County and Walnut Point State Park (223 ha) in Douglas County, were the largest contiguous blocks of forest in their respective counties. The third site, Baber Woods, is a Nature Conservancy preserve that, although much smaller (20 ha), is one of the largest stands of virgin timber in east-central Illinois. Vegetation was sampled at each site, using 12 0.04 ha circular plots (James and Shugart 1970), located randomly along the mist-net line.

We mist netted birds in each woodlot following the methods of Robinson (1992; see also Bollinger and Linder 1994). Twenty nets (black, 36 mm mesh, 12 m) were strung end-to-end along the net line and opened for three consecutive days from 06:00–12:00 CDT. Two, 20-net lines were sampled at Fox Ridge and Walnut Point but only one line at Baber Woods because of its smaller size. Each line was sampled twice, once between 20 June and 6 July 1993 and once between 7 July and 23 July 1993. Lines were located in the centers of each