A PROBABLE GRASSHOPPER × SAVANNAH SPARROW HYBRID
SINGING A SONG SPARROW SONG

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ABSTRACT.—We observed a male sparrow in May 1999 in Stow, Massachusetts, that showed hybrid characteristics resembling both Grasshopper Sparrow (Ammodramus savannarum) and Savannah Sparrow (Passerculus sandwichensis). During 1999 and 2000, this male sang a simplified Song Sparrow (Melospiza melodia) song. However, in 2001 it also sang a typical Savannah Sparrow song and frequently alternated between these two songs. We recorded songs and captured this individual in an area with numerous Song Sparrows and about three pairs of Savannah Sparrows. We compared mitochondrial DNA, morphological measurements, behavior, and audio spectrograms of this hybrid with similar data from Grasshopper, Savannah, and Song sparrows. Genetic analysis indicated that the hybrid’s mother was almost certainly a Grasshopper Sparrow. The hybrid showed morphological traits that were within the range of both Savannah Sparrow and Song Sparrow, but generally were more consistent for Savannah Sparrow. We observed this individual frequently associating with Savannah Sparrows, attempting to copulate with a female Savannah Sparrow, carrying Savannah Sparrow fecal sacs, and feeding young Savannah Sparrows, lending additional support to Savannah Sparrow paternity. We conclude that this individual was a Grasshopper × Savannah sparrow hybrid that learned to imitate the songs of Song Sparrows at an early stage of development. Interestingly, the hybrid’s exposed culmen was considerably longer than culmen measurements of any of the three species of sparrows under consideration. Received 16 October 2002, accepted 19 May 2003.

Approximately 10% of all bird species have been reported to produce hybrid offspring, and 8% of species in the order Passeriformes hybridize (Grant and Grant 1992). Evidence of natural hybridization can provide important insights regarding established phylogenies and can shed light on species relationships (Lewontin and Birch 1966).

We first observed a unique sparrow at DeLANEY Wildlife Management Area (42° 27’ N, 71° 33’ W) in Stow, Massachusetts, on 15 May 1999 that delivered a song similar to that of the Song Sparrow (Melospiza melodia), but that had morphological features more consistent with the Grasshopper Sparrow (Ammodramus savannarum) and the Savannah Sparrow (Passerculus sandwichensis; Fig. 1). We observed this apparent hybrid in a small, flat, open grassland of approximately 5 ha, bordered by shrubs along a stream and woodland edge.

Grasshopper Sparrows are uncommon and local in Massachusetts, with only 18 known breeding sites (Jones 2000). One to two territorial male Grasshopper Sparrows had been recorded at this site since 1993 (Jones and Vickery 1997). Savannah Sparrows are common in Massachusetts (Veit and Petersen 1993) and three to four pairs bred at this site during this period. Both species nest in grasslands, usually with sparse shrubs and weeds, and tend to avoid forested edges (Rising 1996, Vickery 1996). Song Sparrows also are common in Massachusetts and were observed regularly in the brushy habitats bordering this grassland, as well as perched on weed stalks in the grassland (ALJ pers. obs.).

There has been one report of a Grasshopper Sparrow hybridizing with a Savannah Sparrow (Dickerman 1968), but no reports of Grasshopper × Song sparrow hybrids and to our knowledge, this is the first report of a hybrid learning the song that differed from either parent. To determine the parents of this unusual, presumably hybrid sparrow, we compared mitochondrial DNA (mtDNA), morphological characteristics, behavior, and vocalizations of the hybrid with Grasshopper, Savannah, and Song sparrows.
FIG. 1. Presumed Grasshopper × Savannah Sparrow hybrid, Stow, Massachusetts, 25 July 1999. (A) The flat-headed profile and yellow lores closely resemble the Grasshopper Sparrow, (B) the underwing and faintly streaked flank and breast are similar to the Savannah Sparrow, (C) the dark crown with a thin pale median stripe is similar to the Grasshopper Sparrow, and (D) the short tail is similar to Grasshopper and Savannah Sparrows. The very long culmen is considerably longer than Grasshopper, Savannah, or Song sparrows. Photographs by S. A. Perkins.

METHODS
Morphology and behavior.—We captured the sparrow on 25 July 1999 and attached a USFWS metal tag on the left leg and two white plastic color bands on the right leg. We measured the exposed culmen, bill depth at tip of nares, bill length from nape to tip, wing chord, tarsus, tail, and distance between the longest primary and longest secondary feathers (Pyle et al. 1997). We aged, sexed, and checked this individual for fat content and molt, and compared these measurements to morphological measurements in Pyle et al. (1997) and Rising (1996), using the appropriate subspecies and geographic region for these comparisons.

We made > 20 h of detailed observations of the hybrid’s behaviors and songs during the summers of 1999, 2000, and 2001. On 16 July 1999, we recorded songs of the hybrid, a Song
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Sparrow, and a Savannah Sparrow using a cassette recorder with a Sennheiser microphone (Macauley Library of Natural Sounds catalog number 105896). The song was analyzed using a Kay Elemetrics signal analysis workstation. Audio spectrograms were produced using Canary (ver. 1.2.4) with 128-point frame length and 43-Hz frequency resolution. We then compared these recordings to published songs of Song, Savannah, and Grasshopper sparrows (Elliot et al. 1997, Righter and Keller 1999, Fig. 2).

Genetic analysis.—We collected a 0.05-ml blood sample from the presumed hybrid's brachial vein and stored it in a lysis buffer solution for genetic analysis. We isolated total genomic DNA from the presumed hybrid using standard phenol chloroform extraction protocol (Sambrook et al. 1989). A 1.1-kb fragment of the mitochondrial (mtDNA) control region was amplified using Grasshopper Sparrow-specific mtDNA control region primers (NLB unpubl. data) via the polymerase chain reaction. A total of 206 bp of the fragment was sequenced and was visually aligned against 171 Grasshopper Sparrow sequences (NLB unpubl. data) and to the only Song Sparrow sequence available at GenBank (GenBank accession # AF053882). We then determined the number of base pair substitutions among all haplotypes. Unfortunately, we were unable to compare the hybrid's mtDNA to Savannah Sparrow because there were no GenBank submissions for the Savannah Sparrow control region DNA sequence.

RESULTS AND DISCUSSION

Genetic analysis.—The percent sequence similarity among different Grasshopper Sparrow haplotypes was ≥98% (Bulgin 2000), whereas the Song Sparrow haplotype had a maximum of 78% sequence similarity to the Grasshopper Sparrow haplotypes. The hybrid haplotype was identical to one Grasshopper Sparrow haplotype and had a 77% sequence similarity to the Song Sparrow haplotype. The similarity between the hybrid and the Grasshopper Sparrow haplotypes is well within the range of intraspecific variation observed for Grasshopper Sparrow (Bulgin et al. 2003) while the more limited similarity observed between the hybrid and Song Sparrow is representative of a between-species comparison (Bulgin et al. 2003). The mtDNA sequence provided strong evidence that the mother of this individual was a Grasshopper Sparrow and not a Song Sparrow.

Morphological characteristics.—We determined that the sparrow was an after-hatch-year male in 1999 because it had no brood patch but did have a cloacal protuberance (Pyle et al. 1997). This individual was molting heavily on the head and body. In the field, we observed morphological and plumage features that were characteristic of Grasshopper Sparrow: flat head, dark crown with a buffy white median crown stripe, yellow on edge of the wing at the carpal joint, and golden yellow lores (Vickery 1996). The limited streaking across the breast more closely resembled a Savannah Sparrow than a Song Sparrow, but the influence of hybridizing with unstreaked Grasshopper Sparrows could obfuscate this distinction.

The father of this hybrid could have been a Savannah Sparrow or a Song Sparrow. Three of six morphological measurements (nares depth, wing chord, tail) of the hybrid fell within the range of Savannah Sparrows and two of the remaining three measurements (tarsus, primary extension) were slightly longer on the hybrid than reported for Savannah Sparrows (Table 1). Three measurements (wing chord, primary extension, tarsus) fit within the range of Song Sparrows but depth of nares and tail length were considerably smaller in the hybrid. The morphological measurements make it very unlikely that the father was a Grasshopper Sparrow because all six hybrid measurements were beyond the known range of male Grasshopper Sparrows (Table 1). The hybrid's exposed culmen was considerably longer than any of the three species of sparrows (Table 1).

Behavior.—During 1999 and 2000, we observed the hybrid using various perches to sing a simplified Song Sparrow song. We found no evidence of nesting behavior or interactions with other birds during these two breeding seasons. However, in June 2001, we noted that the bird sang different songs than the Savannah Sparrow (Bulgin et al. 2003) while the more limited similarity observed between the hybrid and Song Sparrow is representative of a between-species comparison (Bulgin et al. 2003). The mtDNA sequence provided strong evidence that the mother of this individual was a Grasshopper Sparrow and not a Song Sparrow.
FIG. 2. Audio spectrograms of (A–B) two song types recorded from a presumed Grasshopper × Savannah Sparrow hybrid, and single songs from (C) a Song Sparrow, (D) Savannah Sparrow, and (E) Grasshopper Sparrow. Unlike most Song Sparrows in northeastern North America which have a repertoire of 8–9 songs, the hybrid’s repertoire was limited to two song types (A and B). Songs A–D were recorded in Stow, Massachusetts, 16 July 1999, by W. G. Shriver and song E was recorded in Montana (Righter and Keller 1999).
Measurements from Rising (1996) and Pyle et al. (1997).

<table>
<thead>
<tr>
<th>Measurement (mm)</th>
<th>Savannah Sparrow</th>
<th>Song Sparrow</th>
<th>Grasshopper Sparrow</th>
<th>Hybrid sparrow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exposed culmen</td>
<td>9.6–11.9</td>
<td>11.4–13.2</td>
<td>10.5–12.2</td>
<td>14.0</td>
</tr>
<tr>
<td>Depth at tip of nares</td>
<td>4.9–6.0</td>
<td>6.3–7.2</td>
<td>5.7–6.3</td>
<td>5.2</td>
</tr>
<tr>
<td>Tarsus</td>
<td>18.4–21.6</td>
<td>20.3–23.4</td>
<td>18.3–20.3</td>
<td>22.0</td>
</tr>
<tr>
<td>Wing chord</td>
<td>65.0–74.0</td>
<td>61.0–72.0</td>
<td>58.0–65.0</td>
<td>68.0</td>
</tr>
<tr>
<td>Distance between longest primary and longest secondary</td>
<td>2.0–7.0</td>
<td>4.0–12.0</td>
<td>—</td>
<td>8.0</td>
</tr>
<tr>
<td>Tail</td>
<td>46.0–57.0</td>
<td>61.0–71.0</td>
<td>42.0–50.0</td>
<td>52.0</td>
</tr>
</tbody>
</table>

*Measurements from Rising (1996) and Pyle et al. (1997).*

Sac from this patch and interacted with another sparrow of undetermined gender. When a Savannah Sparrow carried food to the same nest patch, it was repeatedly chased by the hybrid. We saw paired male and female Savannah Sparrows in the vicinity of the nest, and these individuals were aggressive toward the hybrid. By 15 June, the hybrid sang the Savannah Sparrow song only once or twice a day, and we found fledgling Savannah Sparrows near the nest patch. The hybrid remained at this site and was agitated by the presence of other birds, chirping frequently. Later in July 2001, the hybrid repeatedly attempted to copulate with a female Savannah Sparrow and chased other Savannah Sparrows.

We think that the hybrid was more likely genetically related to Savannah Sparrows because of the numerous interactions with Savannah Sparrows and the fact that we never observed it interact with Song Sparrows. There is a previous report of hybridization between Grasshopper and Savannah sparrows (Dickerman 1968), and a case of a female Grasshopper Sparrow “egg-dumping” in a Savannah Sparrow nest (Wiens 1971).

**Song.**—In 1999 and 2000, the hybrid sang only a simplified Song Sparrow song. In 2001, we observed it singing both Song and Savannah sparrow songs, although it delivered the Song Sparrow song more frequently (>75%, n > 60). On at least two occasions, the hybrid alternated between Song Sparrow and Savannah Sparrow songs with no pause between songs. In New England, Song Sparrows (*M. m. melodia*) typically have a repertoire of 8–9 different songs (Peters et al. 2000). Although the hybrid’s songs were similar in quality to that of Song Sparrows, it had a repertoire of only two song types (Fig. 2 A–B), which it alternated (A, B, A, B, A, B). Both of the hybrid’s song types started with typical Song Sparrow introductory notes, but only song type B ended with the standard Song Sparrow trill (Fig. 2B). The hybrid’s song type B was remarkably similar to a Song Sparrow song recorded at the same site (Fig. 2C), providing additional support for the thesis that this bird learned his limited Song Sparrow repertoire from neighboring Song Sparrows. We were unable to record Savannah Sparrow songs from this individual.

**Conclusion.**—Using four types of information to assess the parentage of this hybrid sparrow, we determined that the mother was almost certainly a Grasshopper Sparrow and that the father was probably a Savannah Sparrow. The mtDNA analysis, indicating the maternal line, showed a close sequence similarity with a Grasshopper Sparrow and we think the morphological analyses, behavior, and song were more consistent with Savannah Sparrow than Song Sparrow for the father. In addition, Song Sparrows have been known to hybridize only with White-crowned Sparrows (*Zonotrichia leucophrys*; Dickerman 1961).

The most unexpected aspect of this Grasshopper × Savannah Sparrow hybrid was the fact that this individual usually delivered a simplified Song Sparrow song. Because song normally is inherited from the paternal line or learned from neighboring males in the nestling stage (Slater 1989), especially from species with high population densities (Jung et al. 1994), the hybrid probably learned these songs from neighboring Song Sparrows whose ranges overlapped with Savannah Sparrows. Although the structure of song was similar to
that of Song Sparrows, the limited song repertoire (two song types) was consistent with that of Grasshopper Sparrows. Hybrid sparrows have been reported to sing a mixture of both parental songs, incorporating elements from each parent, e.g., White-throated Sparrow (Zonotrichia albicollis) × Dark-eyed Junco (Junco hyemalis; Jung et al. 1994) and Clay-colored Sparrow (Spizella pallida) × Field Sparrow (Spizella pusilla; Hoag 1999), but we are unaware of a previous case where a hybrid Emberizid sang a song that was not inherited from the father or other conspecifics.

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