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EXTENDED FLIGHT-SONGS OF VESPER SPARROWS

JEFFREY V. WELLS[1] AND PETER D. VICKERY[2]

ABSTRACT.—While conducting fieldwork on the breeding ecology of grassland birds at Kennebunk, Maine, we documented the existence of extended flight-songs of Vesper Sparrows (*Pooecetes gramineus*). In general, we observed this behavior very infrequently, usually less than three times per breeding season. Extended flight-songs were about three times as long as primary songs and contained elements not typically found in primary songs. Extended flight-songs occurred more frequently late in the breeding season. Within the subfamily Emberizinae, extended flight-songs have now been documented for at least 10 species but their behavioral function remains unclear. *Received 8 Nov. 1993, accepted 21 April 1994.*

In a recent review, Spector (1992) classified the song systems of wood-warblers (Parulinae) into subsets. For some genera, he distinguished between "primary" song—a song type used most frequently and often given less frequently after mating—and "extended" song—a song type heard less commonly and often given in flight. Extended songs are best known from the Parulinae (Ficken and Ficken 1962, Spector 1992), most notably Common Yellowthroat (*Geothlypis trichas*) (Ritchison 1991) and Ovenbird (*Seiurus aurocapillus*) (Lein 1981). At least 17 species of Emberizinae also have extended songs, and in at least ten species these songs are typically given in flight (Table 1). Within the Emberizinae, only Cassin's Sparrow (*Aimophila cassinii*), Lark Bunting (*Calamospiza melanocorys*), *Calcarius* longspurs, and *Plectrophenax* buntings regularly sing their primary song in flight (Austin 1968a).

METHODS AND RESULTS

During the course of fieldwork on the breeding ecology of grassland birds in Kennebunk, Maine (43°23′N, 70°37′W), we documented the "extended flight-song" of Vesper Sparrows (*Pooecetes gramineus*). The infrequency of this behavior may explain why it has not been well-documented; it also complicates interpretation of its function. Until July 1993, we had observed this behavior among a population of 50–100 pairs only 24 times during eight of 10 field seasons, despite being in the field for >40 h/week for the entire breeding season. The exception came on the mornings of 28 and 30 July 1993 when Wells noted at least 20 extended flight-songs and recorded several examples (Cornell Laboratory of Ornithology, Library of Natural Sounds Catalog Numbers 55508–55511 and 63000). During this observation period there was an average of one extended flight-song every 15–20 min in an area where 8–10 pairs of Vesper Sparrows had established territories.

Extended songs of Vesper Sparrows differ in several ways from their primary songs (Figs. 1 and 2). They are longer, approximately 6–10 sec in duration compared to primary song

[1] New York Cooperative Wildlife Research Unit, Fernow Hall, Cornell Univ., Ithaca, New York 14853. [2] Wildlife Dept., Univ. of Maine, Orono, Maine 04469. Present address: Center for Biological Conservation, Massachusetts Audubon Society, Lincoln, Massachusetts 01773.

TABLE 1

SPECIES OF EMBERIZINAE FOR WHICH EXTENDED SONGS HAVE BEEN DOCUMENTED

Species	Song characteristics	Reference
California Towhee (*Pipilo crissalis*)	P, U, I	Childs 1968
Bachman's Sparrow (*Aimophila aestivalis*)	F, U, I	Mengel 1951
Field Sparrow (*Spizella pusilla*)	P	Nelson and Croner 1991
Vesper Sparrow (*Pooecetes gramineus*)	F, U, I	Present study, Burroughs 1905
Lark Sparrow (*Chondestes grammacus*)	F, C	Baepler 1968
Grasshopper Sparrow (*Ammodramus savannarum*)	P	Smith 1959
Henslow's Sparrow (*A. henslowi*)	F, U, I	Graber 1968
LeConte's Sparrow (*A. leconteii*)	P?, U, I	Walkinshaw 1968
Sharp-tailed Sparrow (*A. caudacutus*)	F, U	Greenlaw 1993
Seaside Sparrow (*A. maritimus*)	F, U	McDonald 1983
Song Sparrow (*Melospiza melodia*)	F, U, I	Nice 1943
Lincoln's Sparrow (*M. lincolnii*)	F, U, I	Speirs and Speirs 1968
Swamp Sparrow (*M. georgiana*)	F, U, I	Wetherbee 1968, Nowicki et al. 1991
Rufous-collared Sparrow (*Zonotrichia capensis*)	N, U	Lougheed and Handford 1989
Harris' Sparrow (*Z. querula*)	P, U, I	Baumgartner 1968
Dark-eyed Junco (*Junco hyemalis*)	P, U, I	Eaton 1968
Yellow-eyed Junco (*J. phaeonotus*)	F, C, I	Austin 1968b

F = extended song typically given in flight; P = extended song typically given from a perch; C = extended song included in courtship display; U = behavioral context of extended song unclear; I = extended song normally occurs infrequently; N = extended song given at night.

length of 2.4–4.2 sec (Berger 1968). Like extended songs of many species, the extended songs of Vesper Sparrows begin with several "chip" notes then continue with a series of trills at various frequencies and speeds bearing little resemblance to primary songs (Fig. 2).

In most cases, no other Vesper Sparrows were singing when this behavior occurred. During 322 min of observation on 28 and 30 July, the only primary songs heard were delivered by one bird that sang eight times over a 5-min period. On 30 July a recording of the primary song of a Vesper Sparrow that elicited strong response early in the season was played near areas where extended flight-songs had been recently noted. This did not elicit flight songs or any other obvious response. We think that these extended flight-songs were delivered by resident males, most of whom had been on territory since early May; no agonistic territorial behavior was ever observed subsequent to an extended flight-song.

In a typical extended flight-song, the singing Vesper Sparrow ascended to a height of 25–75 m and moved horizontally and in a straight line 100–200 m before descending. Flight-songs were noted throughout the day and often (>50%) occurred under cloudy, overcast skies. Because of the infrequency and apparent unpredictability of this behavior we had few opportunities to examine closely individuals giving extended songs. On 30 July, however, Wells closely examined a bird that had completed an extended flight-song 50 m from him. The bird was clearly an adult as evidenced by its worn plumage.

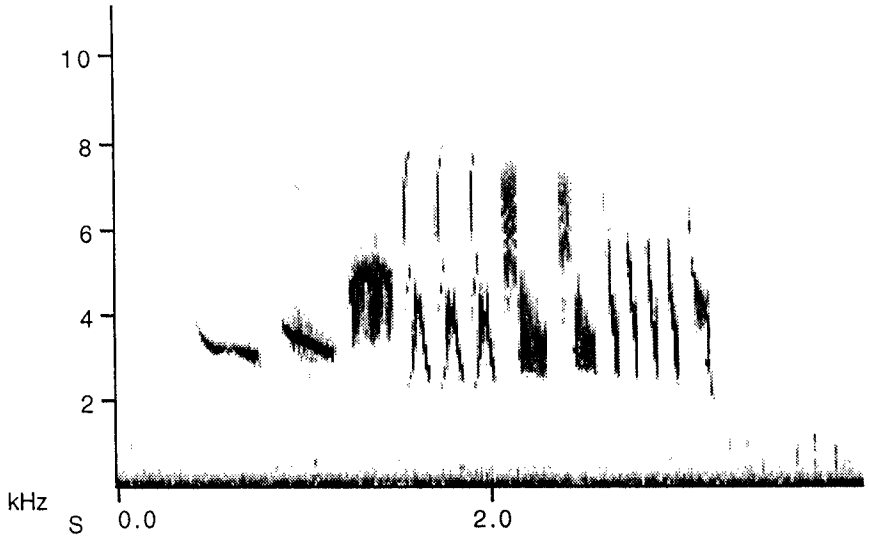

FIG. 1. Sonogram of primary song of a Vesper Sparrow recorded 30 May 1951 near Ithaca, New York (Cornell Laboratory of Ornithology, Library of Natural Sounds Catalog Number 15364). Note that the song lasts approximately three sec. Sonograms were produced using Canary 1.1 software from the Cornell Bioacoustics Research Program.

Extended flight-songs were usually given by Vesper Sparrows late in the breeding season (Fig. 3). Although sparrows arrived at our study site in April and began first nests in May, the earliest date that we noted an extended flight-song was 29 June. All other extended flight-songs occurred between 7 July–10 August. This pattern suggests that the function of Vesper Sparrow extended flight-song is not normally associated with territorial interactions or mate attraction.

DISCUSSION

Ritchison (1991) found that male Common Yellowthroats uttered extended flight-songs more frequently when he was within their territory and proposed that this behavior may function to warn a mate of potential predators and/or to distract the predator away from a nest site. This explanation seems inadequate for Vesper Sparrows at this site because nest predation rates averaged 58% between 1984–1986 (Vickery et al. 1992). If the extended flight-songs of Vesper Sparrows function as a predator warning to mates, one would expect this behavior to occur more frequently and earlier in the season. Other possible explanations include the possibility that extended flight-songs may function as a predator warning to fledglings or may function to bring fledglings together by broadcasting

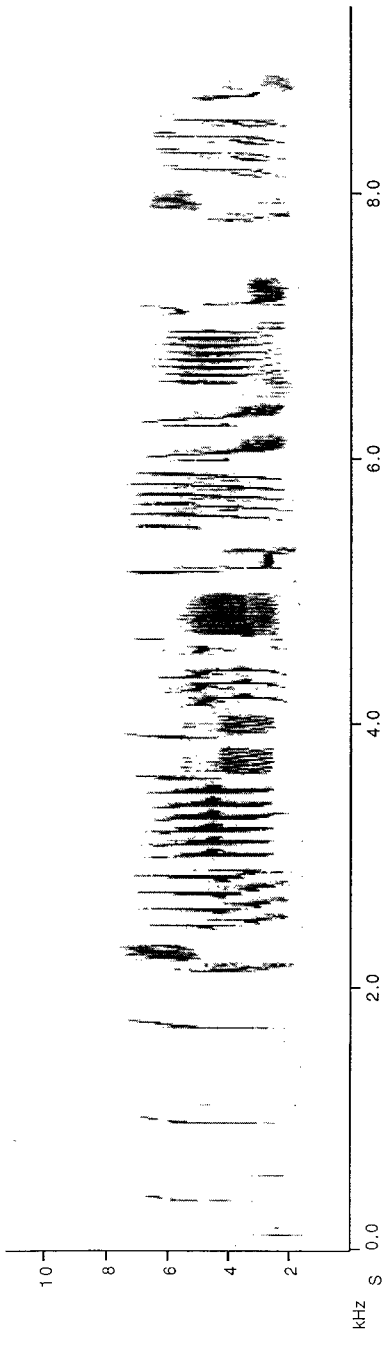

FIG. 2. Sonogram of an extended flight-song of a Vesper Sparrow recorded 30 July 1993 at Kennebunk, Maine (Cornell Laboratory of Ornithology, Library of Natural Sounds Catalog Number 63000). Note that the song lasts approximately nine sec and is different in structure from the primary song in Fig. 1.

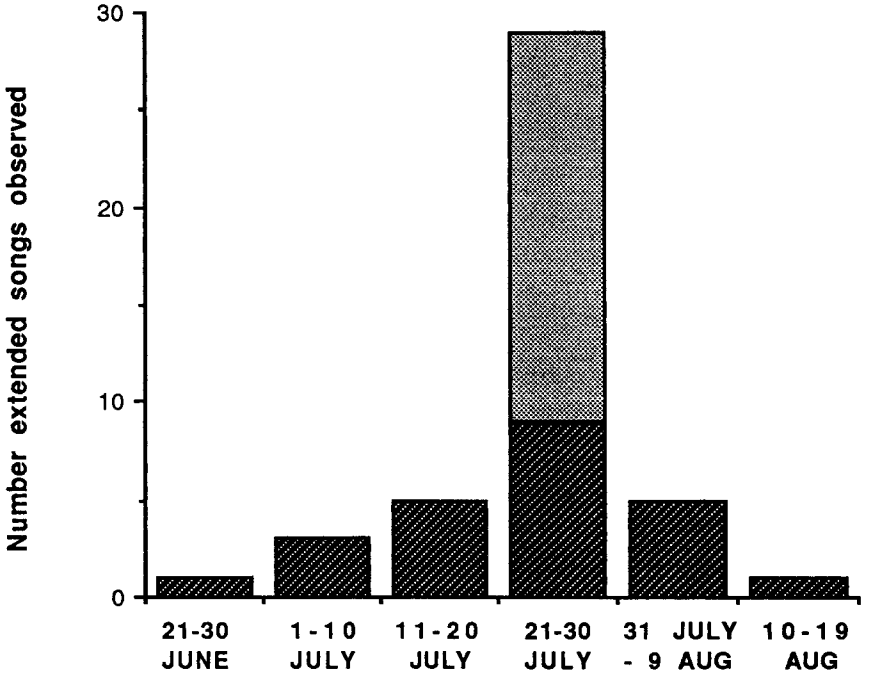

FIG. 3. Number of Vesper Sparrow extended flight songs noted in six ten-day periods from June through August 1984–1993 at Kennebunk, Maine. Observer effort was approximately equal among time periods. Stippled bar represents 1993 observations described in text.

a long, distinctive song from a height that would increase the area of audibility.

The use of extended flight-songs suggests a phylogenetic link between those Paruline warblers with an extended song (*Protonotaria, Helmitheros, Limnothlypis, Seiurus, Oporornis,* and *Geothlypis* [Spector 1992]) and the Emberizines. It is unclear, however, whether or not extended song is homologous in the two groups or whether it could have evolved independently in each. Even if extended flight-song in both groups has a common origin, it may not serve the same function for all species.

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