The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 160 July 2008 No. 1

Am. Midl. Nat. 160:1–6

Use and Possible Functions of the Primary and Sustained Songs of Male Grasshopper Sparrows

DARREN S. PROPPE AND GARY RITCHISON[1]

Department of Biological Sciences, Eastern Kentucky University, Richmond 40475

ABSTRACT.—Ascertaining the functions bird song requires information about when and where a song or, for males with multisong repertoires, songs are used. Because the need for and type of communication with mates and conspecifics changes with breeding stage and social context, detailed observations may reveal differential use of song or of different song types. Our objective was to examine the use, and determine the possible functions, of the two song types (primary and sustained) in the repertoire of male grasshopper sparrows (*Ammodramus savannarum*) by observing males throughout the breeding season and in different behavioral contexts in Madison County, Kentucky. For primary songs, rates varied among breeding stages and were highest before pairing, suggesting that primary song plays a role in mate attraction. However, male Grasshopper Sparrows continued to use primary songs after pairing, and likely functions include territory defense. The use of sustained songs also varied among breeding stages, with none uttered before pairing and rates highest during nest building and incubation. Male grasshopper sparrows also uttered more sustained songs when being observed (with one of us in their territories) then when not (neighboring males). These results suggest that sustained songs may serve to alert females to the presence of potential predators while simultaneously distracting such predators. Songs with such functions appear to be uncommon and have been reported in few other species.

INTRODUCTION

Although it is generally accepted that bird song repels rivals and attracts mates (Slater, 2003), singing also serves other functions (Smith and Smith, 1992) and, in some species, different song types may convey different information. For example, male eastern kingbirds (*Tyrannus tyrannus*) use different song types to signal different levels of aggression (Smith and Smith, 1992) and male common yellowthroats (*Geothlypis trichas*) utter flight songs to distract predators and alert mates (Ritchison, 1991).

Ascertaining song function requires information about when and where songs are used. Because the need for and type of communication with mates and conspecific males changes with breeding stage and social context, detailed observations may reveal differential use of song or song types. For example, singing rates decrease dramatically after pair formation in many songbirds, suggesting that song plays a role in mate attraction (*e.g.*, Eens *et al.*, 1994).

[1] Corresponding author: Telephone: (859) 622-1541; FAX: (859) 622-1359; e-mail: gary.ritchison@eku.edu

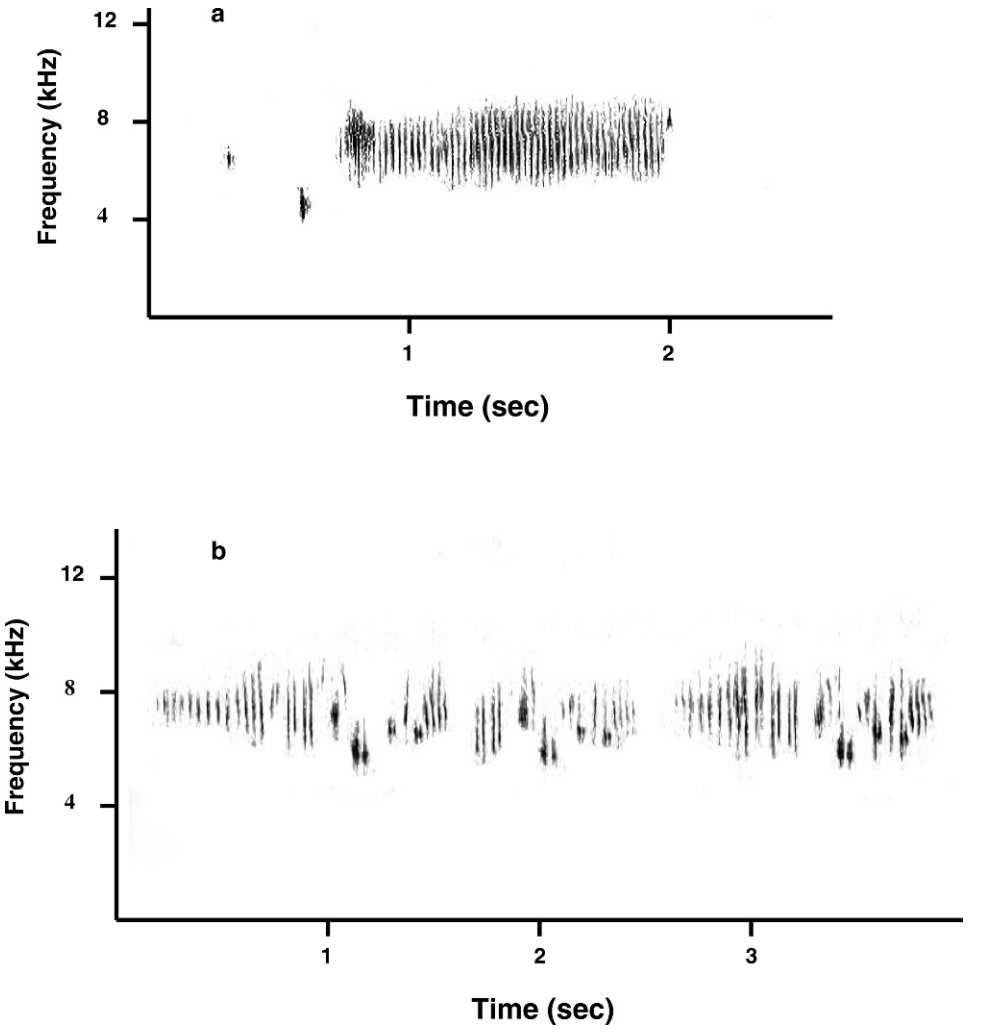

FIG. 1.—Primary (a) and sustained (b) songs of a male grasshopper sparrow recorded in Madison County, Kentucky

Playback experiments with bush warblers (*Cettia diphone*), a species with ''alpha'' and ''beta'' song types, revealed that beta songs signal a higher level of aggression (Park and Park, 2000).

Male grasshopper sparrows (*Ammodramus savannarum*) have two song types, a primary song and a sustained song (Fig. 1; Vickery, 1996). Smith (1959) suggested possible functions, but did not quantify singing rates and use of the two song types among breeding stages and behavioral contexts. As a result, functions of these song types remain unclear (Vickery, 1996). Our objective was to gain insight into the possible functions of primary and sustained songs by determining the rates at which male grasshopper sparrows uttered these

songs during different stages of the breeding cycle and determining if focal males and males in adjacent territories uttered sustained songs at different rates.

METHODS

We studied grasshopper sparrows (N = 18) in grazed and ungrazed grasslands in Madison County, Kentucky, from 27 Apr.–7 Aug. 2004 and 23 Apr.–7 May 2005. Males were captured in mist nets and fitted with a numbered aluminum band plus a unique combination of three colored bands. Territory boundaries were determined by observing the locations and movements of focal males. Territories were located at eight different sites distributed throughout our 3500-ha study area, with sites separated by areas of unsuitable habitat. The number of contiguous breeding territories at these locations varied from two to five.

In 2004 we observed and recorded each male sparrow two or three times weekly, monitoring males from a distance of 10–30 m. Observation periods began when we entered a focal territory and were 20–30 min in duration, and always between sunrise and 1100 h EDT. Songs were recorded using a cassette recorder (Sony TCM-50DV) and a shotgun microphone (Sennheiser ME 88).

We delineated territory boundaries by monitoring the location of focal males, and the locations of interactions between neighboring males, during observation periods. Because territories were small (0.19–0.8 ha), we were, while in a focal male's territory, also able to monitor the singing of males in all adjacent territories as a means of determining whether our presence in a territory might influence singing behavior. Specifically, we noted all bouts of song that included sustained songs.

Nests were located by observing behavior (*e.g.*, nest building) and searching likely sites. The breeding cycle was divided into five stages: (1) pre-pairing (from arrival on breeding grounds until a female was observed on the territory), (2) post-pairing/pre-incubation (from the day of pairing until the day the penultimate egg of a clutch was laid), (3) incubation (laying of the last egg of a clutch until the day before the first egg hatched), (4) nestling (day the first egg hatched until young fledged) and (5) post-fledging (fledging until 10 d after fledging). To determine stages, nests were checked at least twice weekly. Because nests were found at various stages, we sometimes backdated to determine the start of earlier stages. We used the duration of nesting stages provided by Vickery (1996) and Smith (1968), with 3 d for nest building, 4 or 5 d for egg-laying (depending on clutch size), 12 d for incubation and 9 d for the nestling period. Because grasshopper sparrows are multi-brooded, females often began construction of new nests several days after young from a previous nest fledged. The date of initiation of a new nesting attempt was determined either by observation (copulation or nest building) or backdating.

Because focal individuals were observed repeatedly during the breeding season, variation in singing rates among breeding stages and use of songs among different behavioral contexts were examined using repeated measures analysis of variance. The overall rates at which males in focal and adjacent territories uttered sustained songs were also compared using repeated measures analysis of variance. All analyses were conducted using the Statistical Analysis System (SAS Institute, 1999). All values are presented as means ± standard error.

RESULTS

For both song types combined, singing rates of males (N = 18) varied ($F_{4,53} = 9.06$, $P < 0.0001$) among breeding stages, with rates higher before pairing and lower during the nestling and post-fledging periods (Fig. 2). Singing rates for primary songs also varied

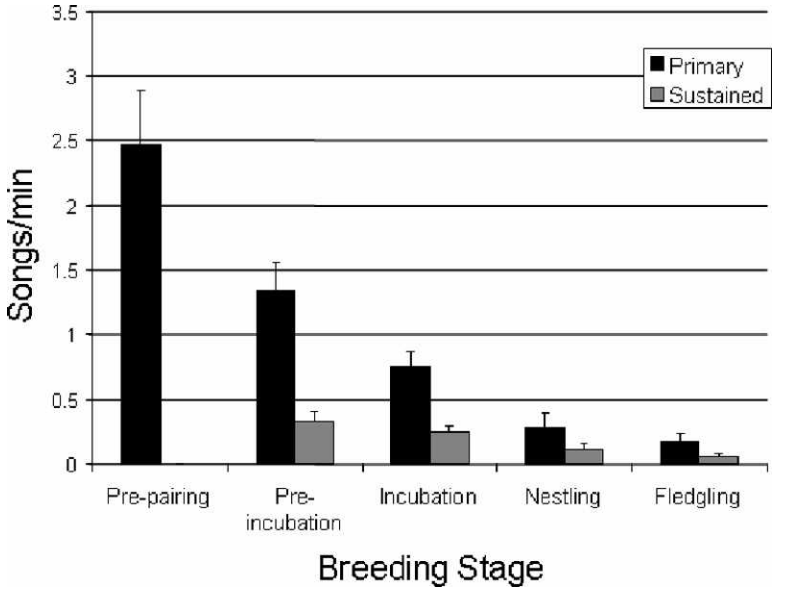

FIG. 2.—Rates at which primary and sustained songs were uttered by male grasshopper sparrows during different breeding stages

among breeding stages ($F_{4,53} = 8.2$, $P < 0.0001$), with rates highest before pairing (Fig. 2). Although lower than before pairing, males uttered primary songs at higher rates during nest building and incubation than during the nestling and post-fledging periods (Tukey's test, $P < 0.05$; Fig. 2).

The rates at which sustained songs were uttered also varied among breeding stages ($F_{4,53} = 3.9$, $P = 0.008$), with rates highest during nest building and incubation (Fig. 2). Sustained songs were not uttered before pairing (Fig. 2).

Adjacent to the territories of the 18 focal males were the territories of 52 male grasshopper sparrows (with those 18 males also considered neighbors when males in adjacent territories were observed). Focal males uttered sustained songs at a higher rate ($F_{1,1} = 675.3$, $P = 0.025$), with mean rates of 2.27 ± 0.22 bouts with one or more sustained songs per hour for focal males and 0.48 ± 0.06 per hour for neighbors.

DISCUSSION

Male grasshopper sparrows did not utter sustained songs before pairing and, for primary songs, singing rates were highest before pairing and then declined. Reduced singing rates after pairing have also been reported for other species (*e.g.*, Otter and Ratcliffe, 1993; Balsby, 2000; Huntsman and Ritchison, 2002), and such post-pairing declines in singing rates provide evidence that singing attracts mates (Kroodsma and Byers, 1991). Although rates declined after pairing, male grasshopper sparrows uttered primary songs throughout the breeding season, suggesting multiple functions. One function may be territory defense. Male grasshopper sparrows arrive on breeding grounds 3–5 d before females (Vickery, 1996) and establish territories. Males only use primary songs during this time, suggesting a role in territory establishment. Smith (1959) also suggested that the primary songs of grasshopper sparrows were territorial in function, and males in other species also sing

throughout the breeding season to repel other males (Nowicki *et al.*, 1998; Amrhein *et al.*, 2002).

During territory establishment, male grasshopper sparrows respond to the primary songs of conspecifics with a 'hostile' wing-fluttering display (Smith, 1959). In addition, after chasing conspecific intruders from a territory, resident males typically sing primary songs (Smith, 1959). Such observations further support the hypothesis that primary song plays a role in the establishment and defense of territories by male grasshopper sparrows.

Male grasshopper sparrows in our study did not utter sustained songs before pairing and Vickery (1996) also noted that unpaired males sang only primary songs. Although Smith (1959) suggested that sustained songs attract mates, songs that attract mates in other species are typically uttered at high rates before pairing and at lower rates thereafter (*e.g.*, Albrecht and Oring, 1995; Gil *et al.*, 1999; Amrhein *et al.*, 2002). Songs given at low rates only after pairing, like the sustained songs of male grasshopper sparrows, are unlikely to be important in mate attraction.

We found that focal male grasshopper sparrows uttered sustained songs at higher rates than neighbors, suggesting that our presence may have stimulated males to utter sustained songs. In addition, males uttered sustained songs at higher rates during the nest building and incubation stages. When nest building, female grasshopper sparrows are often on the ground searching for nest material and, during incubation, they are in nests covered with overhanging grasses (Vickery, 1996). Females, therefore, may be less likely to detect predators and the sustained songs of males may alert females to the presence of a predator. Simultaneously, sustained songs may distract potential predators. The characteristics of sustained songs, long in duration (2.5–5 s) and often uttered in succession at relatively high volumes, may make them easier to detect and more likely to attract a predator's attention.

Males in other species of birds are known to utter calls that apparently alert their mates to the presence of potential predators or other threats, such as brood parasites. For example, the 'seet' and 'chip' calls of male yellow warblers (*Dendroica petechia*) appear to alert mates to the presence of potential threats to their nest (Gill and Sealy, 2003). Similarly, male red-winged blackbirds (*Agelaius phoeniceus*) utter calls that inform mates about the presence of potential predators (Burton and Yasukawa, 2001). The use of song to alert mates, as we suggest for grasshopper sparrows, has, in addition, been reported in at least three other species. Male bush warblers have a song type that functions as an alarm signal and may distract predators from nests and females (Park *et al.*, 2004). Similarly, male common yellowthroats often perform flight songs when a human is in their territories, suggesting that the songs warn mates and direct the attention of a predator to the male and away from females and nests (Ritchison, 1991). In addition, eastern bluebirds utter alarm songs in the presence of potential nest predators (Gowaty and Plissner, 1998) that may serve to alert mates. Although experimental verification is required, our results, and those of several other investigators, suggest that using song to alert mates is, for at least some species, yet another of the many functions served by bird song.

Acknowledgments.—We thank Ben Sutter for help with fieldwork, the Kentucky Ornithological Society and Kentucky Society for Natural History for financial support and two anonymous reviewers for comments that improved our manuscript. Our study was approved by the Eastern Kentucky University Animal Care and Use Committee.

LITERATURE CITED

ALBRECHT, D. J. AND L. W. ORING. 1995. Song in chipping sparrows, *Spizella passerina*: structure and function. *Anim. Behav.*, **50**:1233–1241.

AMRHEIN, V., P. KORNER AND M. NAGUIB. 2002. Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle. *Anim. Behav.*, **64**:939–944.

BALSBY, T. J. S. 2000. The function of song in Whitethroats. *Bioacoustics*, **11**:17–30.

BURTON, N. AND K. YASUKAWA. 2001. The ''predator early warning system'' of red-winged blackbirds. *J. Field Ornithol.*, **72**:106–112.

EENS, M., R. PINXTEN AND R. VERHEYEN. 1994. Variation in singing activity during the breeding cycle of the European starling. *Belgium J. Zool.*, **124**:167–174.

GIL, D., J. A. GRAVES AND P. J. B. SLATER. 1999. Seasonal patterns of singing in the willow warbler: evidence against the fertility announcement hypothesis. *Anim. Behav.*, **58**:995–1000.

GILL, S. A. AND S. G. SEALY. 2003. Tests of two functions of alarm calls given by yellow warblers during nest defence. *Can. J. Zool.*, **81**:1685–1690.

GOWATY, P. A. AND J. H. PLISSNER. 1998. Eastern bluebird (*Sialia sialis*). *In:* A. Poole and F. Gill (eds.). The Birds of North America, No. 381. The birds of North America, Inc, Philadelphia, Pennsylvania, USA.

HUNTSMAN, B. O. AND G. RITCHISON. 2002. Use and possible functions of large song repertoires by male eastern bluebirds. *J. Field Ornithol.*, **73**:372–378.

KROODSMA, D. E. AND B. E. BYERS. 1991. The functions of bird song. *Amer. Zool.*, **31**:318–328.

NOWICKI, S., W. A. SEARCY AND M. HUGHES. 1998. The territory defence function of song in song sparrows: a test with the speaker occupation design. *Behaviour*, **135**:615–628.

OTTER, K. AND L. RATCLIFFE. 1993. Changes in singing behavior of male black-capped chickadees following mate removal. *Behav. Ecol. Sociobiol.*, **33**:409–414.

PARK, S. R., S. CHEONG AND H. CHUNG. 2004. Behavioral function of the anomalous song in the bush warbler. *Korean J. Biol. Sci.*, **8**:89–95.

PARK, S. AND D. PARK. 2000. Song type for intrasexual interaction in the bush warbler. *Auk*, **117**:228–232.

RITCHISON, G. 1991. The flight songs of common yellowthroats: description and causation. *Condor*, **93**:12–18.

SAS INSTITUTE. 1999. SAS user's guide: statistics. SAS Institute, Cary, North Carolina, USA.

SLATER, P. J. B. 2003. Fifty years of bird song research: a case study in animal behaviour. *Anim. Behav.*, **65**:633–639.

SMITH, J. AND S. M. SMITH. 1992. Behavioral information provided by two song forms of the eastern kingbird. *Behaviour*, **120**:90–102.

SMITH, R. L. 1959. The songs of the grasshopper sparrow. *Wilson Bull.*, **71**:141–151.

———. 1968. Grasshopper sparrow, p. 725–745. *In:* O. L. Austin (ed.). Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Nat. Mus. Bull. 237C, Washington, DC.

VICKERY, P. D. 1996. Grasshopper sparrow (*Ammodramus savannarum*). *In:* A. Poole and F. Gill (eds.). The Birds of North America, No. 239. Acad. Nat. Sci., Philadelphia, Pennsylvania, USA.

SUBMITTED 29 JANUARY 2007 ACCEPTED 29 JANUARY 2008