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Diel and seasonal patterns of variation in the singing behaviour of Savannah Sparrows (*Passerculus sandwichensis*)

Ines G. Moran^{1*}, Katrina C. Lukianchuk¹, Stéphanie. M. Doucet¹, Amy E. M. Newman², Heather Williams³, D. Ryan Norris² and Daniel J. Mennill^{1*} 

Abstract

Background: The vocalizations of birds are dynamic traits that often vary in output with time of day and time of year. By quantifying patterns of diel and seasonal variation in vocal output, we can gain insight into the ecology and evolution of birds and the function of their vocalizations. In this investigation, we quantified diel and seasonal variation in song output by studying a breeding population of Savannah Sparrows (*Passerculus sandwichensis*).

Methods: We used autonomous recorders to collect extensive recordings across the breeding season in a long-term, colour-marked study population of Savannah Sparrows in eastern Canada. We described diel and seasonal variation across five different breeding stages based on recordings of more than 50,000 songs from 34 males.

Results: During the pre-breeding stage, prior to female arrival, males sang a pronounced dawn chorus with a peak in song output during the early morning. During the breeding stage, in contrast, the dawn chorus was diminished and males instead exhibited a pronounced dusk chorus with a peak in song output during the evening. Across the breeding season, the highest levels of song output occurred in late April and early May, soon after males arrived on the breeding grounds, and the lowest levels occurred in August, prior to the departure of birds for the wintering grounds.

Conclusions: These patterns suggest that Savannah Sparrows' early-season dawn choruses are directed at males and serve a territorial defense function. Later-season dusk choruses, in contrast, appear to play a role in attracting mates and possibly acoustic mate guarding.

Keywords: Bird song, Breeding activities, Circadian rhythms, Seasonal variation in song

Background

Many animals vary their vocal output seasonally, often in relation to changes in abiotic factors such as light and temperature (Runkle et al. 1994; Stafford et al. 2001; Amrhein et al. 2004), or in relation to the rhythms of social activities such as changes in reproductive status (Slagsvold 1977; Amrhein et al. 2008; Bruni and Foote 2014). Several hypotheses have been proposed to explain why animal signaling behaviour varies seasonally, and these hypotheses fall into three main categories: (1) social

processes, such as changes in social context, influence seasonal changes in vocal output; (2) mechanistic processes, such as the hormones that influence vocal output, influence seasonal changes in vocal output; and (3) environmental features, which place constraints on acoustic communication (for example, through changes in vegetation), influence seasonal changes in vocal output (Kacelnik and Krebs 1983; Mace 1987; Cuthill and Macdonald 1990; Staicer et al. 1996; Burt and Vehrencamp 2005). Many studies have revealed the strong influence of social forces such as pairing status (Catchpole 1973; Cuthill and Hindmarsh 1985; Demko et al. 2013) and breeding status (Hanski and Laurila 1993; Foote and Barber 2009; Bruni and Foote 2014; Zhang et al. 2016) on vocal output, and understanding the correspondence between social

*Correspondence: moran11@uwindsor.ca; dmennill@uwindsor.ca

¹ Department of Biological Sciences, University of Windsor, Windsor, ON N9B3P4, Canada

Full list of author information is available at the end of the article



activities and vocal behaviour has provided insight into the behavioural ecology of animals.

In addition to seasonal variation, many animals vary their vocal output with time of day (reviewed in Staicer et al. 1996). Dawn and dusk choruses are periods of heightened vocal activity that appear to be important for territorial defense, mate attraction, and extra-pair mate attraction (Catchpole 1973; Slagsvold et al. 1994; Burt and Vehrencamp 2005; Kunc et al. 2005; Poesel et al. 2006). Animals with dawn and dusk choruses include primates (Oliveira and Ades 2004), lizards (Ord 2008), and birds (Burt and Vehrencamp 2005). Songbirds are particularly well known for their dawn choruses, and to a lesser degree their dusk choruses. They provide a model system in the field of acoustic communication to study diel variation in vocal output (Staicer et al. 1996).

In this study our goal is to describe seasonal and diel variation in the song output of male Savannah Sparrows (*Passerculus sandwichensis*), and to compare changes in vocal output to the birds' breeding activities. We quantify patterns of diel variation to test the hypothesis that Savannah Sparrows exhibit dawn and dusk choruses. Then we quantify patterns of seasonal variation to test the hypothesis that Savannah Sparrow vocal output varies with breeding stage. We made a priori predictions about the relationship between variation in vocal output and breeding activities. We predicted that if the dawn and dusk chorus of male Savannah Sparrows plays an important role in defending and maintaining territory, then song output should remain constant across breeding stages. Alternatively, if the main function of the dawn and dusk chorus in male Savannah Sparrows is related to within-pair or extra-pair mate attraction, then we predicted that song output should vary across breeding stages, with the highest levels during the period of female fertility and the lowest levels during both the pre-pairing stage (prior to the arrival of females) and later in the breeding season when most individuals are feeding young and no longer reproductive.

Methods

Study species and study site

Savannah Sparrows are small migratory songbirds that live in open grasslands throughout North America (Wheelwright and Rising 2008). In the spring, males migrate from wintering grounds in the southern United States to breeding grounds across the United States and Canada (Bédard and LaPointe 1984; Tufts 1986; Woodworth et al. 2016). We conducted our research at the Bowdoin Scientific Station on Kent Island, New Brunswick, Canada (44°35'N, 66°46'W). Our island-living, colour-marked population of Savannah Sparrows has been studied for more than three decades (Williams

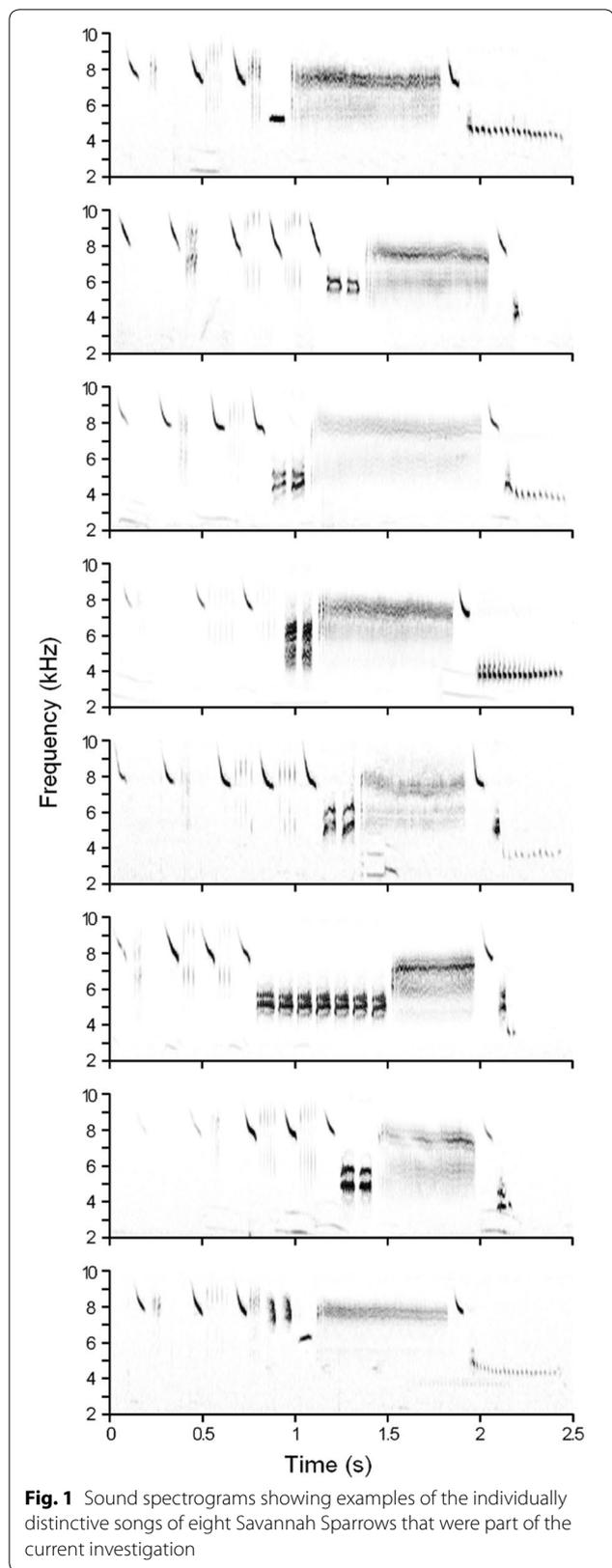
et al. 2013) and is known to exhibit strong site philopatry (Wheelwright and Mauck 1998). Males in this population arrive from migration in mid-April, approximately one month before female arrival, and begin to defend breeding territories from rival males (Woodworth et al. 2016). Males regularly produce songs which they learn by emulating vocal tutors heard during their natal year and at the outset of their first breeding season (Mennill et al. 2018). Songs are made up of a complex series of notes produced in a consistent and stereotyped order (Fig. 1). Each male produces a single song type that is individually distinctive (Williams et al. 2013). Song persists between the arrival from spring migration and departure for fall migration, but the pattern of this variation has not been studied previously in quantitative detail.

Recording technique

In 2014, we recorded male Savannah Sparrows using automated digital recorders (Wildlife Acoustics Song Meters, model: SM2; details in Mennill et al. 2012). We used eight different recorders, each mounted at a height of 1 m on a wooden stake, and moved the eight recorders around among 13 locations at the study site, allowing us to monitor the 34 males. Each recorder location was separated by 100–150 m. Given the small territories of Savannah Sparrows (territory diameter is less than 50 m, and often as small as 25 m), each autonomous recorder allowed us to record between one and seven males simultaneously. We are confident that our recorders sampled all songs produced by males on their territories, because territories are small and songs are routinely heard from at least two territories away. In-person observation sessions confirmed that males only sing from within the boundaries of their territories, and that song posts were within range of the recorders. In total we recorded $n = 34$ males for ten 24-h long recording sessions between mid-April and mid-September, with approximately 14-day intervals between subsequent recording sessions at each of the 13 microphone locations. In all of the recordings where multiple males were present, we distinguished individuals on the basis of their individually distinctive song. The song of each individual was known from in-person focal recording sessions, which allowed us to connect each song to a specific colour-banded individual (as in Williams et al. 2013; Mennill et al. 2018).

Analysis of pairing and breeding status

To determine the breeding activities of the 34 males, we collected behavioural observations and monitored nests every 2 days. We divided the breeding season into five different stages (as in Foote and Barber 2009): (1) the “pre-pairing stage”, a time-period when males had arrived on the breeding ground but had not yet attracted



a mate (in our study population this stage begins in mid-April or late-April and persists for approximately 15 days, until females arrive and pair with males); (2) the “fertile stage”, a time-period when males had paired with a fertile female (8 days prior to the laying of the penultimate egg; in our study population this stage occurs between early and late May); (3) the “incubation stage”, a time-period when males were paired with a female incubating eggs (a period of 12 days; in our study population this stage typically occurs in early June); (4) the “hatchling stage”, a time-period when males were paired with a female who was provisioning nestlings (a period of 9 days; in our study population this stage typically occurs in late June); and (5) the “fledgling stage”, a time-period when males were paired with a female provisioning fledglings (starting with the end of the nestling stage to the start of the next brood, or, if no consecutive brood is attempted, a period of 7 days after the end of the nestling stage). We estimated the length of the fertile period, relative to egg-laying dates, based on the following logic: female Savannah Sparrows are thought to be fertile during the 1–3 days when nests are built and during the following period of 3–5 days when eggs are laid (1 egg per day). In cases where nests were found after laying was complete, we estimated the first day of incubation by back-dating 12 days from known hatch dates (Dixon 1978; Wheelwright and Rising 2008). The first nesting attempts of birds in our study population are quite synchronous. For re-nesting attempts, stages 2 through 5 were repeated later in the summer. Thus the timing of each breeding stage varied individually, especially as the breeding season progressed and the breeding activities of the study animals became asynchronous.

Analysis of diel and seasonal variation

We analyzed field recordings by visually scanning sound spectrograms using Syrinx-PC Sound Analysis Software (J. Burt, Seattle, WA). This software allowed us to visualize 5 min of recording at a time, to compare the field recordings to an on-screen reference recording of each individual, and annotate the songs with a time-stamped annotation. From these annotations we tallied the vocal output of each male.

We defined the “dawn chorus” as songs that occurred during the period 30 min before sunrise until sunrise (as in Liu 2004; Naguib et al. 2016). We defined “daytime song” as songs that occurred between sunrise and sunset. We defined the “dusk chorus” as songs that occurred following sunset. Sunrise and sunset times for each day were obtained from the National Research Council, Herzberg Institute of Astrophysics sunrise/sunset calculator

(www.nrc-cnrc.gc.ca) for the nearby city of Saint John, New Brunswick. In addition to tallying the songs produced by birds during the three periods of sunrise, daytime, and sunset, we also calculated hourly values of song output during 1-h bins. We excluded days where the recordings showed a heavy influence of weather (i.e. very rainy or windy days) and we could not be confident that we had sampled all songs. The number of songs recorded in September was typically zero, and we did not include zero-song recordings in our analysis because we could not be certain if the bird remained in the area of the recorder at that time (birds may have already begun their southward migration, or territory boundaries may have eroded after breeding had concluded). On average, we included 7 ± 3 days of recording spread across the season for each individual.

Statistical analysis

We analyzed diel and seasonal variation in song output using linear mixed models (LMM). Our fixed effects were time of day (subdivided into 1-h periods; or subdivided into bins of dawn, daytime, and dusk), breeding stage (pre-pairing, fertile, incubation, hatchling, or fledgling), and interaction between time of day and breeding stage. We included male identity as a random effect to account for the fact that the same males were sampled repeatedly. For any analysis that showed statistical significance for the fixed effects, we conducted a Tukey's post hoc test of honestly significant differences. We used JMP (v14 SAS Institute Inc. 2019) for all statistical analyses.

Results

Based on analysis of 58,301 songs from 34 male Savannah Sparrows recorded during a 5-month time span, we found substantial variation in song output, both with time of year (Fig. 2a) and with breeding stage (Fig. 2b). We analyzed variation in song output on an hourly basis, and found that song output varied with time of day (LMM: $F_{19,132} = 10.1$, $p < 0.0001$); song output showed no systematic variation with breeding stage ($F_{4,132} = 0.1$, $p = 0.98$); song output varied with the interaction between time of day and breeding stage ($F_{76,132} = 6.9$, $p < 0.0001$); and song output varied between males (random effect of 34 repeatedly sampled individuals: $F_{33,132} = 9.8$, $p < 0.0001$). The interaction effect was explained by a peak of singing during the early morning (i.e. a dawn chorus) and low song output at dusk during the pre-pairing stage, low song output during the morning and a peak of singing at sunset (i.e. a dusk chorus) during the fertile stage, and relatively consistent output across the day during the incubation, hatchling, and fledgling stages (Fig. 3).

We also analyzed variation in song output across the five breeding stages for three time periods: the dawn

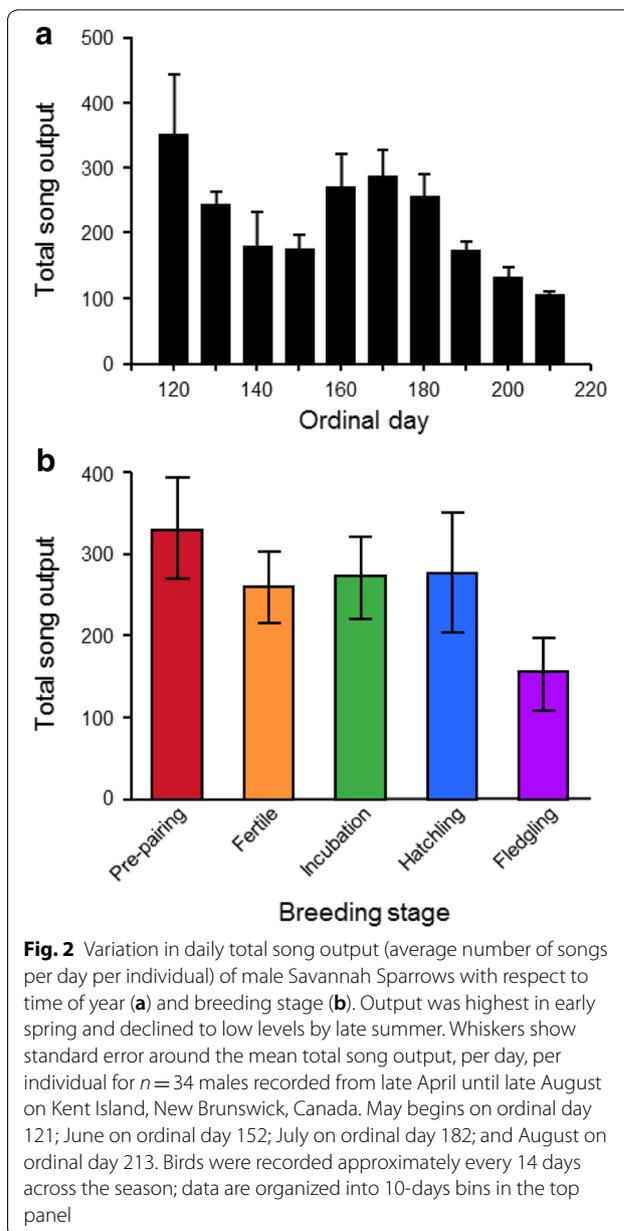


Fig. 2 Variation in daily total song output (average number of songs per day per individual) of male Savannah Sparrows with respect to time of year (a) and breeding stage (b). Output was highest in early spring and declined to low levels by late summer. Whiskers show standard error around the mean total song output, per day, per individual for $n = 34$ males recorded from late April until late August on Kent Island, New Brunswick, Canada. May begins on ordinal day 121; June on ordinal day 152; July on ordinal day 182; and August on ordinal day 213. Birds were recorded approximately every 14 days across the season; data are organized into 10-days bins in the top panel

chorus, the period between dawn and dusk, and the dusk chorus. Song output during the dawn chorus varied with breeding stage (LMM: main effect of breeding stage: $F_{4,38} = 4.3$, $p = 0.003$; random effect of individual: $F_{33,38} = 1.9$, $p = 0.007$) and post hoc analysis revealed higher dawn chorus output during the pre-pairing stage than all other breeding stages (Fig. 4a). Song output between dawn and dusk showed little variation with breeding stage (LMM: main effect of breeding stage: $F_{4,38} = 1.2$, $p = 0.31$; Fig. 4b; random effect of individual: $F_{33,38} = 0.9$, $p = 0.62$). Song output at dusk varied with breeding stage (LMM: main effect of breeding

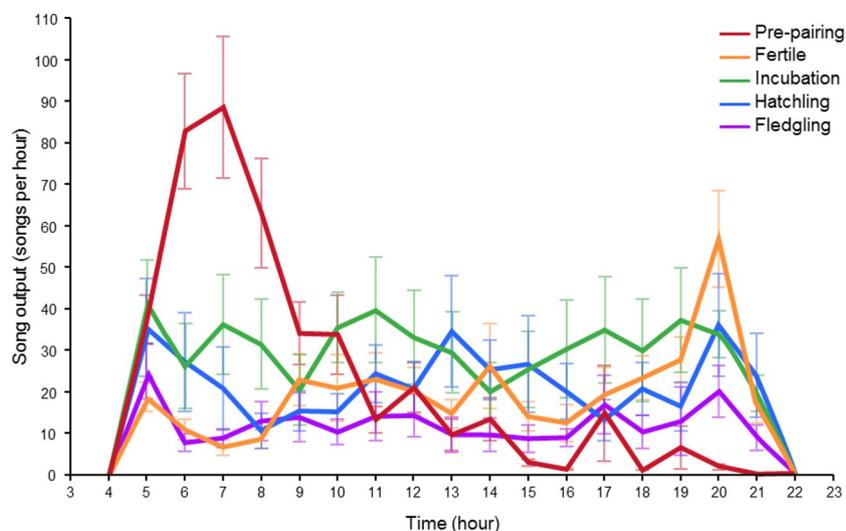


Fig. 3 Variation in hourly song output of male Savannah Sparrows with respect to breeding stage (pre-pairing, fertile, incubation, hatchling, and fledgling). Before pairing, male singing activity peaked in the morning (i.e. a dawn chorus) and was nearly absent at dusk. During the fertile stage, after pairing, male singing activity was low until the end of the day (i.e. a dusk chorus). Whiskers show standard error round the mean value for each hour, per individual, for $n = 34$ males

stage: $F_{4,38} = 3.7$, $p = 0.008$; random effect of individual: $F_{33,38} = 0.9$, $p = 0.66$) and post hoc analysis revealed low dusk output during the unpaired stage, high dusk output during the fertile stage, and intermediate output during the remaining stages (Fig. 4c).

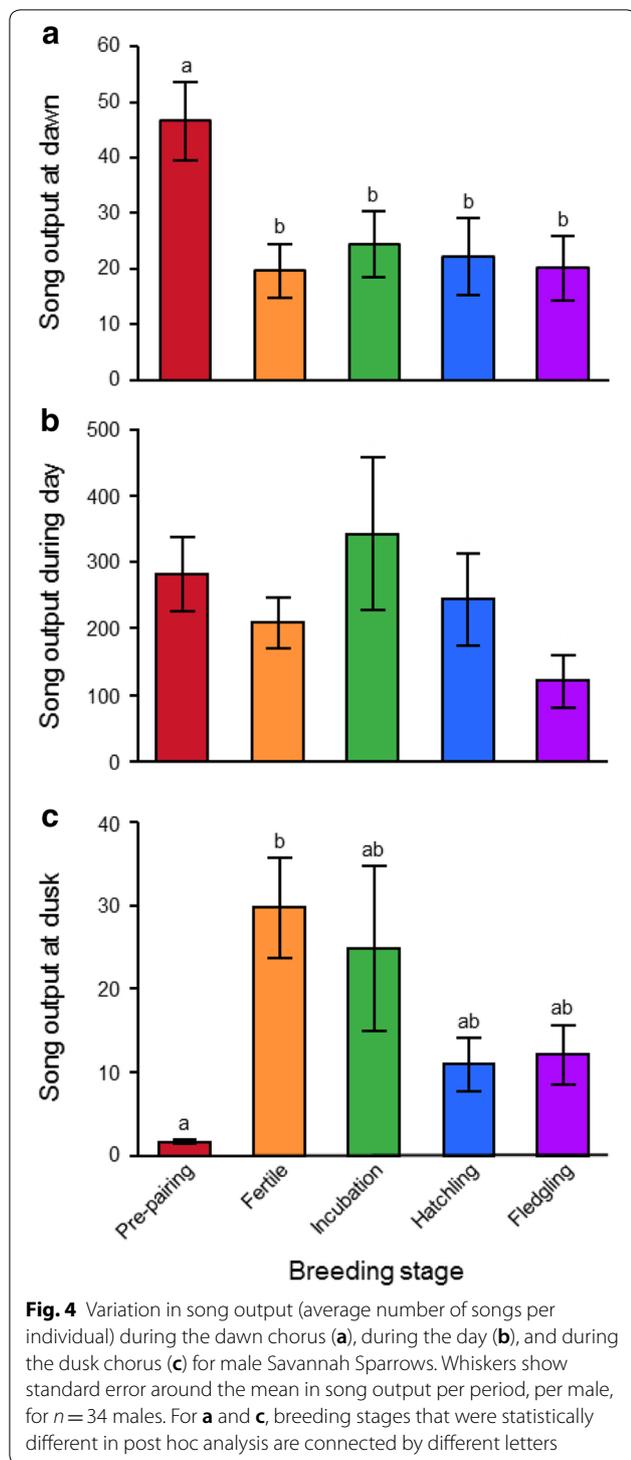
Discussion

Savannah Sparrows showed diel and seasonal variation in song output. When males arrived from spring migration, prior to female arrival, they showed the highest song output during the dawn chorus and lower song output during the daytime and dusk periods. The dawn chorus was commonplace during the pre-breeding stage, before females arrived from migration, but dawn song output was lower thereafter. Upon female arrival on the breeding grounds, males showed their highest song output during the dusk chorus. These results suggest that dawn-chorus singing behaviour is an important intra-sexual signal during territory establishment, whereas dusk-chorus singing behaviour is an important signal during the peak reproductive period, when male song may play a role in attracting extra-pair mating opportunities or in acoustic mate guarding.

The pattern of variation in Savannah Sparrows supports the idea that songs have an important territorial function early in the breeding season and early in the morning. The high singing activity in the mornings of pre-pairing Savannah Sparrows, when females are absent from the island altogether, suggests that the morning is a period of importance for territorial interactions when

males are claiming and defending territories. Establishing a territory is a critical prerequisite for attracting a breeding partner in this species (Potter 1972). Previous studies have suggested that pairing success in Savannah Sparrows appears to be influenced by both male territory size and by male song rate (Reid and Weatherhead 1990). This may explain why males arrive at the breeding grounds as much as a month before of females (Woodworth et al. 2016) and, as we show here, devote significant attention to singing upon their arrival.

Once females arrived and breeding partnerships formed, male Savannah Sparrows' morning singing activity decreased by a factor of two or more, and remained at a similar level throughout the remaining breeding stages. This pattern suggests that the dawn chorus activity plays a less-important role after territorial establishment and pairing. Yet in spite of the decrease in dawn output after pairing, song output at dawn was still considerable, and often ranked among the highest hours of song output across the day during the post-pairing breeding stages. In other bird species, post-pairing dawn choruses appear to play a role in territory maintenance (Amrhein and Erne 2006; Erne and Amrhein 2008; Foote et al. 2011), strengthening the pair bond (Erne and Amrhein 2008), or soliciting extra-pair copulations (Poesel et al. 2006). For example, the dawn chorus is an honest signal of male quality in Eastern Kingbirds, *Tyrannus tyrannus* (Murphy et al. 2008); male Eastern Kingbirds that sing more, and earlier, during the morning have a higher chance of obtaining extra-pair copulations. Savannah Sparrows



have high rates of extra-pair paternity (Freeman-Gallant et al. 2005, 2006), where approximately half of the nestlings born in this study population arise through extra-pair paternity. Dawn song during later stages may also be important in attracting extra-pair mates.

Our study provides the first quantitative evidence that Savannah Sparrows produce a dusk chorus. Dusk choruses showed a striking pattern of seasonal variation: male song was almost absent at dusk before females arrived on the breeding grounds, but after pairing males sang pronounced dusk choruses. During the fertile period, in particular, male song reached its highest levels at dusk. This pattern strongly suggests that the Savannah Sparrow dusk chorus is intended for a female audience. In other species, the dusk chorus has been hypothesized to function as a period during which males defend territories, obtain extra pair copulations, or advertise their mated status (Cuthill and Macdonald 1990; Erne and Amrhein 2008). The heightened output of song at dusk in male Savannah Sparrows with fertile mates suggests that song may be important for males advertising their mated status (thereby reducing the likelihood of paternity loss to extra-pair sires; i.e. acoustic mate guarding) or advertising themselves to prospective extra-pair partners. Future observational studies and playback experiments on dusk chorus songs could shed light on the function of songs during the dusk chorus songs in Savannah Sparrows.

Outside of the early-season pre-pairing stage, Savannah Sparrows also sang a pronounced dusk chorus when males were paired with an incubating female. The fertility announcement hypothesis suggests that singing activity peaks with the fertile period of the females (Møller 1991), yet many species do not follow this pattern. European Redwings (*Turdus iliacus*) and Acrocephalus warblers show a peak in song activity a few days after egg laying (Catchpole 1973; Slagsvold 1977; Lampe and Espmark 1987); Song Sparrows (*Melospiza melodia*) sing most often during incubation (Foote and Barber 2009); and Willow Warblers (*Phylloscopus trochilus*) do not sing during females' fertile periods (Gil et al. 1999). Previous investigators have argued that an increase in song output during the incubation stage can act as either a mate guarding strategy, a stimulus that promotes incubation by females (Foote and Barber 2009), an all-clear signal to indicate to females that the male is nearby and that no predators are around (Johnson and Kermott 1991), or as a strategy to advertise to potential extra-pair partners. Given the high rates of extra-pair copulations in Savannah Sparrows, and the fact that predation often leads to asynchronous breeding activities in our study population, it is entirely possible that the heightened output during incubation is consistent with males advertising for extra-pair copulations.

Conclusions

In conclusion, we explored the relationship between singing activity and breeding activity, and what this relationship might reveal about the function of song in Savannah

Sparrows. We showed that singing activity varied at both a diel and seasonal time scales. Pre-pairing territorial males had the most pronounced dawn chorus, whereas males paired to fertile females had the most pronounced dusk chorus. Savannah Sparrows exhibit dynamic patterns of diel and seasonal variation, where vocal output at dawn and dusk varies with the changing social context at different stages of their breeding season. Analysis of seasonal variation of singing, as demonstrated in our study, can provide insight into the complex communication systems of songbirds.

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Authors' contributions

All authors shared in designing the project and collecting field data. IGM, KCL, and DJM conducted the acoustic analyses. IGM and DJM drafted the manuscript, and all authors shared in editing and revising the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The data are available from the senior author (DJM) on reasonable request.

Ethics approval and consent to participate

This research complies with the current laws of Canada, and the research was approved under a University of Windsor Animal Care Permit to DJM and a University of Guelph Animal Care Permit to AEMN and DRN.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

¹ Department of Biological Sciences, University of Windsor, Windsor, ON N9B3P4, Canada. ² Department of Integrative Biology, University of Guelph, Guelph, ON N1G2W1, Canada. ³ Biology Department, Williams College, Williamstown, MD 01267, USA.

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