


Singing on the nest is a widespread behavior in incubating Northern Mockingbirds and increases probability of nest predation

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ABSTRACT

In this study, we documented for the first time singing on the nest (SOTN) in 74% of 65 Northern Mockingbird (*Mimus polyglottos*) nests that were monitored with continuous-running video cameras (8,353.9 hr sampled). As predicted, higher rates of SOTN significantly decreased daily survival rates of nests. SOTN occurred almost exclusively by females during the egg stage and in 86% (48 of 56) of nests for which we had sampling from the egg stage. While extensive at the population level, the average rate of SOTN per individual was low (5.24 ± 1.24 s SOTN per hour of video sampled). We found mixed support for the hypothesis that SOTN functions in territory maintenance. We found no support for the hypotheses that SOTN functions to coordinate parental care, defend nests, or aid in vocal learning. Given the limited attention SOTN has received and the mostly anecdotal accounts of it, our understanding of its costs and benefits is lacking. We conclude that while individual rates of SOTN are quite low, SOTN may be more widespread in populations than previously thought and that studies specifically designed to test hypotheses regarding potential functions are critically needed.

Keywords: female song, nest predation, Northern Mockingbirds, singing on the nest, song function, song type matching

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LAY SUMMARY

- In some bird species, individuals will sing while sitting on the nest (SOTN); however, little is known about this behavior. Why do birds that hide their nests engage in this conspicuous behavior that could draw the attention of nest predators?
- We used video recordings from 65 Northern Mockingbird nests to provide the first evidence that mockingbirds sing on the nest. Singing on the nest occurred in 86% of nests with sampling during the egg stage, but rates of singing on each nest were low. Almost all singing events were by females incubating eggs.
- As predicted, higher rates of singing led to increased rates of nest predation.
- We found mixed evidence that singing functions in territory maintenance and no evidence that singing functions in coordination of parental care, nest defense, or vocal learning.
- We conclude that rare SOTN may be more widespread than previously thought and needs further study to understand its function.

Cantar en el nido es un comportamiento muy extendido en *Mimus polyglottos* en incubación y aumenta la probabilidad de depredación del nido

RESUMEN

En este estudio, documentamos por primera vez el canto en el nido en el 74% de los 65 nidos de ruiseñor común (*Mimus polyglottos*) que fueron monitorizados con cámaras de vídeo de funcionamiento continuo (8.353,9 horas muestreadas). Como se predijo, las mayores tasas de SOTN disminuyeron significativamente las tasas de supervivencia diaria de los nidos. El SOTN se produjo casi exclusivamente por parte de las hembras durante la fase de huevo y en el 86% (48/56) de los nidos de los que se tomaron muestras desde la fase de huevo. Aunque extensa en el nivel

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de población, la tasa media del canto en el nido por individual fue muy baja ($5,24 \pm 1,24$ s SOTN por hora de video muestreada). Encontramos un apoyo mixto a la hipótesis de que la cantas en el nido funciona en la defensa del territorio. No encontramos apoyo para la hipótesis de que la canto en el nido funciona para coordinar el cuidado parental, defender los nidos o ayudar en el aprendizaje del canto. Dada la escasa atención que ha recibido la SOTN y los relatos mayoritariamente anecdóticos sobre ella, carecemos de conocimientos sobre sus costes y beneficios. Llegamos a la conclusión de que, mientras tasas de la canto en el nido de individuales son bajas, la canto en el nido en las poblaciones puede estar más extendida de lo que se pensaba y que se necesitan urgentemente estudios diseñados específicamente para poner a prueba las hipótesis sobre sus posibles funciones.

Palabras clave: canto de pájaro femenino, depredación de nidos, *Mimus polyglottos*, cantando en el nido, función canto de pájaros, concordancia de tipo de canción de pájaro

INTRODUCTION

Singing is one of the most conspicuous behaviors of songbirds and has been studied extensively from both proximate and ultimate perspectives (Catchpole and Slater 2003). Historically, the majority of such studies have focused almost exclusively on male song, although recent work has begun the shift to include females (e.g., Odom *et al.* 2014, Odom and Benedict 2018, Riebel *et al.* 2019). An even less well understood facet of bird song is singing on the nest (SOTN), which is the production of song by an incubating or brooding, often female, bird (Leonard 2008). While SOTN has been anecdotally recognized for a long time (e.g., Gibbs 1893), there have been few studies that directly focus on it (but see Halkin 1997, Leonard 2008, Kleindorfer *et al.* 2016) and rare female song, in general, has historically been viewed as an anomaly (Langmore *et al.* 2008).

Vocalizing on nests, and singing on them in particular, would seem to increase the likelihood of eavesdropping by both predators and brood parasites, which could result in complete reproductive failure for that nesting attempt (Leonard 2008). While this intuitively makes sense, few studies have experimentally assessed the relationship between SOTN and rates of nest predation and parasitism (Yasukawa 1989, Haff *et al.* 2015, Kleindorfer *et al.* 2016). Kleindorfer *et al.* (2016) demonstrated both observationally and experimentally an increase in nest predation of Superb Fairy-wrens (*Malurus cyaneus*) with higher rates of female SOTN. Likewise, experimental nests that broadcast female Red-winged Blackbird (*Agelaius phoeniceus*) songs on the nest experienced higher rates of nest predation, but active nests with calling females were more successful, presumably because of increased nest defense by males (Yasukawa 1989). Parasitism by Brown-headed Cowbirds (*Molothrus ater*) was positively associated with singing near the nest for Red-winged Blackbirds (Clotfelter 1998) and Willow Flycatchers (*Empidonax traillii*) (Uyehara and Narins 1995). Likewise, SOTN was positively associated with nest parasitism in multiple species of vireos (Banks and Martin 2001, Walker and Marzluff 2017). On the other hand, SOTN appears to decrease the risk of both nest predation (Peterson *et al.* 2004) and parasitism in Bell's Vireo (*Vireo bellii*) (Sharp and Kus 2006, Steckler and Conway 2012). With the lack of focused studies on SOTN, it is difficult to make generalizations about the costs of this conspicuous behavior.

Leonard (2008) estimated that at least 10% of North American bird species sing on the nest and it is possible the number is higher (e.g., MacDonald *et al.* 2019). Incubation is an energetically costly behavior (reviewed in Williams 1996, Tinbergen and Williams 2002, Nord and Williams 2015); therefore singing (which also entails energetic costs; Oberweger and Goller 2001) during incubation would further increase the energetic demands of incubation. These energetic costs plus the potential costs of predation and parasitism

make SOTN an unlikely behavior to evolve, unless the benefits of doing so are great enough to outweigh these costs. A variety of functions of SOTN have been hypothesized (reviewed in Leonard 2008, Haff *et al.* 2015; and see Supplementary Material Table S1 for a summary of hypotheses), including coordination of parental care, territory maintenance, nest defense, pair bonding, solicitation of extra-pair copulations, and vocal learning (Colombelli-Négrel and Kleindorfer 2017, Kleindorfer *et al.* 2018). Alternatively, SOTN may be a byproduct of high levels of androgen in incubating males (Nice 1937, Kern and King 1972, Catchpole and Slater 2003) and females and not have an adaptive function. While few studies have directly examined SOTN, a handful of studies have found support for some of these hypotheses. For example, male Northern Cardinals (*Cardinalis cardinalis*) respond to female SOTN by adjusting their provisioning rates dependent upon the female's singing behavior (Halkin 1997). However, before we can fully understand the function, or lack thereof, of SOTN, we need more detailed studies on intraspecific variation in the behavior.

As part of another study (Stracey 2011), Northern Mockingbird (*Mimus polyglottos*) nests were continuously monitored with video cameras in 2008 and 2009 in north central Florida and several cases of SOTN were discovered. The purpose of the present study was to follow up on these initial observations of SOTN by documenting the extent to which the Northern Mockingbird sings on the nest, describe properties of SOTN (e.g., rate, length, and timing of singing), and test for an association between SOTN and nest predation. We also collect preliminary data related to hypothesized functions of SOTN including coordination of parental care, territory maintenance, nest defense, and vocal learning.

METHODS

Study System

The Northern Mockingbird is an opencup nesting, altricial bird that occurs throughout the United States, southern Canada, Mexico, and the West Indies (Farnsworth *et al.* 2020). Pairs are socially monogamous with both sexes participating in parental care: females exclusively incubate eggs and nestlings, and both sexes provision nestlings and defend nests (Farnsworth *et al.* 2020). Mockingbirds are perhaps best known for their ability to mimic the songs and calls of other bird species, as well as other sounds in their environment (Farnsworth *et al.* 2020). Males are prolific singers during the breeding season, whereas females rarely sing in the spring and summer and only do so when their mates are not on the territory (Farnsworth *et al.* 2020). Both male and female mockingbirds sing in the fall at a lower rate than males do during the breeding season (Breitwisch *et al.* 1986). While male mockingbirds engage in song matching during countersinging, its function is unknown and it is unknown if

females countering or song match (Farnsworth *et al.* 2020). As in most species (Odom and Benedict 2018), the extent and acoustic structure of female mockingbird songs have not been well studied (but see Gammon and Stracey 2022).

To explore SOTN in mockingbirds, we analyzed video recordings from a previous study (Stracey 2011). Stracey (2011) placed continuous-running video cameras near 128 mockingbird nests located in residential neighborhoods, pastures, and a wildlife reserve near Gainesville, Florida in 2008 and 2009 (see Stracey and Robinson 2012 for a map of study sites). Cameras were placed near nests once the clutch was complete (or upon discovery of a nest that was farther along) and were removed when the nest was empty as a result of fledging or predation. The cameras were placed ~0.5–1 m from the nest cup such that there was a clear view of the bird on the nest; however, this precluded us from seeing what was happening outside of the nest itself. The cameras (OPCM Weatherproof Security Camera BS08; 6 cm × 4 cm × 4 cm) recorded in black and white with sound onto a DVR (Archos 504, Igny, France) and were transferred to external hard drives and later to a server for storage.

We haphazardly selected 65 nests to sample for SOTN for a combined 8,353.9 hr of video footage. To identify instances of SOTN we used a two-step process that included both automated and manual approaches. The automated step consisted of running the videos through a computer program to determine likely intervals of SOTN based on a frequency and then a decibel filter. Timestamps with potential singing events were written to an output file. Researchers then reviewed videos of all outputted timestamps for all nests to determine whether SOTN occurred and, if so, recorded descriptive behavioral data.

Automated Analysis

We developed an automated analysis program using Python to produce timestamps with potential singing events based on frequency and amplitude (Figure 1; see <https://github.com/dakota-hawkins/SOTN> for the code). For the automated analysis only, the audio track was isolated from each video file and broken into 1-min sections for analysis to prevent computer crashes. Sounds were transformed into the frequency domain using the Fast Fourier Transform. Sound files were then run through a frequency filter that excluded any 1-min samples with sound frequencies outside of 2–7 kHz, the characteristic frequency range of avian species (Nemeth *et al.* 2015).

To better distinguish SOTN from background singing, samples with 2–7 kHz sounds were run through an amplitude filter. We assumed that if SOTN occurred, the proximity to the camera would result in large decibel values relative to other sounds in the background. The amplitude of each of these samples was then compared to the amplitude of a random 1-min sample of average background noise. If the decibel value of the sound sample was >0 and in the 90th percentile of amplitudes in the sample, then the sample was kept, otherwise the sample amplitude was forced to zero to exclude it from further analysis. To better determine when SOTN occurred within the sampled interval, the program compared the percent change of amplitude of each 1-min section before and after filtration over a series of 15-s time intervals. If the percent change was <10%, the starting timestamp was recorded. If any timestamp fell within 10 s of another, it was removed; and a final output file was created that contained timestamps of potential SOTN occurrences.

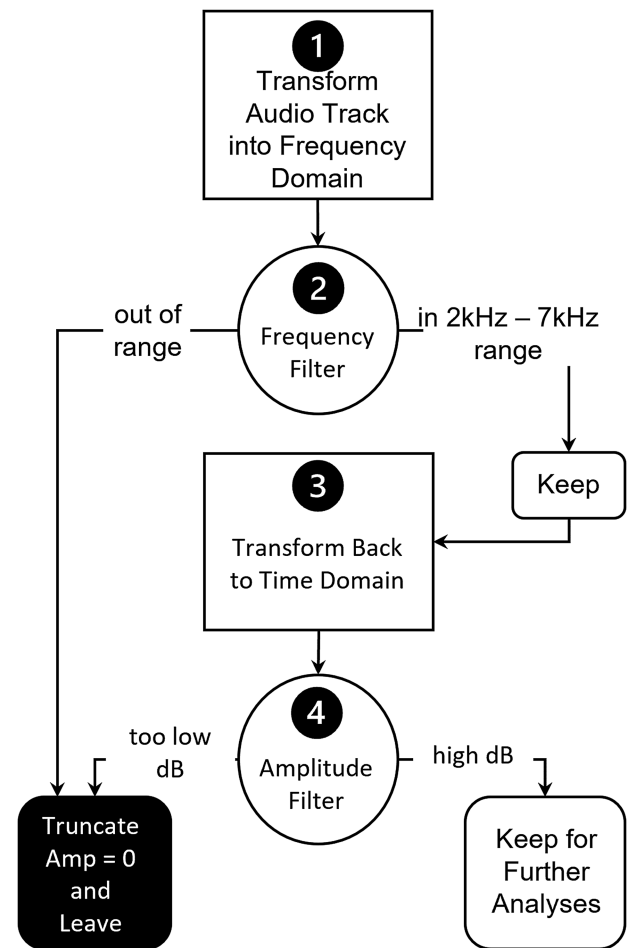


FIGURE 1. Graphical representation of the automated identification of potential SOTN occurrences. (1) Audio files were transformed into the frequency domain using the Fourier Transform, then (2) files were passed through a frequency filter and only samples between 2 and 7 kHz were (3) transformed back into the time domain with the Inverse Fast Fourier Transforms and passed through (4) an amplitude filter that compared the amplitude of the sample to the background amplitude, lastly (5) samples that had a decibel value >0 and were in the 90th percentile of samples were kept for further analysis.

We validated the automated analysis by watching 7 test files in their entirety comprising 980 min of video. In these 7 test files, the program was able to detect all singing intervals without producing false negatives. False positives were present, including from nestling begging, and accounted for 63% of timestamps generated in these 7 files. During manual inspection (see below), we came across a number of false negatives, which occurred most frequently on videos with extensive wind noise, but we were unable to adjust our filters to account for this without substantially increasing our rate of false positives. We collected data on all false negatives that we came across; therefore, our estimates of SOTN are minimum estimates of the true rate of SOTN.

Manual Inspection

Because other sounds can display the same acoustic characteristics as SOTN and we had a high rate of false positives, we manually inspected all 32,471 timestamps generated from the automated analysis for all 65 nests to validate the

presence of SOTN. For each timestamp, we viewed the original video files starting 1 min prior to the timestamp and continuing 1 min after the timestamp to determine if SOTN occurred. For every instance of SOTN that occurred, we recorded additional data for each singing event. We considered any pause in singing that lasted longer than 10 s as a new event of SOTN. For each SOTN event, we recorded song duration, time of day, nest stage (eggs or nestlings), and, when possible, the sex of the singing bird to verify that it was the female and not the male singing. A subset of adult birds in the videos were color-banded, but we were unable to read the colors from the black and white footage and so could only identify sex when one member of the pair was banded and the other was unbanded ($n = 19$ nests). In cases where we had data from the same female across multiple nesting attempts, we averaged the data across her renests and used that in our analyses. We recorded the same data for instances of SOTN that were not timestamped, but that we came across incidentally.

Characterization of SOTN

To determine how widespread SOTN is in the Northern Mockingbird, we calculated the percentage of nests that had at least one SOTN event. Because SOTN occurred almost exclusively during the egg stage (see Section 3), we recalculated the percentage of nests with at least one SOTN event by excluding 9 nests that had no sampling during the egg stage from the initial calculation. To further characterize SOTN, for each nest, we calculated the average SOTN event length and summed all events for the total SOTN duration for that nest. We also calculated the rate of SOTN. Because of the complexity of defining discrete mockingbird songs and because we had unequal sampling times on each nest, we calculated this rate by dividing the total SOTN duration in seconds by the total hours sampled for that nest. We then calculated the average rate of singing across all nests that had at least one SOTN event.

To describe the relationship between SOTN and time of day, we determined time of sunrise on the date of each singing event using the *getSunlightTimes* function in the *suncalc* package (Thieurmel and Elmarhraoui 2019) in R Studio 1.2.1335 (R Core Team) and converted the time of singing to minutes before or after sunrise, with sunrise equal to 0 min. For each nest, we calculated the rate of singing during the following time periods: dawn chorus (1 hr before sunrise to 1 hr after sunrise), morning (1 hr after sunrise to 5 hr after sunrise), afternoon (5 hr after sunrise to 2 hr before the end of nautical twilight), dusk (2 hr before end of nautical twilight to end of nautical twilight), and overnight (end of nautical twilight to 1 hr before sunrise). We chose these intervals because they roughly correspond with daily singing patterns of male mockingbirds (Merritt 1985). Because we were interested in describing temporal patterns of singing for birds that engage in SOTN, we compiled data on all nests with singing that were also sampled in all 5 time periods ($n = 43$). We calculated the rate of SOTN within each time period for each nest by dividing the total duration of singing by the number of hours of video sampled for that time period. A Kruskal–Wallis test was conducted using SAS Studio 3.8 (SAS Institute, Cary, North Carolina, USA) to see if the rate of SOTN differed significantly based on time of day. We then performed a Dunn post-hoc pairwise test with a Bonferroni correction

to determine which intervals differed significantly using R Studio 1.2.1335.

To describe the extent of female and male SOTN, we identified the individual responsible for singing based on the presence/absence of leg bands when only one member of the pair was banded and singing occurred ($n = 13$). We then calculated the total number of SOTN events for each nest, the percentage of events performed by females, the percentage of events performed by males, and the percentage of unknown events (when the bird's legs were not visible). We also calculated the average SOTN event length for females and males.

Cost of SOTN

We predicted that increasing rates of SOTN would lead to a higher probability of nest predation (Peterson *et al.* 2004, Kleindorfer *et al.* 2016, Walker and Marzluff 2017). To test the relationship between the rate of SOTN and nest predation, we calculated daily nest survival rates using the logistic-exposure method (Shaffer 2004). We used a modified logit-link and set the SOTN rate as a fixed effect and nest ID and year as random effects to account for annual variation and pairs using the *glmmTMB* (Brooks *et al.* 2017) package in R Studio 4.2.1 (R Core Team 2018). Five out of the 65 nests sampled in this study failed for reasons other than nest predation. Because we were only interested in the effect of SOTN on nest predation, nests that failed due to predation ($n = 37$) were the only ones we considered in the model as not surviving (survival = 0). We reviewed model residuals to assess normality. Models presented in results fulfilled this requirement.

Exploration of Potential Function of SOTN

Coordination of parental care.

To explore the hypothesis that SOTN functions in the coordination of parental care (Halkin 1997, Haff *et al.* 2015), we counted the number of events in which the mate returned to the nest during or within 1 min of the end of the SOTN event. In addition, we compared the rate of SOTN in the egg stage to the nestling stage ($n = 65$). We predicted that SOTN should be low during the egg stage because male mockingbirds do not incubate or feed the incubating female, whereas during the nestling stage, SOTN should be higher because males are assisting with nestling provisioning. We calculated the rate of SOTN for each nest in each stage and tested for a difference in rate using a linear mixed model using the *lme4* package (Bates *et al.* 2015) in R Studio 4.2.1 (R Core Team 2018). We used egg stage as the predictor variable, singing rate as the response variable, and site nested within year as a random effect. We reviewed model residuals to assess normality.

Territory maintenance.

If SOTN is related to territory maintenance, then we predicted that rates of SOTN should be positively associated with population density (Arcese *et al.* 1988, Yoon *et al.* 2012), occur in response to background mockingbird song (e.g., Hathcock and Benedict 2018), and include song matching (Akçay *et al.* 2013).

We predicted that if SOTN functions in territory maintenance, then study sites with higher population density would have higher rates of SOTN since previous studies have found a correlation between rates of territory defense and

population density (Arcese *et al.* 1988, Yoon *et al.* 2012, but see Dargis *et al.* 2021). We estimated population density in two ways: by calculating territory density and nearest neighbor distance. We used territory density of each site, as calculated by Stracey (2010). Mockingbird nests were located in the 5 study sites and nests were assigned to a territory based on color-bands or the location and timing of egg laying when individuals were unbanded. The number of territories in each year at each study site was divided by the area of the study site. Data for territory density were available for 2006, 2007, and 2008 while SOTN data were available for 2008 and 2009. We, therefore, used the average territory density across 2006–2008 for our analysis. We attempted to run generalized linear mixed effect models using average territory density; however, we were unable to adequately fit a model to our data. Because sites varied in their density (0.054–0.270 territories ha^{-1}), we visually explored the relationship between site and average rate of SOTN as a preliminary assessment of this hypothesis.

We also calculated the distance between each nest from 2008 ($n = 26$) and the closest Northern Mockingbird nest (that was not a re-nest of the same pair) based on GPS latitude and longitude coordinates. We calculated the pairwise distance between GPS coordinates using the *coordinates* function in the *sp* package (Pebesma *et al.* 2005), and the *distm* function in the *geosphere* package (Hijmans *et al.* 2021). All packages were run in SAS Studio 3.8 (SAS Institute, Cary, North Carolina). To test for a relationship between the distance of the nearest neighbor and the rate of SOTN, we attempted to run linear and generalized linear models. Once again however, we were unable to fit a model to our data and instead, we visually explored the relationship between rate of SOTN and nearest neighbor using a scatterplot.

We attempted to quantify SOTN in response to a mockingbird singing in the background, as well as the percentage of SOTN events that involved song matching. Unfortunately, we were unable to do so systematically because the audio from the built-in microphones on the cameras were not set up to study vocalizations and thus recording volume and distance from nests were not standardized or documented. In addition, the cameras used were not of high enough quality to consistently capture singing in the distance or allow us to make detailed acoustic measurements. We therefore simply noted instances when either of these behaviors was particularly obvious and counted the number of nests when each was documented at least once; these estimates therefore represent the minimum extent of response to background singing. We predicted that we would observe clear instances of SOTN in response to singing by a mockingbird in the background (Hathcock and Benedict 2018), as well as song matching (Akçay *et al.* 2013), if SOTN functions in territory maintenance.

Nest defense.

Mockingbirds are not known to destroy conspecific nests (Stracey 2011, Farnsworth *et al.* 2020) and they are not a common host for Brown-headed Cowbirds (Farnsworth *et al.* 2020); therefore, if SOTN is used in nest defense (Haff *et al.* 2015), it would be for defense against nest predators. If SOTN functions in nest defense, then we predicted that there would be a negative relationship between rate of singing and probability of predation. If, on the other hand, nest predation

is a cost of SOTN, then we predicted that there would be a positive relationship between rate of singing and probability of predation. To assess the relationship between SOTN and nest predation, we modeled the probability of nest predation as a function of rate of SOTN (see Cost of SOTN above for details of analysis).

Vocal learning.

Vocal learning was traditionally thought to occur beginning in the fledgling stage (Marler and Peters 1981); however, a growing body of literature demonstrates that vocal learning begins while developing birds are still in the egg (e.g., Katsis *et al.* 2018, Rivera *et al.* 2018, Colombelli-Négrel *et al.* 2021). We, therefore, predicted that if SOTN functions in vocal learning, then SOTN should occur during both the egg and nestling stages (see Coordination of Parental Care above for details of analysis).

All averages are reported \pm SE and all *P*-values reported are for 2-tailed tests with an α level of 0.05.

RESULTS

Characterization of SOTN

We sampled a total of 8,353.9 hr of video footage across 65 nests with an average of 128.5 ± 12.8 hr sampled per nest. The minimum hours sampled per nest was 8.9 while the maximum sampled was 542.1 hr. Of the 65 nests that we screened, SOTN occurred at least once in 48 nests (74%). Of the 17 (26%) nests without SOTN, 9 exclusively had recordings during the nestling phase. When we remove these 9 nests with no egg sampling from our calculation, SOTN was detected in 86% (48 of 56) of nests screened. While 8 nests sampled during the egg phase had no SOTN, these 8 nests had limited sampling during the egg phase: an average of 11.9 hr sampled (range: 6.8–18.5 hr) as compared to an average of 90.3 hr sampled (range: 8.7–231.1 hr) in the egg phase for nests in which we detected SOTN. Average SOTN event duration was 20.00 ± 1.29 s with an average of 29.44 ± 5.69 singing events per nest. The average rate of SOTN was 5.24 ± 1.24 (seconds of SOTN per hour sampled).

The rate of SOTN significantly differed across time intervals ($\chi^2 = 44.3$, $df = 4$, $P < 0.001$). Rates of SOTN were highest during the dawn chorus and morning and then decreased as the day went on (Figure 2).

For the 13 nests where we could definitively identify the female and male, there were 502 SOTN events with 475 produced by the female (95%), 12 produced by the male (2%), and 15 unknown because we could not see the bird's legs (3%). In 11 of the 13 nests, all SOTN events were by the female. In the remaining two nests, the same banded male produced the SOTN. For his first nest, there were 21 total SOTN events with 10 by the female and 11 by the male. For his second nest, there was only one SOTN event detected and it was produced by the male. The average event duration by females was 20.02 ± 3.21 s hr^{-1} and the average SOTN event duration by the male was 21.86 ± 4.37 s hr^{-1} .

Cost of SOTN

As hypothesized, there was a decrease in nest survival with increasing rates of SOTN. Our linear mixed model found that the SOTN rate significantly predicts lower daily survival ($P = 0.006$, Figure 3, Table 1).

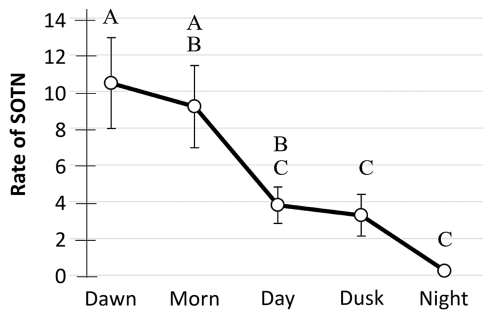


FIGURE 2. Least-square means with standard error for the average rate of SOTN (seconds of singing per hour of video sampled) for each time-of-day interval ($\chi^2 = 44.3$, $df = 4$, $P < 0.001$). Dawn = dawn chorus, Morn = morning, Day = afternoon, Night = overnight. Letters indicate significance at $\alpha = 0.05$ after a Bonferroni correction for Dunn's pairwise comparisons.

Exploration of Potential Function of SOTN

Coordination of parental care.

In only 5 out of 48 nests, the mate returned to the nest during or within a minute of the end of the SOTN event and for each of these 5 nests, this only occurred once. SOTN occurred at a higher rate during the egg stage (5.38 ± 1.18 s hr^{-1}) than the nestling stage (0.16 ± 0.09 s hr^{-1} ; $P < 0.001$; [Figure 4](#); [Table 1](#)).

Territory maintenance.

There was no relationship between territory density or distance to the nearest neighbor with rates of SOTN ([Figure 5](#)). In 19 out of 48 nests, SOTN clearly occurred at least once in response to a singing mockingbird in the background. In 12 nests there was at least one obvious instance of clear song matching and for 3 of those nests obvious song matching occurred extensively.

Nest defense.

The probability of nest predation did not decrease with increasing rates of SOTN and instead increased with higher rates of singing (see above).

Vocal learning.

SOTN occurred at a higher rate in the egg stage than the nestling stage (see above).

DISCUSSION

SOTN is widespread at the population level in the Northern Mockingbird with at least 74% of birds in this study singing on the nest at least once. When we restrict our data to nests with at least 2 hr of sampling during the egg stage, then 86%

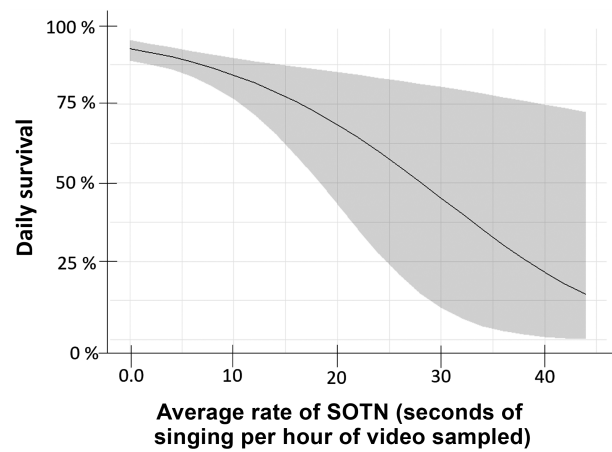


FIGURE 3. Linear mixed model predicted daily survival rate of Northern Mockingbird nests as a function of the average rate of SOTN (seconds of singing per hour of video sampled). Black line is the fitted line for predicted daily survival, gray shaded area is the 95% confidence interval for the predicted relationship between daily survival and average rate of SOTN.

of mockingbirds sang on the nest. To the best of our knowledge no one has documented this behavior in mockingbirds, despite their breeding biology being relatively well studied ([Farnsworth et al. 2020](#)). [Leonard's \(2008\)](#) survey of the Birds of North America found that 10% of songbird species had at least anecdotal accounts of SOTN (but not mockingbirds). Leonard concluded that SOTN is much more widespread than previously thought and our results further support this conclusion.

While the majority of nests had at least one instance of SOTN, rates of SOTN by individual birds were low (ranging between 0.04 and 44.01 s of singing per hour of video sampled) and they peaked during the dawn chorus ([Figure 2](#)). This rate calculation includes overnight periods when SOTN is rare and the automated sampling produced false negatives, therefore the rates we present here should be viewed as minimum estimates of the true rate of SOTN. Even if our conservative estimates of SOTN are off by an order of magnitude, we would still conclude that SOTN is widespread at the population level in mockingbirds, but that individual birds sing at low rates. We restrict the following discussion to SOTN and do not include a broader discussion of calling on the nest (COTN), as that has been treated elsewhere ([Haff et al. 2015](#)).

Cost of SOTN

The main reason SOTN is considered a paradoxical behavior is that vocalizations from a nest are assumed to attract

TABLE 1. Results for daily survival modeled as a function of SOTN rate and rate of SOTN modeled as a function of nest stage.

	Estimate	SE	<i>z</i>	<i>P</i>
Model: Daily survival as a function of SOTN rate				
Intercept	3.38	0.24	14.17	<0.001
Average rate of SOTN	-0.084	0.03	-2.98	0.003
Model: Rate of SOTN as a function of nest stage				
Intercept	5.38	0.84	6.41	<0.001
Stage (nestling)	-5.22	1.17	-4.46	<0.001

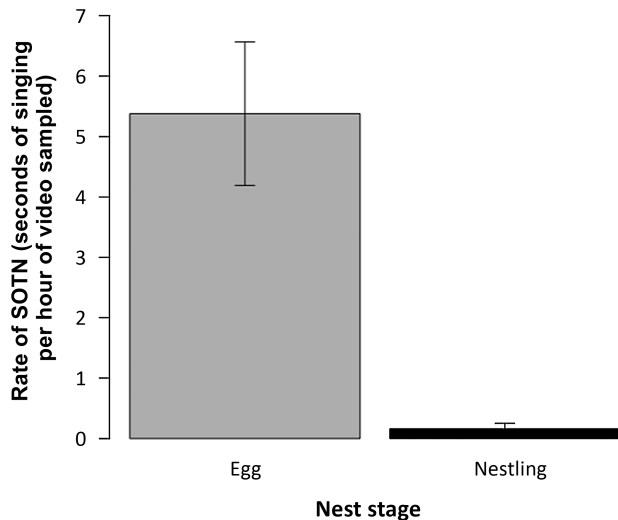


FIGURE 4. The average rate of SOTN in the egg stage and nestling stage of Northern Mockingbirds ($n = 65$, $P < 0.001$). Rate of SOTN is seconds of singing per hour of video sampled \pm standard error (SE).

the attention of nest predators and parasites, thereby reducing nest success and resulting in selection against SOTN (Leonard 2008). As predicted, we found that increasing rates of SOTN led to decreasing daily survival rates of Northern Mockingbird nests (Figure 3). None of the 65 nests in this study were parasitized, which is consistent with low rates of parasitism across most hosts by Brown-headed Cowbirds in north-central Florida (Reetz *et al.* 2007); therefore, we cannot address that hypothesized cost of SOTN.

Previous studies that correlated SOTN with nest predation have found mixed results, with some studies finding an increase in nest predation with singing (Kleindorfer *et al.* 2016, Walker and Marzluff 2017) and others finding no relationship (Leonard 2008) or even a decrease in nest predation with SOTN (Yasukawa 1989). The strongest study to date (Kleindorfer *et al.* 2016) experimentally manipulated rates of SOTN on Superb Fairy-Wren nests and found a positive correlation between rate of SOTN and nest predation. The extremely low rates of SOTN that we document could be the result of the tradeoff between achieving the function of SOTN while minimizing its predation cost. Additionally, birds may adjust SOTN based on the presence of predators in the area (Schmidt and Belinsky 2013, Haff *et al.* 2015, Walker and Marzluff 2017), which could further reduce the costs of SOTN.

On the other hand, other studies have failed to document a link between SOTN and nest predation (Peterson *et al.* 2004, Leonard 2008). For example, Peterson *et al.* (2004) found no association between SOTN and nest predation of Least Bell's Vireos. This study, however, limited the correlation between SOTN and nest predation to SOTN in the 1-hr preceding the predation event and excluded all night predation events. The link between nest detection and nest predation might be more complex than we currently understand (e.g., Krama and Krams 2005). For example, we have video evidence of a house cat that visited a mockingbird nest on multiple nights during the egg stage, but did not depredate the nest until after the eggs had hatched (C. Stracey personal observation) demonstrating a lag of days between nest detection and nest predation. A more complete

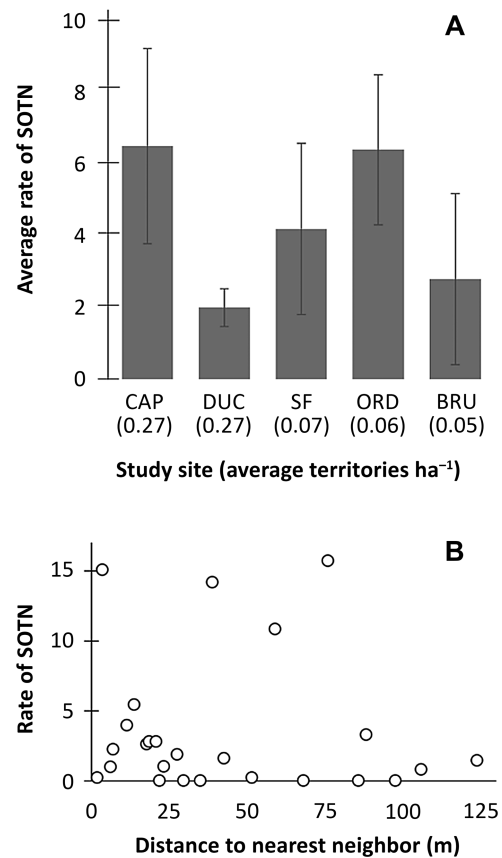


FIGURE 5. Relationship between rate of SOTN (seconds of singing per hour of video sampled) and population density. (A) Average rate \pm SE of SOTN in 2008 and 2009 for each study site. Sites are ordered by decreasing mean territory density (averaged from 2006, 2007, and 2008) with territory density displayed under each study site for illustrative purposes. (B) Rate of SOTN for nests in 2008 based on the distance to nearest neighbor (m).

understanding of the foraging ecology of predators is necessary to fully understand the relationship between SOTN and nest predation. Future experimental research is also needed on the cost of SOTN in terms of both nest predation and parasitism.

Potential Functions of SOTN

With the exception of one male that engaged in SOTN, all other SOTN events were by female mockingbirds and SOTN occurred almost exclusively during the egg stage (Figure 4). Female mockingbirds are known to sing in the fall (Breitwisch *et al.* 1986) and only rarely during the breeding season (Farnsworth *et al.* 2020). Given the pervasiveness of SOTN in the Northern Mockingbird, the hypothesis that this rare female song is an aberrant behavior that results from unusually high levels of androgens (Nice 1937, Kern and King 1972, Catchpole and Slater 2003), seems unlikely, although we are unable to eliminate this hypothesis with our data. Testosterone levels in female birds in general (Ketterson *et al.* 2005), and the Northern Mockingbird specifically (Logan and Wingfield 1995), peak during the pre-laying and laying periods and not during incubation, which is when we recorded SOTN. However, our understanding of how hormones regulate singing at an individual level is limited, particularly for females, and recent work highlights the need to

integrate sex differences across hormonal responses, the nervous system, and gene expression (Ball and Balthazart 2008, Frank-Vilches and Gahr 2018, Riebel *et al.* 2019). Without a better understanding of the neuroendocrine basis of singing for mockingbirds specifically, it is difficult to make clear predictions for any byproduct hypotheses and additional research is needed to assess this hypothesis for SOTN.

While it is likely that hormones play a proximate role in SOTN, we need to consider that SOTN has an adaptive function given how widespread it is (Leonard 2008). The limited evidence available from previous studies on the function of SOTN supports the hypothesis that SOTN coordinates parental care (Howes-Jones 1985, Halkin 1997, Neudorf *et al.* 2013). If SOTN serves this function in mockingbirds, then we predicted that SOTN should occur more frequently during the nestling stage because males do not incubate eggs and do not provision incubating females, but they do feed nestlings (Supplementary Material Table S1). Contrary to this prediction, we found that rates of SOTN were significantly higher during the egg stage than during the nestling stage when SOTN was extremely rare (Figure 4). Therefore, we conclude that SOTN in the Northern Mockingbird is not used to coordinate parental care. Instead, mockingbirds appear to use calls instead of song during male–female interactions at the nest (B. Brown personal observation), as is the case for some other species (e.g., Boucaud *et al.* 2016, 2017; Ferree *et al.* 2021). Whether a species employs singing or calling to coordinate parental care may depend on habitat characteristics and the distance over which they need to communicate (Bradbury and Vehrencamp 1998). Future research is needed to understand the role of calling vs. singing in parental communication at the nest.

While the coordination of parental care has received the most support in previous studies of SOTN, studies of female song more generally tend to support the hypothesis that song functions in the context of resource defense (e.g., territoriality; reviewed in Langmore *et al.* 2008). In terms of SOTN, however, there is limited evidence that it serves this function (Kasumovic *et al.* 2003, Chiver *et al.* 2007).

While the function of female mockingbird song is unknown (Farnsworth *et al.* 2020), female mockingbirds are known to sing, albeit infrequently, during fall territory establishment (Breitwisch *et al.* 1986) and rarely during the breeding season when their mate is off territory (Farnsworth *et al.* 2020). If SOTN functions in territoriality, then we predicted that (1) rates of SOTN would be higher at study sites with higher population densities, (2) SOTN would occur in response to background mockingbird song, and (3) there would be song matching with background song. The relationship between population density and singing rate is ambiguous (e.g., Yoon *et al.* 2012 vs. Dargis *et al.* 2021) and we did not find an association between territory density and SOTN (Figure 5A) or nearest neighbor distance and SOTN (Figure 5B). There were clear instances when the incubating bird became alert immediately following the start of a nearby singing mockingbird and then began to sing, but this was not the case for every nest. There were also numerous times we were able to detect obvious song matching between a nearby singing mockingbird and the bird that was engaged in SOTN, but again this was not always the case. The amplitude of SOTN that we detected varied from “quiet song” to a volume that seemed consistent with typical male songs. Unfortunately, because of audio

quality, we were unable to systematically quantify the amount of SOTN in response to background singing, the amount of song matching, or the amplitude of song. We also have no way of knowing if the bird singing in the background that she seemingly responded to, or was song matching with, was her mate or an intruder. The function of song matching varies across species and sexes (Todt and Naguib 2000, Rogers *et al.* 2006, Moser-Purdy *et al.* 2019). While male mockingbirds engage in song matching during countersinging, its function is unknown (Farnsworth *et al.* 2020) and to the best of our knowledge there have been no previous reports of song matching in female mockingbirds. Given that we were unable to directly test the hypothesis that SOTN functions in territory maintenance and the fact that our predictions for this hypothesis are weak to begin with, these results should be interpreted with caution.

SOTN has also been hypothesized to function in nest defense (reviewed in Haff *et al.* 2015) and could occur in three ways: (1) the cessation of singing alerts predators to unattended nests (Watchman’s song sensu Wickler 1985), (2) males are tricked into returning to the nest to defend against predators because female song is perceived as a rival male (Morton *et al.* 1978, Ritchison 1983), or (3) singing signals to the mate that a predator is near so that the mate can return to defend the nest (Yasukawa 1989). The first explanation likely does not apply to mockingbirds because they only rarely sing on the nest, unlike species in which SOTN is relatively constant (e.g., Howes-Jones 1985). It is possible that mockingbirds sing to alert their mate of a nearby predator; however, given the extensive and complex alarm calls that mockingbirds produce in response to nest predators (Savage *et al.* 2020) this explanation also seems unlikely. Furthermore, we documented an increase in nest predation with increasing rates of SOTN (Figure 3). Based on our preliminary evidence, we, therefore, reject the hypothesis that SOTN functions in nest defense against predators for mockingbirds. However, more studies are needed to address potential nest defense against brood parasites.

Two more potential hypotheses for SOTN are that it is used for song learning and parent identification (reviewed in Haff *et al.* 2015). Traditionally, song learning in birds is thought to occur during a critical period during the late nestling and fledgling stages (Marler and Peters 1981), but growing evidence indicates that developing bird embryos respond to and are shaped by their prenatal acoustic environment (e.g., Katsis *et al.* 2018, Rivera *et al.* 2018, Colombelli-Négrel *et al.* 2021). We found that SOTN rate was significantly higher during the egg stage; however, the role of acoustic signals during the egg stage of mockingbirds remains unstudied and our results suggest this needs further investigation. Likewise, how fledglings locate their parents is also unknown. Anecdotally, on one of the nests with a relatively high rate of SOTN (14.18 s hr⁻¹ sampled compared to the average of 5.24 ± 1.24 s hr⁻¹), a fledgling repeatedly appears at the nest when the female is incubating and singing. In re-nesting mockingbirds, the male typically feeds the fledglings while the female incubates the next clutch (Farnsworth *et al.* 2020). Perhaps, song is a cue used by fledglings to locate the parent responsible for feeding. Whether song during the egg stage facilitates this is also a mystery.

Lastly, SOTN has been proposed to play a role in the maintenance of pair bonds (Beletsky and Orians 1985, Leonard 2008, Haff *et al.* 2015), the solicitation of extrapair

copulations (EPC's; Leonard 2008), and could shape offspring quality via maternal investment (*sensu* Mariette and Buchanan 2016). With our data, we were unable to explore the potential for SOTN to function in pair bonding or maternal investment. The SOTN that we recorded occurred after clutch completion and, therefore, incubating females would not be fertile indicating that solicitation of EPC's was not the function of SOTN in our study. All of these hypotheses, however, warrant further evaluation.

Collectively, our results failed to strongly support a particular hypothesis for why female mockingbirds engage in SOTN. We found no support for the hypotheses that SOTN functions to coordinate parental care, defend nests, or aid in vocal learning. We were unable to assess the byproduct hypothesis or the hypotheses that SOTN functions in pair bonding or maternal investment. We did, however, find mixed support for the hypothesis that SOTN functions in territory maintenance. Future studies involving playback experiments of territorial intruders, including assessment of song matching, could test this hypothesis directly.

Our data demonstrate that a species that was thought not to sing on the nest not only does so, but the majority of incubating females engage in the behavior. This suggests that low rates of SOTN could be much more widespread than currently appreciated. Given the limitations of our study, we can only draw preliminary conclusions about the potential function(s) of SOTN, but we are able to offer tantalizing clues that should be followed up on with both observational and experimental studies. Likewise, most previous studies on the relationship between SOTN and nest predation/parasitism are correlational; therefore, it is critical that future studies experimentally assess the predation and parasitism cost of SOTN to fully understand this behavior. Continuous video monitoring of nesting birds, combined with automated screening have the potential to drastically revise our understanding of SOTN and the breeding biology of birds.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

This research was conducted in compliance with the Guidelines to the Use of Wild Birds in Research and IACUC protocol #D984.

Author contributions

C.M.S. formulated the questions and supervised research; C.M.S., K.S., and B.B. collected data; C.M.S. wrote the paper with assistance from K.S. and B.B.; D.H. and T.S. developed automated analysis; K.S. and B.B. performed statistical analyses; C.M.S., K.S., and D.H. contributed funding.

Data availability

Analyses reported in this article can be reproduced using the data provided by Stracey *et al.* (2023).

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