Proceedings of The National Conference
On Undergraduate Research (NCUR) 2014
University of Kentucky, Lexington, KY
April 3-5, 2014

How Does Song Sequence Duration Vary Between Breeding Stages in the Northern Mockingbird (*Mimus polyglottos)*?

Helen L. Wright
Biology Department
Elon University
East Haggard Avenue
Elon, North Carolina 27244 USA

Faculty Advisor: Dr. David E. Gammon

Abstract

During their spring breeding season, male Northern mockingbirds sing continuously for up to several hours while frequently switching between different song types. Singing behavior is thought to influence female mate choice. A previous observational study found that males produced a greater number of song types per unit of time during the nest building stage and declined once incubation began. Using song data from nine free-living mockingbirds on Elon University's campus, I measured the duration of song sequences during the different breeding stages. I found that males sang more continuously when females were fertile. This increase in song duration during female fertility periods indicates the possible importance of song duration in stimulating a female mate. It also suggests that it is evolutionarily advantageous for males to sing longer sequences during times of female fertility.

Keywords: breeding season, song duration, Northern mockingbirds

1. Introduction

Seasonal variation in behavior, hormones, and physiology is noticeable across all taxa. For certain species, the breeding behavior can vary tremendously. For many organisms, hormonal signals are used to regulate sexual behavior which may cause an increase in gamete production and sexual activity. Whether animals are closely related or not, they tend to have the same set of hormones controlling sexual behavior and development: testosterone and estrogen. For example, British red deer stags produce more testosterone and consequently become aggressive in September, as their mating season approaches[7]. One group of organisms that is characterized by drastic changes in breeding behavior is birds. In temperate zones, the emergence of bird song in the spring is a great example of this seasonally-based behavioral change[3]. Most songbirds sing on an annual cycle reflecting breeding activity such as occupying territory and attracting a mate. One study by Slagsvold indicated that in a few different species, the peak song activity was followed by female egg-laying[13]. Multiple studies have established this pattern of increased song to attracting a mate among many species[5, 8]. This suggests that one purpose of bird song is to attract a female mate at their point of highest fertility[13]. Specifically, the increased duration of song sequences is important during the breeding season for attracting a mate. One study by Payne and Payne observed a community of indigobirds in Africa and concluded that the most successful males were those who sang more songs per hour than the less vocal birds[12]. This suggests the length of song serves as a sexual attractor. One species that is known for its continuous singing behavior is the Northern mockingbird. Logan observed mockingbird song behavior and found that overall song became most continuous during the nest building phase through to the egg-laying stage and became less continuous during the incubation and nestling phases[8]. With these results, it was suggested that male singing behavior changes in association with the female fertility and may have a stimulating effect on the female [8].

The Northern mockingbird (*Mimus polyglottos)* was chosen as the study organism because of its complex, continuous singing behavior. Although they sing year round, the males typically begin singing extensively in

February and continue through August[5]. They form monogamous pair bonds with a mate that usually lasts anywhere from two to four years, but have been recorded to remain paired for up to eight years[10]. Table 1 illustrates the typical progression of the mockingbird breeding stages[5].

Table 1. The table summarizes the usual pattern of progression through the breeding season from stage to stage.

Stage	Time-Frame
Nest building	15-25 days
Egg-laying	3-4 day
Incubation	12-13 days
Nestling	~12 days in nest post-hatching
Fledgling	Post-leaving nest, flight develops ~8 days after leaving nest
Nest building (2nd clutch)	1-3 days after fledglings leave the nest, males being nest building

My study describes how song length varies with each breeding stage. Mockingbirds typically have several overlapping clutches of eggs between February and August, so the goal of this study was to quantify the differences in song duration of the breeding season relative to a bird's first clutch of eggs[5]. The timing of the transitions between breeding stages varied for each bird. For some birds, nests failed, while others were successful in beginning a second brood of eggs immediately after the first. In a previous study, Logan monitored song behavior of Northern mockingbirds through the breeding cycle and found that the most overall song behavior was observed during the nest building stage and the egg-laying stages, or when the female was approaching peak fertility[10]. Although Logan evaluated the overall song produced, she did not focus specifically on the changes in song sequence durations[8]. In my study, I was focused on analyzing the changes in song sequence durations through each breeding stage.

Previous research suggests that high song activity correlates with increased mating behavior; therefore I would expect to observe changes in male singing behavior in order to successfully attract and mate with a female when she is most fertile[4]. A study conducted by Wasserman and Cigliano examined the response of white-throated sparrow females to variation in male song. By manipulating the song playback to lengthen and shorten song sequences, the researchers observed that females displayed more to the increased song output and longer song sequence durations[14]. In birds that are continuous singers, such as the Northern mockingbird, increased song output behavior often times means that there are shorter pauses between longer sequences of song[3]. With the accepted understanding and knowledge about the function of bird song, I predicted that the males would produce longer song sequence durations at the stage in the breeding season when females are most fertile, during the egg-laying stage[11].

2. Materials and Methods

2.1 Central Goals

My goal was to quantify changes in duration of song sequences of the Northern mockingbird through a single breeding season by observing multiple pairs during each breeding stage. I observed the behavior and recorded song from birds across Elon University's Campus, Elon, NC, USA.

2.2 Methodology and Data Collection

I recorded the song and observed the physical behavior of nine male mockingbirds at Elon University four to five times per week between February and May of 2013. These nine focal mockingbirds were identified and distinguished by a unique combination of colored bands on each of their legs. Data collection began at civil twilight and would continue for two consecutive hours by myself and my research advisor, Dr. David Gammon. Due to the territorial nature of mockingbirds, especially during the breeding season, I rarely observed a mockingbird travelling very far outside of its territory for more than a few minutes[5]. Due to the unique leg bands and the bird's territorial nature, I am confident that I was sampling data from nine distinct individuals.

I planned to collect at least ten minutes of song from each bird during each stage of the breeding season. This goal was logistically difficult due to variables in the ecosystem out of my control. Several factors such as nest predation, weather, and infertility prevented me from collecting data during the later breeding stages for some birds. I was unable to collect the entire ten minutes for all birds in each breeding stage.

During a sampling period for any focal mockingbird, I gathered continuous audio recordings of the song using a Tascam DR-100 recorder or a Zoom H4 solid-state recorder. These recording devices were connected to a Sennheiser ME62 microphone mounted inside a 60-cm Telinga Pro Universal parabola. I commented on their behavior throughout the audio recording and noted which breeding stage the bird was in. As mentioned in the Introduction, I broke down the breeding season into five sequential breeding stages: nest building, egg-laying, incubation, nestling, and fledgling stages[5]. My field observations allowed me to categorize and identify the breeding stages for each bird. Specifically, if I saw a male mockingbird carrying twigs to a bush, I categorized that as nest building behavior. Once I knew where the established nest was, I checked for eggs and female presence during every observation to determine if she had started egg-laying or incubating. I continued to check the nest until the eggs hatched to determine the start of the nestling stage and the survival, growth, and fledging of the offspring. Each day I never left the area until I was certain of the male's breeding stage. Due to my frequent observations of each focal male, (i.e., approximately every two days), I accurately estimated the dates of the first laid eggs within one day or less. Once the audio recordings were made, I transferred them to a computer and analyzed the song using Audacity software (http://audacity.sourceforge.net/) and Syrinx software (John Burt, available online at: www.syrinxpc.com/).

2.3 Observational Variables

I analyzed the collected song data in order to quantify differences in song sequence durations through the breeding season. I used spectrograms to visualize the song, which allowed me to define song sequences, create a silence threshold, and therefore measure the song duration. I defined a song sequence as a chain of songs between longer breaks. Even though these sequences usually contained different song types, I was only interested in measuring the overall duration of each sequence. The number of different song types and the species were not taken into consideration when measuring the sequence duration: rather the sequence duration was a measurement of the number of seconds of continuous song. After reviewing 100 mockingbird song sequences from the recorded data, I observed that the duration of breaks between song sequences varied continuously. However, it was essential to establish a threshold in order to quantify the start and stop of each song sequence. A common break length between sequences of song was 3.5 seconds, which I categorized as the silence threshold. At any point in a song sequence where there was a silent pause of more than 3.5 seconds, I identified this as a transition to a new sequence of song. To quantify song duration, I used the 3.5 second silence threshold to separate song sequences and measured the length of song in between these pauses.

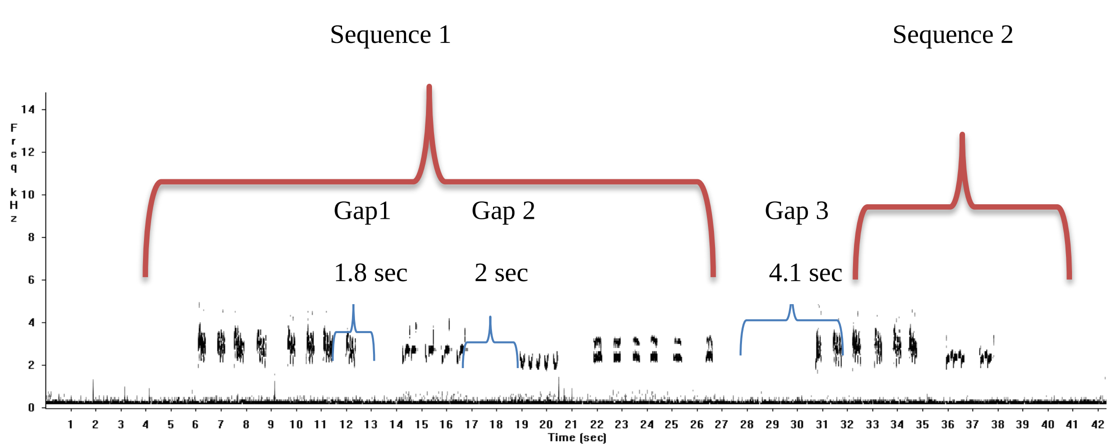

Figure 1. Song sequence spectrogram.

Figure 1. This spectrogram contains three gaps, but only Gap 3 exceeds the 3.5 second silence threshold. Thus the spectrogram shows just two song sequences.

2.4 Data Analysis

Initially I listened to and viewed the spectrograms of the data I had collected for all seasons and all birds to record the length of each song sequence and noted the gap lengths between song sequences (see Fig 1). Audio tracks were ignored if there was excessive background noise, such as construction or traffic. Once I had the sequence durations for all audio recordings for all birds, I was able to compare each breeding stage to the sequence duration for all birds. The average sequence durations varied greatly between birds. Therefore, before averaging the durations for all birds, I normalized the duration data of each bird to itself. To accomplish this, I determined the bird's average duration for any given stage minus the average duration across all stages for that bird divided by the bird's standard deviation across all stages. This allowed me to directly compare the relative sequence durations between birds in a meaningful way. I compared the normalized average durations between breeding stages using a Two-Way ANOVA that blocked by bird.

My methods had at least two limitations. First, I often did not push the "record" button on my audio recorder until just after a focal male began singing, which effectively truncated the beginnings of several of my song sequences. However, because this problem was equally distributed across all breeding stages, it should not have affected my ability to determine temporal changes in the durations of song sequences. Another limitation was that for each bird I recorded different amounts of song from each of the breeding stages (see Table 2). This problem was unavoidable, however, because I had no control over how long a focal male sang, and because breeding cycles ended early for some birds because of infertility or predation. This limitation effectively reduced sample sizes for certain breeding stages and may have reduced the statistical power of my data analysis.

3. Results

3.1 Data Set

One of the nine birds, Ari, had a complete data set with at least 600 seconds (10 minutes) of song in each breeding stage. Sunshine had some song from every stage, but not the full 600 seconds. The nestling stage has the most data gaps, with only 4 out of the 9 birds having any recorded song. Table 2 illustrates the number of sequences and overall song collected for each stage for each bird.

Table 2. Number of sequences and total song duration table for each bird in each breeding stage.

Bird	Nest building	Egg-laying	Incubation	Nestling	Fledgling
Ari	48 (1661.2 s)	30 (1675.5 s)	25 (878.1 s)	39 (639.9 s)	22 (1059.8 s)
Rhodes	34 (874.4 s)	No song	47 (1015.2 s)	148 (2001.4 s)	107 (1872.2 s)
Delta	177 (2912.1 s)	34 (1229.5 s)	12 (447.2 s)	No song	No song
Sunshine	41 (965.8 s)	28 (1776.6 s)	32(513.5 s)	16 (384.1 s)	78 (1136.5 s)
Hardy	38 (891.1 s)	78 (1209.7 s)	35 (191. 3 s)	No song	No song
Zeta	33(659.1 s)	42 (820.6 s)	29(604.1 s)	No song	No song
Nutty	143 (794.2 s)	20 (1088.1 s)	10 (960.8 s)	No song	61 (832 s)
Rudd	85 (1121.6 s)	53 (928.1 s)	14 (839.8 s)	18 (114.7 s)	No song
Walter	18 (1161 s)	5 (435.7 s)	8 (176.8 s)	No song	No song

Table 2. The table lists the birds and indicates the number of song sequences obtained for that particular stage and in parentheses, the total duration in seconds of that stage. Several birds have no song at all collected from a particular stage, due to external causes such as predation or infertility. If this was the case, it is indicated in the table as "no song."

3.2 Duration Results

The average relative duration of song sequences in the egg-laying stage was significantly longer than sequences in all other stages ($F_{4, 1593}$= 26.6, p<0.001). In order to directly compare the sequence durations of different birds without skewing the pattern, the data were normalized to account for the variation in sequence length between birds. By using all of the normalized data for each breeding stage, Figure 2 highlights the longer average sequence durations during the egg-laying stage compared to the much shorter sequences recorded in all other stages. As predicted, male mockingbirds sang the longest song sequences during the egg-laying stage when the female is most fertile. These results are consistent with my hypothesis, although they do not support Derrickson's predictions that longer sequence durations would also be presented during the nest building stage[4].

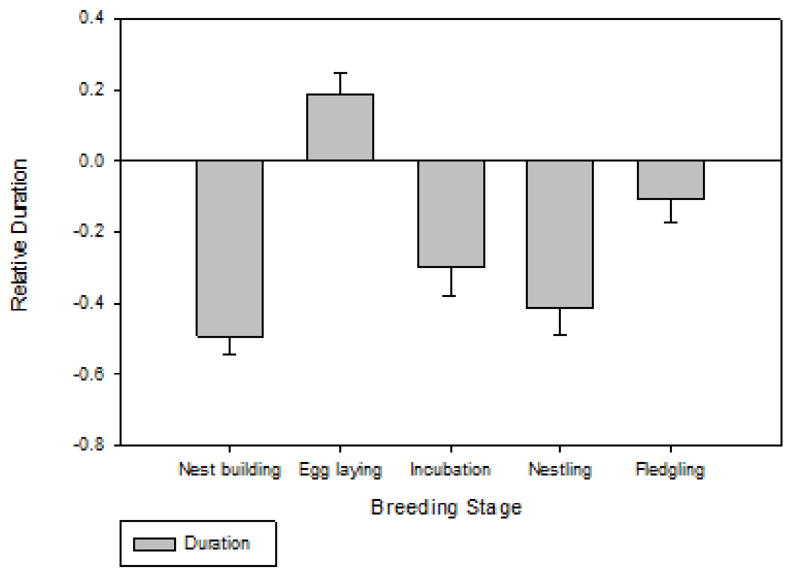

Figure 2. Longest Sequence Durations During Egg-laying Stage.

Figure 2. The relative sequence durations are longest in the egg-laying stage when compared to all others stages. The data were normalized due to the extreme variation in the average sequence durations between individual birds. After normalizing the data, the y-axis reflects the normalized sequence durations for the average bird in each stage. A value of 0 for any bird in any given stage indicates the bird sang average-length sequence durations for that particular stage. A value less than 0 means that the bird was singing shorter sequences than normal during that stage. A value greater than 0 indicates that the bird sang longer sequences than was normal for that stage. As expected, the longest normalized sequence durations occurred during the egg-laying stage.

In order to make my results clearer, I organized the sequence durations so that I could compare them to the relative date of the first egg laid and thus the peak of female fertility[3]. Figure 3 illustrates that on most days sequences were relatively short, but within a few days of the female's highest fertility, sequences were often much longer.

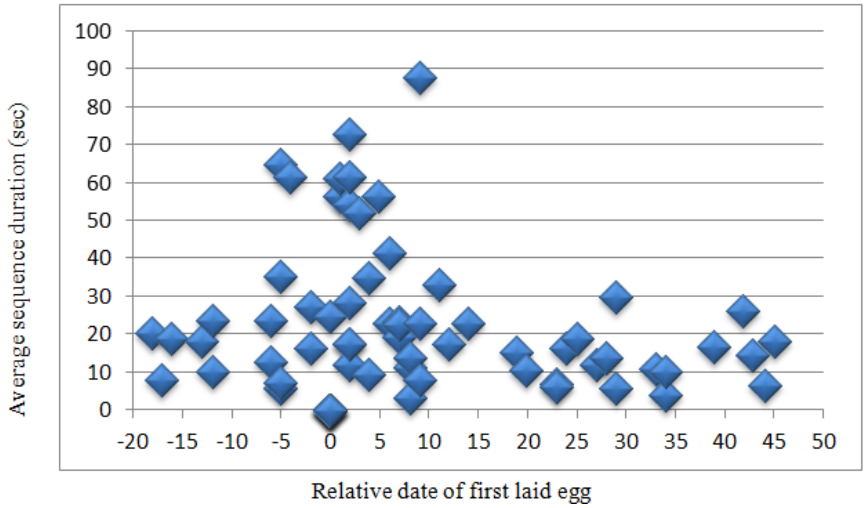

Figure 3. Longer Sequences during female peak fertility

Figure 3. The figure shows the average sequence durations relative to the average day of the first laid egg, indicating that the closer the date of the first laid egg, the longer the sequences became. Each point represents the average sequence duration for a given bird on any given day. I ignored data recorded 18 days prior to the first laid egg, because they are less closely related due to the timing of the breeding stage. Data points were included in this figure only for birds that had at least five recorded sequences that day. The data indicate that on most days sequences are fairly short, but within a few days of the female's highest fertility and the first egg laid, the sequences were often longer.

4. Discussion

The data demonstrated that, as predicted, Northern mockingbird males sing longer sequence durations on average during the egg-laying stage, when the females are most fertile[3]. After the egg-laying stage, the average song duration declined significantly through both the incubation and nestling phases. Song durations lengthened again in the fledgling stage. Since Northern mockingbirds tend to have several clutches of eggs through the spring and summer, often times the second clutch of eggs may be laid in a new nest when the first clutch is late in the fledgling stage. Even though mockingbirds typically form monogamous pair bonds, some birds participate in extra pair copulations with other males to increase their fitness, which is an evolutionary measure of passing along genes[10]. Increased singing activity during the period of female fertility suggests that song serves both to solicit extra pair copulations with other females and prevent a male's female from participating in these extra pair copulations [5].

One female I observed in this study, Trina, frequently interacted with two males, until she settled with one. What is it that attracts a female to settle with one male over another? I hypothesize that the duration of song sequences is not only vital in initially attracting a mate, but also stimulating the female and keeping her from participating in these extra pair copulations. The data support the pattern that as the males began to approach the second egg-laying phase during the end of the fledgling period, the song sequence durations became longer for these previously stated reasons. Overall these results support the hypothesis that that the mockingbird song functions to attract a female and preserve their pair bond.

Although I found a clear pattern regarding the changing duration of average song sequences through the breeding season, I was unable to conclude any direct causal relationship between these factors since this was an observational study. For a future study, it would be fascinating to explore whether the female mockingbirds respond to song sequences of different durations. Logan compared experimental mockingbirds that were exposed to twice as much song to those exposed to half as much song daily. With more song, the birds began re-nesting much earlier, indicating that song does have an effect on their reproductive physiology[9]. A similar play back study could be conducted to test the physiological development and reaction of the females to song sequences of different lengths.

Perhaps being exposed to long song sequences early on in the breeding season would cause an increase in hormone production and early egg-laying. In addition, it would be interesting to see how the females react to unchanging male mockingbird song through the entire breeding season. Would they ever lay eggs and become fertile, or are they reliant on male song to impact their fertility? Another future study could investigate the changes of testosterone levels of the male mockingbird in relation to changes in song sequence durations. Justice and Logan demonstrated that male northern mockingbirds induced with higher levels of testosterone in the blood caused increased singing behavior[6]. Perhaps this increase in testosterone triggers the males to sing longer song sequences and initiate the breeding behavior.

Changes in the behavior during the breeding season are universal across songbird species. Song functions as a mechanism to attract females, but some research suggests that male song has a direct physiological effect on the reproductive development of the females. Brockway demonstrated that playback song could trigger ovarian development and egg-laying in captive female budgerigars[2]. This type of seasonal variation occurs across all taxa and often times certain behavior or courtship displays can trigger physiological development[1]. More research is required across all organisms in order for us to better understand the driving factors behind various mating systems and behaviors.

5. Acknowledgments

I would like to thank my research mentor, Dr. David Gammon, who has supported me extensively with this research. I sincerely appreciate all his efforts and guidance. Additionally, this research would not be possible without the Elon University Biology Department and the Undergraduate Research Program, Dr. Kim Derrickson, and the Northern mockingbirds on campus.

6. References Cited

1. Alcock, J. 2013. Sexual Selection. In: *Animal Behavior. 10th ed*., p 414. Sinauer Associates, Inc., Sunderland, MA.
2. Brockway, B.F. 1965. Stimulation of ovarian development and egg-laying by male courtship vocalizations in budgerigars, *Melopsittacus undulatus. Animal Behaviour*, 13, 575-579.
3. Catchpole, C.K. and Slater, P.J.B. 2008. *Bird Song: Biological themes and variations. 2nd ed*., p 115-178. Cambridge University Press, New York.
4. Derrickson, K.C. 1988. Variation in repertoire presentation in Northern Mockingbirds. *The Condor*, 90, 592-606.
5. Farnsworth, G., Londono, G.A., Martin, J.U., Derrickson, K.C., Breitwisch, R. 2011. Northern Mockingbird (*Mimus polyglottos*), The Birds of North America Online. Ithaca: Cornell Lab of Ornithology.
6. Justice, M.J. and Logan, A.C. 1995. The effects of exogenous testosterone on male Northern mockingbirds during the breeding season. *Wilson Bulletin*, 107, 538-542.
7. Lincoln, G.A., Guinness, F., Short, R.V. 1972. The way in which testosterone controls the social and sexual behavior of the red deer stag (*Cervus elaphus). Hormones and Behavior*, 3, 375-396.
8. Logan, C.A. 1983. Reproductively dependent song cyclicity in mated male mockingbirds (*Mimus polyglottos). The Auk*, 100, 404-413.
9. Logan, C.A., Hyatt, L.E., Gregorcyk, L. 1990. Song playback initiates nest building during the clutch overlap in mockingbirds, *Mimus polyglottos. Animal Behaviour*, 39, 943-953.
10. Logan, C.A. 1997. Mate-reassessment in an already-mated female Northern mockingbird. *The Chat*, 61, 108-112.
11. Marler, P. and Slabbekoorn, H. 2004. Nature's music: the science of birdsong. p 57-59. Elseiver Academic Press. San Diego.
12. Payne, R.B. and Payne, K. 1977. Social organization and mating success in local song populations of village indigobirds *Vidua chalybeate. Zeitschrift für Tiërpsychologie,* 45, 133-173.
13. Slagsvold, T. 1977. Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. *Ornis Scandinavica*, 8, 197-222.
14. Wasserman, F.E. and Cigliano, J.A. 1991. Song output and stimulation of the female in white-throated sparrows. *Behavioral Ecology and Sociobiology,* 29, 55-59.