

THE NOCTURNAL BEHAVIORS OF YELLOW-BREASTED CHATS

BY

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THESIS

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ABSTRACT

Yellow-breasted Chats (*Icteria virens*) are a Neotropical migratory bird species that breeds in shrubland habitat in Illinois. Chats are a diurnally active species but males are known to sing often at night. This behavior suggests that chats may engage in other behaviors related to breeding at night. I investigated whether chats engage in significant movements at night, and if so, why. I used an automated radio telemetry system to quantify the nocturnal movements of male and female chats. I found that males and females moved at night, and that they moved significantly more often when the female of a given pair was fertile. Both males and females moved most often on nights when the moon was least illuminated, but there was no indication that birds engaged in more movements at a certain time of night or during a specific stage of the breeding season. These data, combined with data from other studies of extra-pair copulations and extra-territorial movements of chats, suggest that birds might engage in these movements to assess potential mates and/or copulate with an extra-pair mate. Foraging nocturnally on dark nights by females may allow them to stay undetected by their mates.

Night song may also serve as a cue of habitat quality to migrants during both the spring migration and during the breeding season. Like most other passerines, chats migrate at night and likely select a place to land, either their final destination or a stopover site, while it is still dark or shortly after sunrise. I attempted to attract migrating chats to a predetermined site that lacked appropriate habitat by playing chat song at night. If nocturnal song was used by chats when selecting breeding or stopover sites, then I expected to capture chats on nights when I played chat songs. Significantly more individuals (eight males, seven females) were captured on mornings following treatments (playbacks conducted) relative to control nights when no songs were broadcast (2.5 vs. 0.0 birds/morning, respectively).

This research has documented that nocturnal behaviors are common in chats and that these behaviors may be important in the selection of mates and habitats. Little attention has been paid to what diurnally active birds do at night; however, this study highlights the potential importance of nighttime activity.

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CHAPTER 1

NOCTURNAL MOVEMENTS OF YELLOW-BREASTED CHATS (*Icteria virens*) DURING THE BREEDING SEASON

ABSTRACT

At night, most diurnally active birds are assumed to be inactive and presumably sleeping; however, some diurnally active species engage in nocturnal behaviors, including singing and foraging. One behavior that has been largely investigated during the day, but not at night, is movement outside of one's territory (extra-territorial forays). Traditionally, birds with radio transmitters are frequently tracked by hand only during the day. Many of these studies have found that females and males engage in extra-territorial forays, and often, females engage in extra-pair copulations while foraging. I used an automated radio telemetry system to quantify the nocturnal movements of male and female Yellow-breasted Chats (*Icteria virens*). Both males and females moved significantly more at night when the female was fertile. Individuals moved most often on dark nights when the moon was least illuminated. There was no indication that birds engage in more movements at a certain time of night or during a specific part of the breeding season. On average birds engage in one or two movements per night, and these movements average 170 m. This behavior is consistent with females engaging in extra-territorial forays for extra-pair copulations. Engaging in extra-territorial forays on dark nights may reduce the chances of their social mate harassing or even being aware of the female's behavior. Male chats may be foraging themselves or moving between song posts attempting to attract foraging females on dark nights.

INTRODUCTION

Several bird species that are diurnally active also sing extensively at night (Barclay 1985, Amrhein et al. 2002, 2004, Canterbury 2007). This behavior suggests that these species may also engage in other nocturnal behaviors associated with breeding. Many studies have investigated the movements of territorial birds into conspecific territories (i.e., extra-territorial forays), and many of these studies have found that both males and females enter other territories to potentially assess mates and engage in extra-pair copulations (Double and Cockburn 1999, Mays and Ritchison 2004, Stutchbury et al. 2005, Pedersen et al. 2006, Chiver et al. 2008, Evans et al. 2008). Extra-pair fertilizations are common in many socially monogamous species and many studies have illustrated the sex-specific costs and benefits of engaging in extra-pair copulations. Additionally, researchers have documented that in many species females control paternity (Neudorf et al. 1997, Double and Cockburn 1999, Roth et al. 2009). Often, females engage in extra-territorial forays during their fertile period in order to copulate with males that are not their social mate.

Females are often secretive when engaging in extra-territorial forays (Johnsen et al. 1998, Mays and Ritchison 2004), and males often engage in mate guarding and harassment (Edinger 1988, Mays and Ritchison 2004) to dissuade them from leaving their territory. Female secrecy is likely due to the potential costs experienced by females if extra-pair mating is detected by their social mate (Birkhead and Møller 1992). One of the likely costs is harassment by their social mate (Edinger 1988, Mays and Ritchison 2004). Also, if a male detects a female engaging in extra-territorial forays he may provide less parental care to the female's offspring (Birkhead and Møller 1992, Dixon et al. 2002). Because of the potential costs, if females can secretly engage in extra-territorial forays then the female can receive the benefits associated with extra-pair

fertilizations without the potential costs. Although extra-territorial forays can result in copulations, some forays are probably to simply gather information on the quality of potential mates (Neudorf et al. 1997).

One obvious difficulty in investigating extra-territorial forays is the time and resources associated with tracking the movements of individuals. Due to these difficulties, many studies are constrained to tracking birds during daylight hours or soon before sunrise. I used an Automated Radio Telemetry System (ARTS) to gather data on whether male and female Yellow-breasted Chats (*Icteria virens*) moved and engaged in extra-territorial forays nocturnally. The chat is an ideal species to investigate extra-territorial forays for several reasons. This shrubland species sings at night (Canterbury 2007), so females may potentially move at night to other territories to assess males. Extra-pair paternity has been documented in the species, and both males and females engage in extra-territorial forays (Mays and Ritchison 2004). Using conspecific models of chats, Mays and Hopper (2004) demonstrated that females are likely the sex that controls extra-pair copulations. Finally, Mays and Ritchison (2004) documented that males engage in mate guarding, harass females that attempt to leave their territory, and that females in dense habitats were less likely to be guarded by males, suggesting the denser the habitat the less likely that females would be detected during their extra-territorial forays. I documented whether male and female chats move at night, when they move at night, and if they move more when the female of a pair is fertile. Specifically, I predicted that male and female chats engage in more nocturnal movements when females are fertile (without a nest with eggs or nestlings). I also predicted that birds would move more with increased moon illumination, which would provide increased visibility and possibly reduce the chances of colliding with vegetation.

METHODS

Study species and site. Yellow-breasted chats are Neotropical migrants that breed in shrubland habitat, primarily in eastern North America. Female chats build the nest and incubate alone, whereas both males and female care for nestlings (Schadd & Ritchison 1998). Females may renest after nest failure but few (8%) are double brooded (Thompson and Nolan 1973). I conducted this research at Kennekuk Cove County Park in Vermilion County, Illinois from May-July of the 2008 breeding season. Kennekuk is approximately 1200 ha with scattered patches of shrubland habitat ranging from 4-24 ha dominated by Autumn Olive (*Elaeagnus umbellate*), Bush Honeysuckle (*Lonicera maackii*), and Multiflora Rose (*Rosa multiflora*). I captured male and female chats using targeted mist netting with song playbacks or by flushing females from their nests into a mist net. Upon capture, birds were aged and sexed according to Pyle (1997) and fitted with a USGS numbered leg band and a unique combination of three color bands. Birds were also fitted with a 0.8 g radio transmitter, which is approximately 3% of the adult's body weight. Transmitters were attached at the base of the central rectrices using heat-shrink tubing (Alessi et al. 2009).

I located chat nests from 1 May to 31 July 2008 by incidentally flushing females or by observing parental behavior. I recorded nest locations, and checked nests every two to three days until nestlings fledged or the nest failed. I separated moon phase into four categories: 1) 0-25% illumination, 2) 26-50%, 3) 51-75%, and 4) 76-100%. I considered females to be fertile if they did not have a nest with eggs or nestlings. A male was categorized as fertile if his mate was fertile, and all radio tracking was completed by 10 July.

Automated Radio Telemetry System (ARTS). The ARTS uses six directional yagi antennas to provide data that allows researchers to continuously record the location and activity of radio-tagged animals (Crofoot et al 2008, Rattenborg et al. 2008). Antennas were mounted on a 14.3 m tower and were connected to an Automated Receiving Unit (ARU; Cochran 1980). The ARU was programmed to search for all radio-tag frequencies every three minutes. The output from the ARU is the signal strength (dBm) from each antenna during each search. Signals are strongest for the antenna oriented directly toward the transmitter and vary in strength with the distance between the transmitter and antenna. Therefore, movement by the tagged animal can be estimated from radio signals because any change in the position of a transmitter will result in a change in signal strength (Cochran and Lord 1963, Cochran 1980). Estimating bearings from the tower has been done previously with ARTS (Crofoot et al. 2008).

Using signal strength to estimate distance from a tower is more challenging than estimating bearing and has not been done previously. Changes in signal strength can occur on three planes: signal strength decreases as the transmitter moves away from the receiver, signal strength decreases as the transmitter moves closer to the ground due to increasing attenuation from vegetation, and the direction in which the transmitter's antenna is facing relative to the tower will affect the signal strength. To develop the algorithm for using signal strength to estimate distance, I used radio-tagged females that were incubating in known nest locations as test transmitters. I used 200 samples from nine incubation or brooding events for each of eight nests and averaged the two strongest antennas per sample to establish mean signal strength (S) for each female. Only brooding and incubation events that lasted longer than 15 minutes were used to be certain the female was on her nest. When females were on their nests, the signal strengths of the transmitters were static, whereas when females were off of their nests, the signal

strengths were much more variable. Nests were checked when females were thought to be on their nest to confirm that prolonged periods of inactivity were actual brooding/incubation events. All nests were within 2 m of the ground. I then determined the relationship between mean signal strength and known distance (d) of each nest from the tower as a quadratic relationship using linear regression. The equation ($d=0.2792(S)^2 + 43.509(S) + 1693.5$) explained 99% of the variation between signal strength and distance (Fig. 1). This algorithm was appropriate for documenting female movement because female chats restrict nearly all their activity to within 2 m of the ground (Mays and Ritchison 2004). Male chats often perch in the highest vegetation to sing, however, so to determine whether the algorithm could be applied to males I examined signals from a transmitter placed at varying heights and distances from the tower. The 16 dB variation in signal strength resulting from differences in transmitter height (Fig. 2) was so large that it would make estimates of distance for males unreliable. This meant that although it was still possible to determine when a male moved, it was not possible to determine how far the male moved. Using signal strengths to determine when an animal is active has been done before (Crofoot et al. 2008) and conveys the information that the animal is moving but not where it is going.

Estimating bearing, distance, and errors. I determined bearings using the difference in signal strengths between the two strongest antennas (Crofoot et al. 2008). If a signal is coming from directly between two antennas, then each antenna will receive the same amount of energy from the transmitter. To calibrate the system, I used the same eight nest locations that had a radio-tagged female on the nest. This approach was taken instead of using humans on a test walk so I could assess the natural variation that occurs when a bird is stationary. Females often rotate their

eggs or change positions on the nest, so fluctuations can occur while a female is located at a single position; therefore, using the bird as the mechanism to ground truth when a movement actually occurred was the best approach. Using ARCGIS, I measured the difference between actual and calculated bearings as well as the difference in actual and calculated distances. I averaged the values for the eight locations to determine an average bearing error and average distance error associated with the bearing. The average bearing error was $\pm 2.0^\circ$ ($\pm 0.4^\circ$ [SE]), which can be converted to an average distance error of ± 12.0 m (± 3.6 m [SE]). The average signal strength standard deviation for the eight nest locations was 3.2 dBm ± 0.5 [SE]. I then used the distance function (see Fig. 1) to generate distances for each of the 200 samples per location. Because the location of the transmitter was known (i.e., at a nest), I subtracted the actual distance from the tower from the estimated distance (i.e., from the function). I then averaged the distance error for the eight nest locations and generated an average distance error (51.3 m ± 5.7 [SE]). Both the bearing and distance error estimates are accurate because I knew transmitter locations when females were on their nests and I knew they were not changing locations.

Estimating movements. I recorded a movement only if both the signal strength and bearing changed simultaneously. This meant that changes in signal strength resulting just from a bird changing its orientation relative to the tower were not erroneously documented as movement. Because movements off a territory are likely to take at least several minutes, I defined a movement to be from the initial change in bearing and signal strength until the bearing and signal strength stopped changing for at least six minutes. I chose a conservative measure of when a bird moved to exclude erroneous readings. This conservative threshold removed many small

movements (< 50 m). Because I was interested in documenting extra-territorial forays, I defined a movement as an occasion when the bearing exceeded the average bearing standard deviation (5.2°) and the signal strength was twice the average signal strength deviation (6.4 dB), and these changes occurred both at the same time. Consequently, birds likely moved considerably more than I report, but again, I was interested in movements that would result in them leaving their core-use area (Fig. 3).

Statistical analyses. I used Generalized Linear Mixed Models (SAS PROC GLIMIX; Littell et al. 2006) to examine the effects of fertile vs. non-fertile stage, sex, moon phase, and day of year, and their interactions on nocturnal movements. I subsequently removed non-significant effects in the model and report only the significant models. Because the number of nocturnal movements per night represents count data, I modeled these relationships using the Poisson distribution with a log link function, and, to account for repeated measurements of movements for individuals, I treated an individual as a random effect. I conducted a linear regression on the average number of movements per night with the time these movements occurred. I recognized statistical significance when $P < 0.05$, and followed significant main effects and interactions with pairwise contrasts to explore differences (Littell et al. 2006).

RESULTS

I tracked six females and six males during the 2008 breeding season. Eight of the 12 birds were paired when they were tracked, while four of the birds were tracked without their mate being tracked. However, knowing where the pair were temporally in the nesting cycle permitted analysis. Two females renested after their first nests failed, providing a total of eight

nests; these nests were used to calibrate the ARTS data. The ARTS recorded data for 276 bird-nights, and one or more birds engaged in off-territory forays on 142 of these (51.4%). All day-of-year models were not significant and were removed from the final model. Males ($n=6$; 1.4 ± 0.7 movements/night) and females ($n=6$; 1.1 ± 0.4 movements/night) did not differ in the average number of movements per night (Table 1; $F_{1,7}=0.19$, $P=0.67$). However, the interaction between sex and reproductive status was significant, with both females ($t_{240} = -6.96$, $P < 0.01$) and males ($t_{240} = -2.61$, $P=0.01$) moving more during the fertile phase than the non-fertile phase (Fig. 4). Additionally, males (1.1 ± 0.5 movements/night) moved nearly twice as much during the non-fertile stage than females (0.7 ± 0.3 movements/night). There was a difference in the number of nocturnal movements among moon phases (Table 2; Fig. 5). Birds moved significantly more on nights with 0-25% moon illumination than on nights with greater illumination ($t_{240} > 2.53$, $P < 0.01$). The interaction of sex and moon phase was not significant. There was no tendency for birds to move during certain times of night (Fig. 6; $n=12$, $P=0.66$, $R^2 < 0.01$). Three of the 12 birds with a transmitter left the area during the study. Before leaving, however, these birds were not more likely to move than the birds that did not leave. Also, there was no effect of day of year. The average distance of a nocturnal movement for females was $170.4 \text{ m} \pm 11.7 \text{ m}$ [SE] and the longest nocturnal movement recorded was estimated at 493.0 m (Fig. 7). This average is likely skewed by my conservative estimate of what constitutes a movement. Although both the male and female of a pair were more likely to move when the female was fertile, the male and female never moved at the same time at night.

DISCUSSION

The territory size for a Yellow-breasted Chat has been estimated at 1.2 ha \pm 0.5 [SD] (Thompson and Nolan 1973). Therefore, many of the nocturnal movements I documented would have resulted in the bird leaving its territory and are consistent with extra-territorial forays. Yellow-breasted Chats moved often during the night and female chats moved long distances. Both male and female chats engaged in nocturnal movements throughout the breeding season, but were more likely to move when the female of a pair was fertile.

An increase in extra-territorial forays during the fertile period in birds has been documented in females of several species (Neudorf et al. 1997, Double and Cockburn 2000, Pedersen et al. 2006, Evans et al. 2008) during daylight hours. Although both individuals of a pair engaged in movements when the female was fertile, I found no evidence that males and females moved together. Additionally, the number of movements per night was greater for males than for their non-fertile females (1.1 vs. 0.7 movements per night, respectively). These data are consistent with females engaging in nocturnal extra-territorial forays for either male assessment and/or extra-pair copulations.

Yellow-breasted Chats are in the minority of passerines in that they frequently sing at night (Canterbury 2007). Because males are singing, it provides an ideal situation for females to assess future mates acoustically. Two species that exhibit similar nocturnal behaviors are the Nightingale (*Luscinia megarhynchos*; Roth et al. 2009) and Reed Warblers (*Acrocephalus scirpaceus*; Bulyuk et al. 2000, Mukhin et al. 2005). Female nightingales appear to use nocturnal song as an indicator of male pairing status and possibly to evaluate male quality (Roth et al. 2009). Additionally, translocated female nightingales in an unfamiliar location traveled an average of 1.1 km nocturnally when unpaired males were singing, and five of ten (50%) females

settled in the territory of a male that was singing at night (Roth et al. 2009). Mukhin et al. (2009) radio-tagged 12 breeding pairs of Reed Warblers and simulated nest predation on the females while translocating their males away from their territories. They found that the majority of adult reed warblers nocturnally emigrated after their nest was depredated, and the translocated males attempted to relocate their territories nocturnally, suggesting that some species are active at night when necessary. Male reed warblers moved between 1.7 and 20.6 km nocturnally when attempting to locate their territories after being translocated (Mukhin et al. 2009).

One of the unexpected results of this study is that chats (both males and females) were more likely to move at night when the moon was less illuminated. Double and Cockburn (2000) report that female Superb Fairy-Wrens (*Malurus cyaneus*) initiated forays 20.5 min before sunrise and returned before sunrise. The authors suggest that these females may be able to avoid being guarded by their mate if they move in low light. Dark nights may provide more cover for female chats to engage in extra-territorial forays; however, it is not clear why males would also move more on these nights. The average number of movements per night was nearly the same between males and females on “dark” nights, but on nights with greatest illumination, males were nearly twice as likely to engage in nocturnal movements. Males may have been moving around on dark nights searching for females entering their territory or were singing more at night from many song posts.

Movements on dark nights may also be associated with predation as several studies have found that several species are more active on dark nights due to predation pressure (Mougeot and Bretagnolle 2000, Duriez et al. 2005). However, none of the radio-tagged chats were lost to predation and it is unlikely that nocturnal predation is very frequent. In some species, juveniles will engage in nocturnal behaviors as the fall migration approaches, possibly developing their

stellar compass (Mukhin et al. 2005). Yet, I observed no evidence that nocturnal movements are associated with birds leaving the study site. Nine of the 12 (75%) adult birds with transmitters did not leave the study area and still exhibited nocturnal activity. Therefore, it appears that adult chats are not moving nocturnally in preparation for departure. Both females and males are moving more when females are fertile and these results are consistent with extra-territorial forays.

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TABLES

Table 1. The results from the Generalized Linear Mixed Model I conducted. Significant models are bolded. Birds were moved more on dark nights and when the females were fertile.

Effect	DF	<i>F</i>	<i>P</i>
Sex	1, 7	0.19	0.67
Moon phase	3, 240	15.64	<0.01
Fertile	1, 240	41.38	<0.01
Sex × moon phase	3, 240	1.68	0.17
Sex × fertile	1, 240	5.80	0.02

Table 2. The differences among moonphases. Significant differences between two phases are highlighted in bold. Moonphase 1=0-25% illumination, 2 =26-50%, illumination, 3= 51-75% illumination, and 4= 76-100% illumination.

Moonphase	Moonphase	DF	T	P
1	2	240	2.53	0.01
1	3	240	3.74	<0.01
1	4	240	6.65	<0.01
2	3	240	1.09	0.28
2	4	240	3.52	<0.01
3	4	240	2.33	0.02

FIGURES

Figure 1. The relationship between distance from the receiver and signal strength. Each point represents 200 locations from 8 known nest locations.

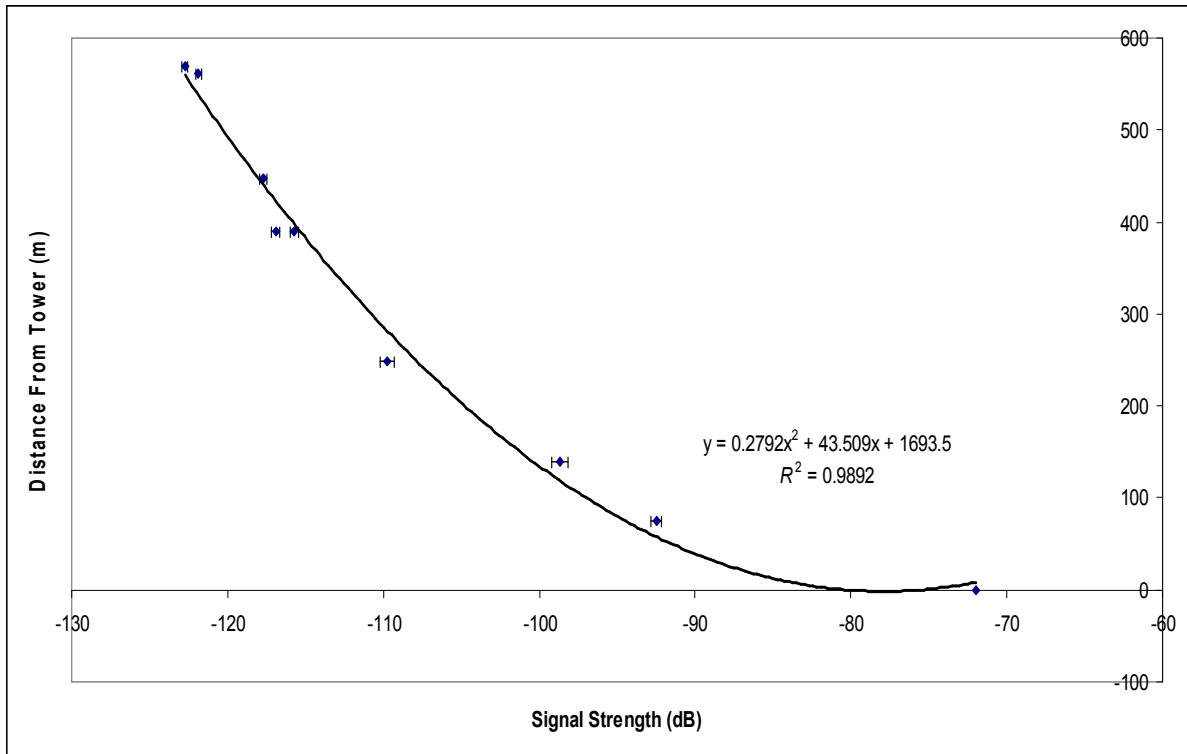


Figure 2. Average signal strengths for varying heights (0, 3, and 6 meters) and distances (10, 200, 400, and 600 meters) at Kennekuk County Park, Illinois. Averages were computed using a transmitter in a stationary location.

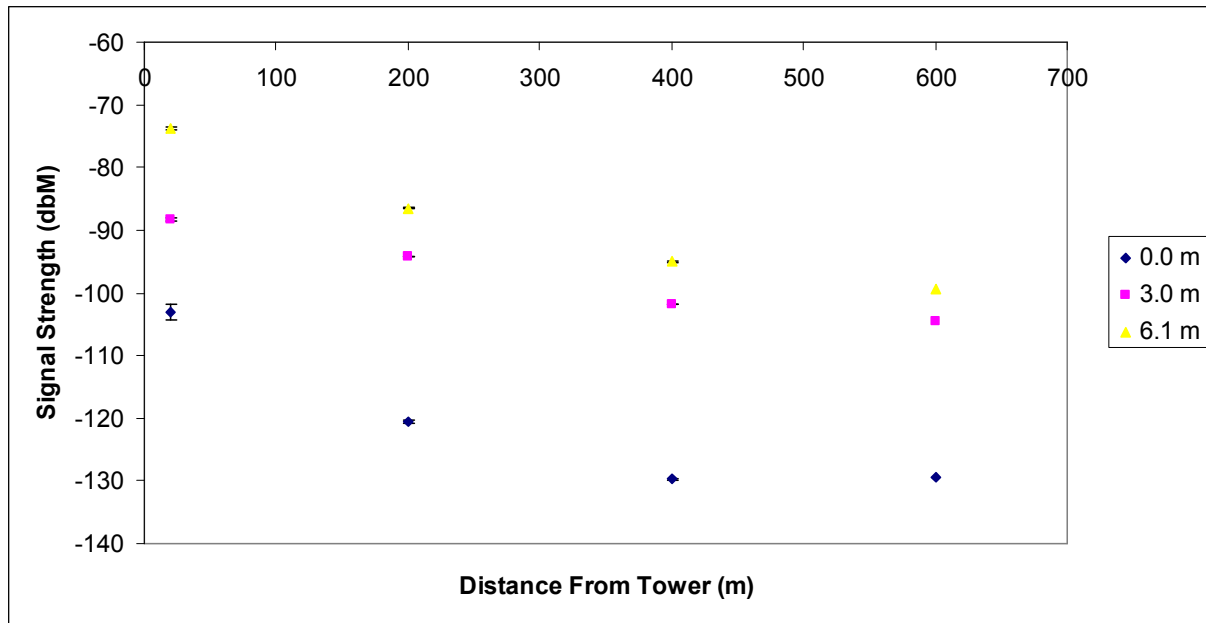


Figure 3. Non-fertile nocturnal locations of a female during the non-fertile (blue dots) and fertile (green dots) phase. Many movements during both the fertile and non-fertile phase occurred, but this figure represents long-distance movements during the fertile phase.

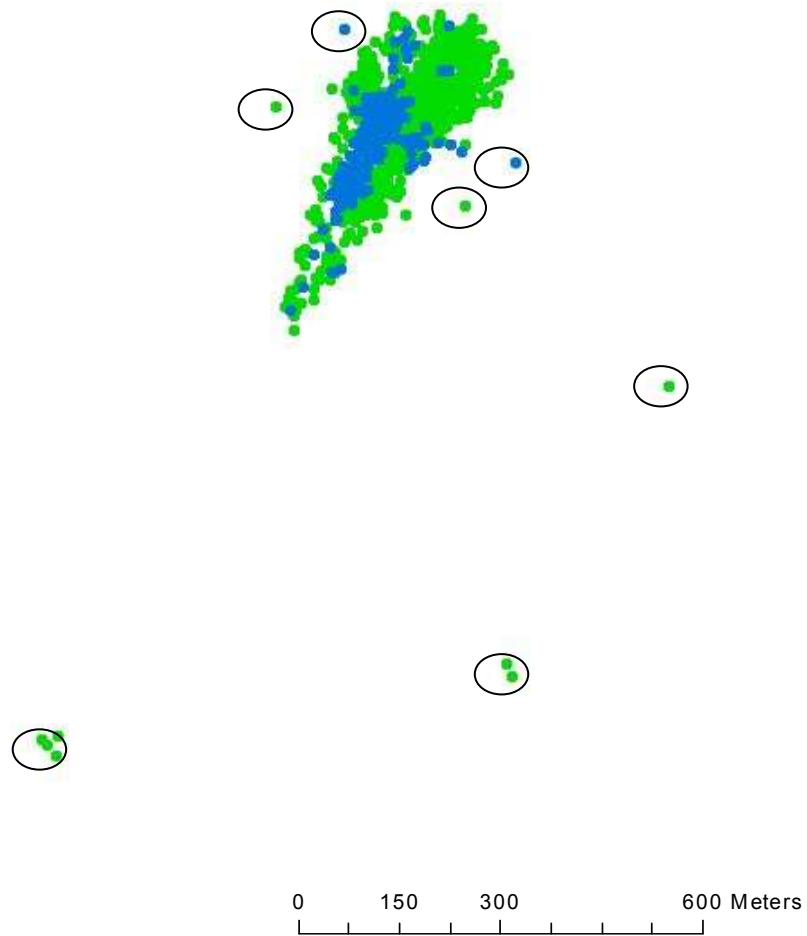


Figure 4. Effect of fertile stage and sex on the average number of movements per night for Yellow-breasted Chats. Mated female and male chats were significantly more active during the female's fertile stage than her non-fertile stage. ** $P < 0.01$, *** $P < 0.0001$.

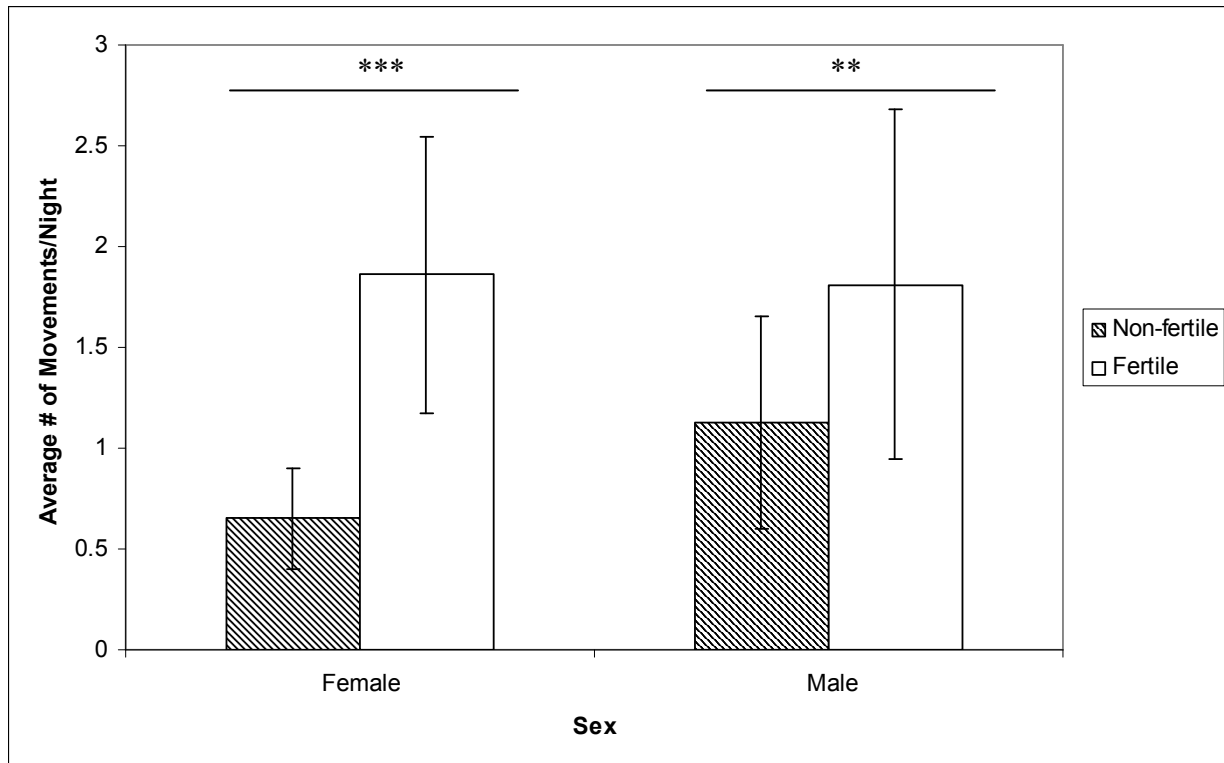


Figure 5. Relationship between nocturnal movements and moon phase. There was a significant negative trend in the average number of movements per night in regards to the moon phase- birds moved less during moonlit nights. $P < 0.05$ among all phases except between the 2 (26-50%) and 3 (51-75%) category ($P = 0.28$)

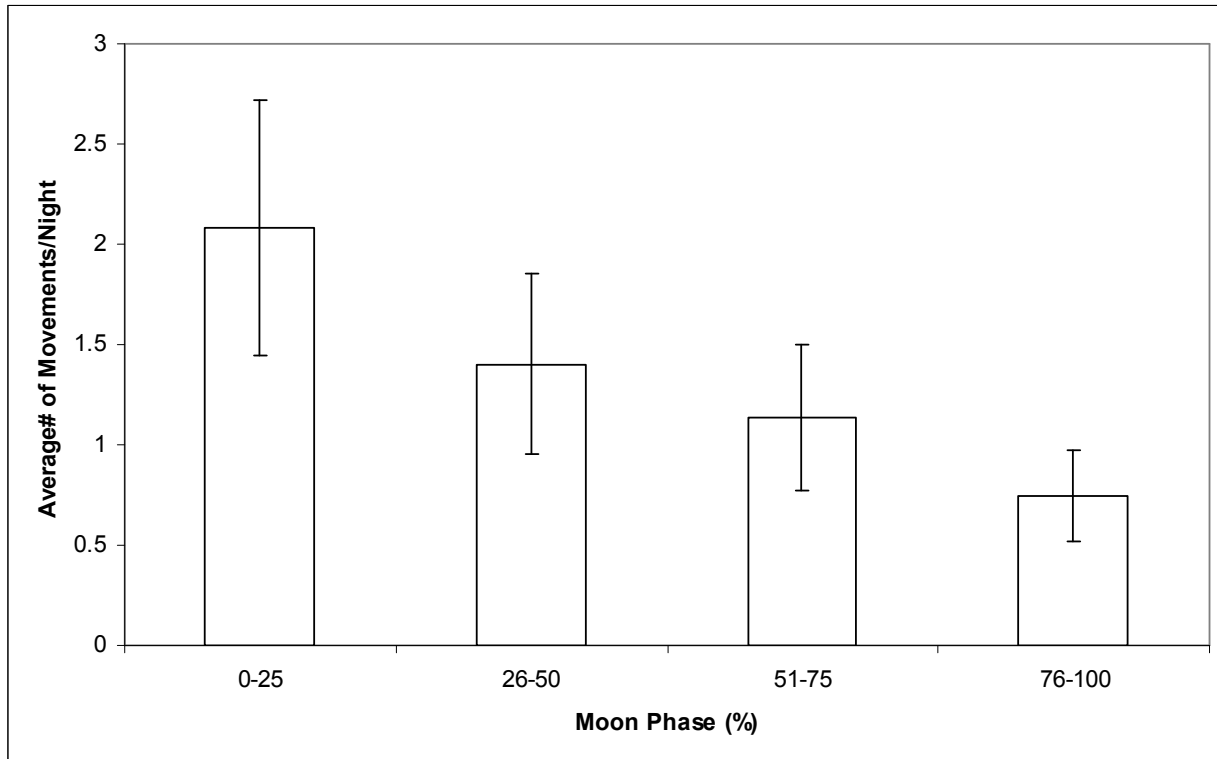


Figure 6. The effect of time on the average number of nocturnal movements. There was no trend associated with the time at which birds ($n=12$) moved nocturnally.

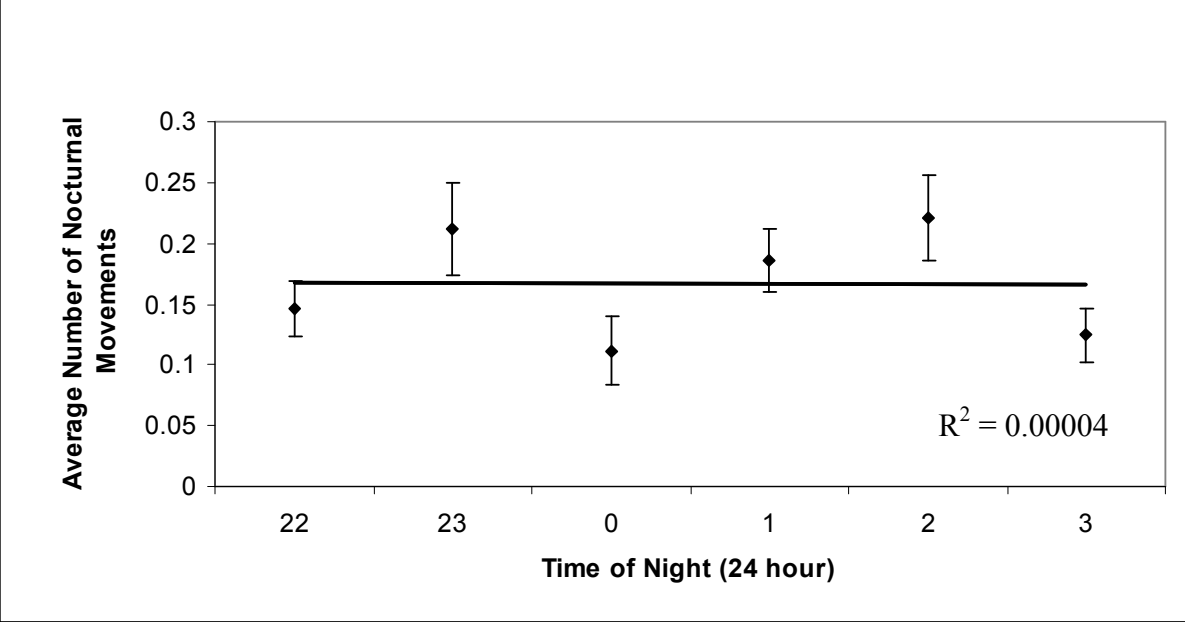
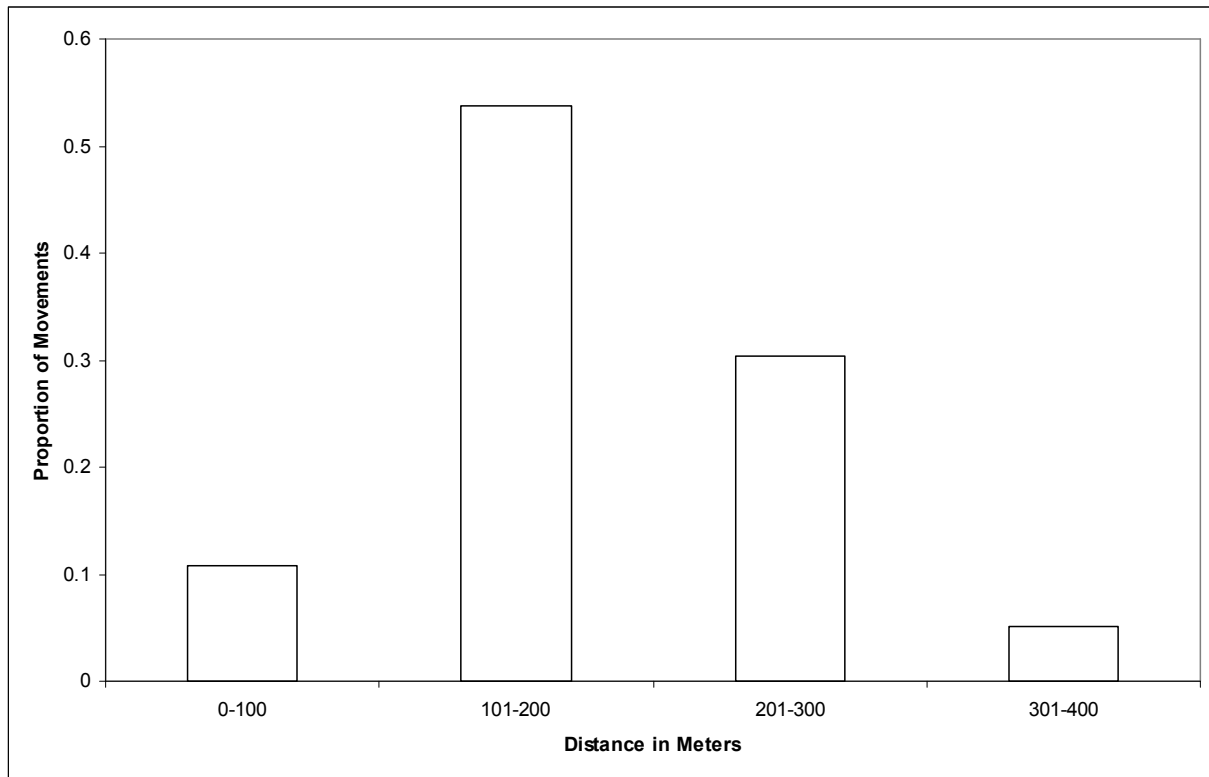


Figure 7. Females moved 100-200 m most often but more than 30% of the movements were greater than 200 meters ($n=277$). There were probably many more short movements; however, the conservative values I used to define a movement excluded most short movements.



CHAPTER 2

NOCTURNAL SOCIAL CUES ATTRACT MIGRATING BIRDS

ABSTRACT

Nocturnally migrating birds use a suite of cues to navigate from their wintering to their breeding grounds; yet, how these birds select specific stopover and breeding habitats is largely unknown. One factor that may influence habitat selection are social cues, specifically conspecific vocalizations. Although most songbirds sing at dawn, dusk, or periodically throughout the day, some diurnally active songbirds also sing at night. Males may sing at night in order to attract females or to defend their territories, but regardless of the reason why a male may sing, the song may be a cue for migrating birds signaling the presence of appropriate habitat. I tested the hypothesis that migrating birds may use nocturnal conspecific song when selecting habitat using the Yellow-breasted Chat (*Icteria virens*). I broadcasted nocturnal song in unsuitable habitat on certain nights and on other nights with no song. I predicted that migrating chats would use male nocturnal song as an indicator of suitable habitat and would land at the site and evaluate the site. Once they determined there was no appropriate habitat they would leave the site. I caught significantly more individuals (eight males, seven females) on mornings following treatments relative to control nights when no songs were broadcast (2.5 vs. 0.0 birds/morning, respectively) and no new birds were captured. Only one bird was recaptured at the site and only one male was detected singing at the site, suggesting that individuals quickly left the area after determining the habitat was unsuitable. Conspecific nocturnal songs appear to be an important cue used when chats are selecting stopover and breeding habitat.

INTRODUCTION

Reliable cues of high-quality habitat are imperative for migratory birds because energetic and fitness costs of not locating suitable habitat can be high (Cochran and Wikelski 2005). Migratory birds use a suite of navigational cues to migrate between their wintering and breeding grounds (Able and Bingman 1987); however, the specific cues used to select stopover and breeding habitat remain largely unknown. Studies suggest that both visual (Moore et al. 1995) and acoustic cues (Ward and Schlossberg 2005; Mukhin et al. 2008) may be involved. However many nocturnal passerine migrants select stopover locations prior to sunrise (Cochran et al. 1967; Moore and Aborn 2000) when visual cues may be absent or difficult to evaluate. Therefore, cues that facilitate locating suitable habitat are likely highly valuable for migrating birds, and one such cue may be nocturnal song.

Nocturnal song by diurnally active birds is uncommon; however, recent research suggests that nocturnal song may be an important habitat location cue (Mukhin et al 2008). Also, several diurnally active species that do sing at night have specific nocturnal songs. For example, research on Nightingales (*Luscinia megarhynchos*) suggests that males sing at night primarily to attract females (Amrhein et al. 2002). The whistle song of male Nightingales (Glutz von Blotzheim 1988) appears to function primarily for mate attraction, and female Nightingales assess males at night while they are using these songs (Roth et al. 2009). The nocturnal song of Yellow-breasted Chats (*Icteria virens*) is also given at a frequency and amplitude that may allow detection farther away than their diurnal song (Canterbury 2007). If the function of nocturnal song is to attract females, then females would use this song as an indicator of suitable habitat and mates. However, relative importance of conspecific vocalization vs. habitat cues is unknown.

I broadcasted the nocturnal song of male Yellow-breasted Chats, a song that is consistently sung at night during spring migration (Canterbury 2007), in unsuitable habitat during chat migration. Because the shrubland habitat in which chats breed is patchy, the probability of a migrating individual quickly locating suitable habitat at dawn is unlikely, and birds would benefit by using pre-dawn cues to locate appropriate areas. I hypothesized that both male and female chats use nocturnal song as an indicator of suitable habitat and that both males and females would select areas with conspecific nocturnal song regardless of habitat suitability. Further, I predicted that chats attracted to unsuitable habitat would quickly leave the site.

METHODS

This experiment was conducted on University of Illinois property in southeast Urbana, Champaign County, Illinois, USA (Fig. 8a) during spring migration between 29 April and 15 May 2009. The site was a 210×30 m linear strip of six rows of apple (*Malus* spp.) trees spaced 6.5-m apart with mowed strips of grass between each column of trees (Fig. 8b). The habitat north and east of the site was residential and commercial property while the habitat to the west and south was a mixture of agricultural land with additional patches of apple trees. The area was selected because it offers woody vegetation, but lacked the size and dense shrub layer that chats require for both breeding habitat (Thompson and Nolan 1973) and stopover habitat (Parnell 1969). Chats have never been recorded at this site and the site was repeatedly treated with pesticides and mowed to facilitate fruit production.

I alternated between control nights, when no songs were broadcast, and treatment nights with song playbacks when the weather allowed (not raining). I used a mixture of commercially available chat songs (Stokes 2000) and chat songs I recorded from individuals in east-central

Illinois. The recording included a male whistle song, the song only used at night (Canterbury 2007). The entire recording was 100 sec long and was repeated continuously using a Fox Pro FX3 playback system. I placed the system in the center of the site in a weatherproof plastic container and aimed the device at a 45-degree angle southward toward the sky. On treatment nights, songs were broadcast from sunset to 1.5 hr after sunrise. I placed mist nets approximately every 30 meters on the site to increase the probability of capturing all chats moving through the vegetation; nets were numbered 1 (South net) to 6 (North net) and were opened for 1.5 hr before and after sunrise each morning for both treatment and control nights. I sexed and banded all captured chats with a USGS band, and recorded the net in which each individual was captured prior to releasing them back into the site. To supplement the capture data after closing the nets, I conducted 5-min, unlimited-radius point counts each morning in two locations at the site to quantify the number of singing chats. One point was located at the southernmost end of the strip while the other was located at the northernmost end. I conducted a one-tailed t-test to examine whether I captured more chats on treatment mornings than on control mornings.

RESULTS

I captured 15 chats (8 males, 7 females) during 4 of the 6 mornings that I broadcast chat song at night, and I captured no new individuals during any of the 5 control mornings (Fig 9a; $t_9=2.02$, $P=0.04$). Eight of 15 chats (53%) were captured in the nets closest to the speaker (chat song), while seven of 15 (47%) were captured in the southernmost nets (Fig. 9b). Over the course of 11 mornings, only one male chat was heard singing during point counts and it was during the morning he was captured. No male chats were recorded singing on control days,

which emphasizes that this location was not suitable habitat. I only recaptured one individual; a female three days after her initial capture.

DISCUSSION

Migrating chats were captured only on mornings following treatment nights and no birds were captured during the mornings following control nights. Both migrating male and female chats responded to experimental addition of nocturnal male song, suggesting that male chat song functions as a cue for stopover or potentially breeding habitat selection. Male chats did not establish territories and likely continued migration until suitable habitat was found. It appears that the lack of appropriate habitat does not preclude chats selecting a site as long as conspecific songs are present.

Nocturnal song of diurnally active birds has been documented primarily in species that breed in patchy or ephemeral habitat (Barclay et al. 1985, Walk et al. 2000). For example, male common Nightingales breed in ephemeral habitat (Hewson et al. 2005) and also sing nocturnally for mate attraction (Amrhein et al. 2002). Similar to Nightingales, male chats appear to primarily use long-range whistle songs only at night (Canterbury 2007). Further, male chats will sing continuously at night for up to six days after arrival on the breeding grounds, potentially providing abundant social cues early in the season when most females are returning from their wintering locations (Canterbury 2007).

Because I broadcasted nocturnal song between sunset and 1.5 hours after sunrise, I attracted birds either during the night or shortly after sunrise. Selecting stopover habitats at sunrise may be adaptive if the increased visibility allows for better habitat assessment (Bolshakov and Bulyuk 1999); however, these results suggest that, at least for chats, individuals

are selecting habitat based on social cues rather than habitat suitability. The extent to which this mechanism is found in other species is currently unknown.

Conspecific attraction has received increasing attention in recent years, and is important for both habitat selection and planning conservation and management actions (Ahlering and Faaborg 2006). Several studies have demonstrated that birds use conspecific attraction to assess and select habitat (Serrano et al. 2004, Ward and Schlossberg 2004, Ahlering 2005, Mukhin 2004, Betts et al. 2006). To date, most conspecific attraction studies have not attempted to attract birds to unsuitable habitat, nor have studies focused exclusively on nocturnal song (but see Mukhin et al. 2008). Attracting birds to unsuitable rather than suitable habitat is a more reliable method of assessing the importance of acoustic social cues (Chernetsov 2006, Betts et al. 2006). Further, if this site had been suitable males may have defended territories and both males and females may have remained to breed at the site. Thus, this mechanism likely holds true for both stopover and breeding site selection.

If chat nocturnal song reflects the presence of high-quality habitat, heterospecifics may also use these cues (Mönkkönen et al. 1999). In this study, I did capture other shrubland bird species on mornings following treatments, such as Orchard Orioles (*Icterus spurius*), Brown Thrashers (*Toxostoma rufum*), and Field Sparrows (*Spizella pusilla*). To fully assess the potential of nocturnal song for heterospecific attraction, a separate playback experiment would be necessary to determine if these species use chat song rather than vegetation structure to select suitable habitat. Since nocturnal song is prevalent in patchily distributed habitats such as wetlands, grasslands, and shrublands in North America (Barclay et al. 1985, Walk et al. 2000), many of these bird species may be using nocturnal heterospecific song as a cue during migration,

and future research is needed to address conspecific and heterospecific attraction in shrubland birds.

ACKNOWLEDGEMENTS

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FIGURES

Figure 8. (A) Aerial photo of Champaign-Urbana. The circle indicates where the study site was located. (B) Aerial view of the site where I conducted the nocturnal song playback experiment. The agricultural field east of the orchard was residential and commercial property.



Figure 8 (cont.)

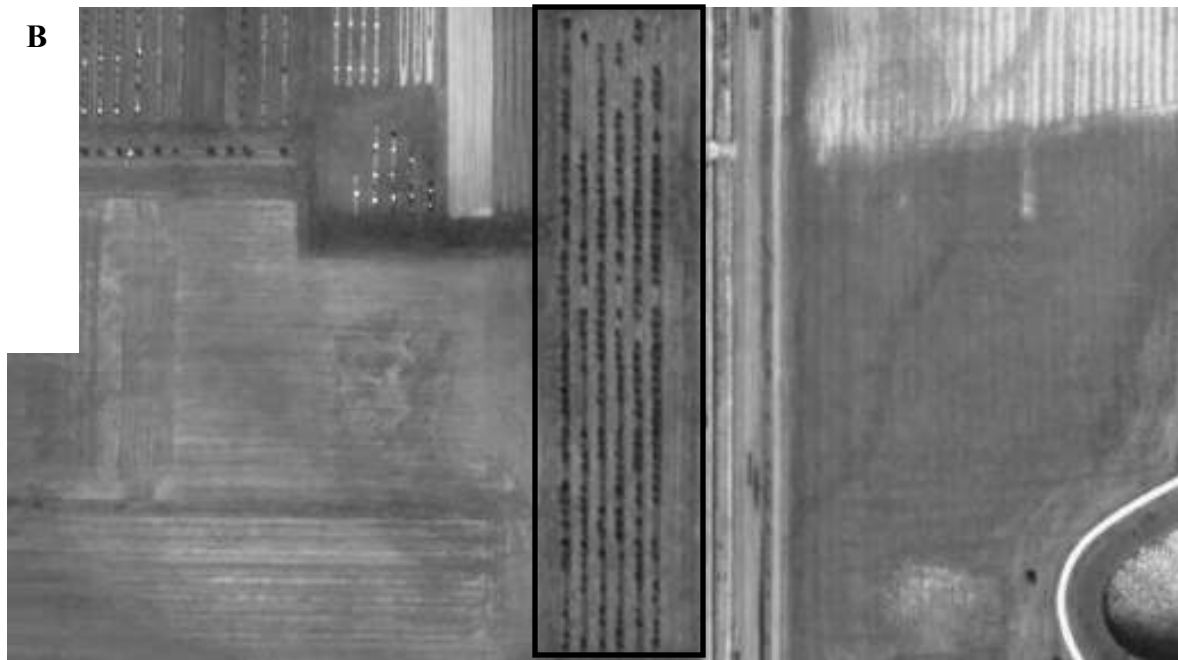


Figure 9. (A) I captured significantly more chats after song playback nights (T- 2.5 birds per day) versus control nights (C- 0 birds per day). (B) The majority of chats were captured at the two nets that surrounded the playback device. The arrow indicates where the speaker was located.

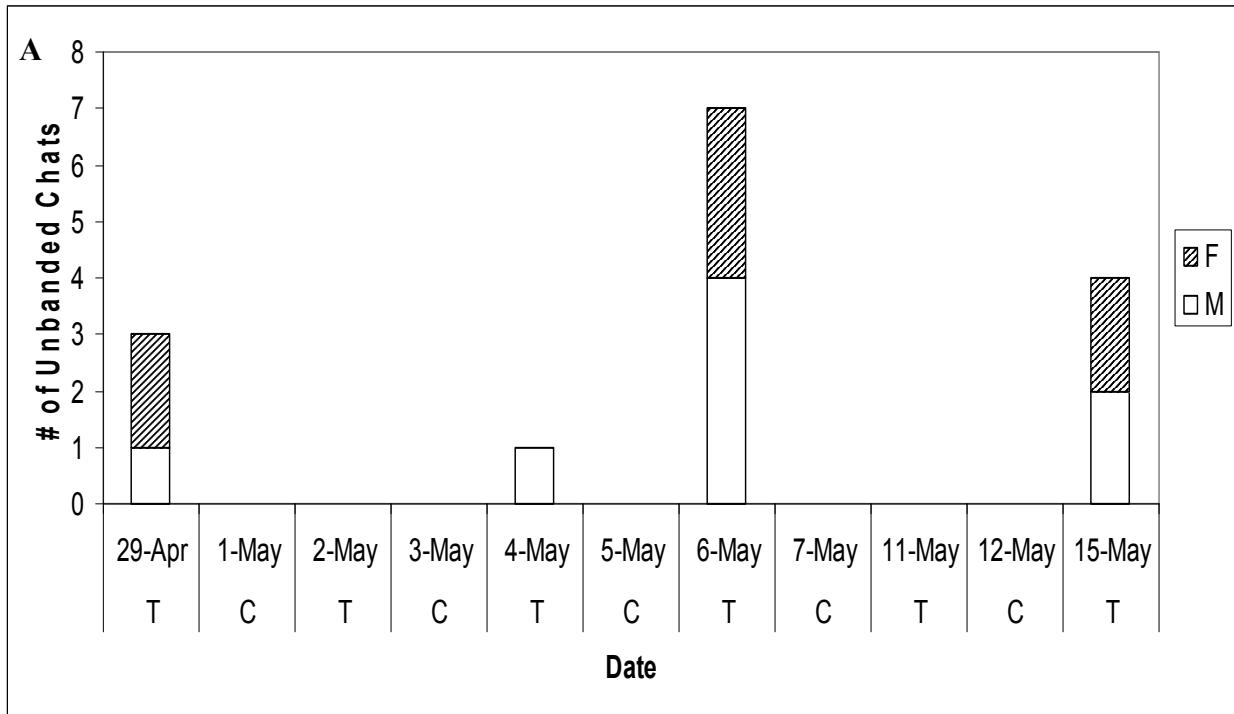
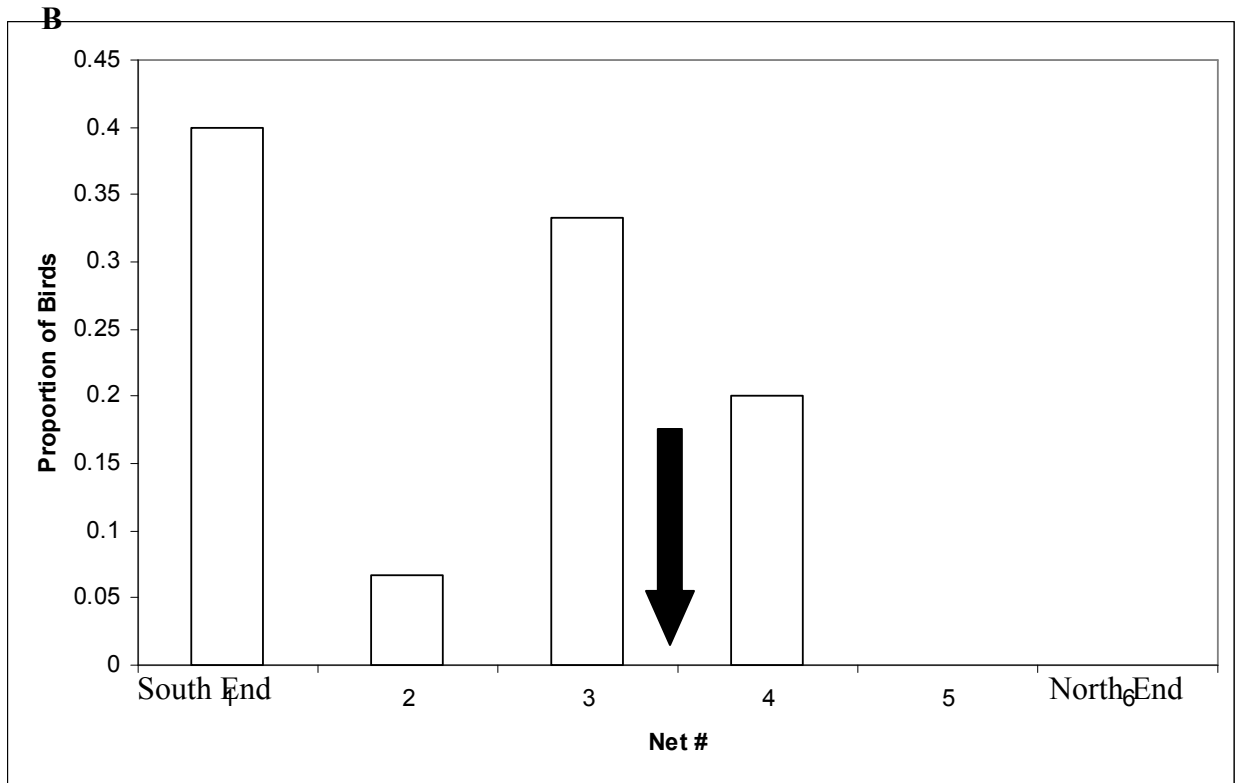


Figure 9 (cont.)



CHAPTER 3

SUMMARY

In summary, my research shows that both male and female chats are moving nocturnally during the breeding season, and these movements appear to be correlated with female fertile status. Therefore, I suggest that female chats are engaging in extra-territorial forays and/or extra-pair copulations nocturnally when they are fertile. I propose that male chats are switching song posts or engaging in extra-territorial forays themselves. Because male chats sing nocturnally, I predicted that male chats sing at night to attract females and that migrating males would also eavesdrop on this accessible cue. I tested this during the 2009 spring migration and caught significantly more chats the mornings after I played nocturnal playbacks. Chats have been suggested to have a clustered and patchy distribution. This is likely the result of the patchiness of their habitat, and a method to attract females in a patchy landscape is to vocalize nocturnally when they are migrating and/or assessing males. Heterospecifics may also use these vocalizations during migration when selecting suitable habitat because it is a reliable cue.