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# THE INFLUENCE OF WEATHER AND AMBIENT LIGHT ON THE DAWN CHORUS START TIMES OF NORTH TEMPERATE BIRDS

By

ADRIANNA BRUNI

A Thesis

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2013

# The influence of weather and ambient light on the dawn chorus start times of north temperate birds

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## Declaration of Co-authorship

I hereby declare that this thesis incorporates material that is the result of joint research, as follows:

I am the sole author of chapters 1 and 4, and the principal author of chapters 2 and 3. Both chapters 2 and 3 were conducted under the co-supervision of Dr. Dan Mennill (University of Windsor) and Dr. Jennifer Foote (Algoma University) who contributed input on the experimental design, analyses, and writing of the manuscripts, as well as logistical and financial support for field research; they share authorship on both chapters 2 and 3. For both chapters 2 and 3, I am responsible for the primary written contribution, with input and feedback provided by both Dr. Mennill and Dr. Foote.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and obtained written permission from each of the co-authors to include the above materials in my thesis.

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## Abstract

The dawn chorus is a bout of increased song output performed by birds prior to sunrise during the breeding season. Although nearly ubiquitous among avian species, the dawn chorus is poorly understood compared to daytime song. Little is known about how extrinsic variables influence dawn chorus performance. In this thesis, I measured relationships between dawn chorus start times and moon brightness, cloud cover, precipitation, ambient temperature, and artificial light exposure in a community of north temperate birds. I found that birds begin their dawn choruses significantly earlier with increasing moon brightness and ambient temperature, and significantly later with presence of cloud cover and precipitation. I found no significant changes in dawn chorus start times when birds were exposed to short-term overnight artificial lighting. This research serves as the first comprehensive study of the effects of extrinsic factors on dawn chorus start times in north temperate birds.

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# Chapter 1

# General Introduction

## Introduction

Communication facilitates survival, growth, and reproduction for many animal species (McGregor 2005). Vocal communication is a particularly important component of fitness given its prominent role in animal reproduction (Bradbury and Vehrencamp 1998). In birds, for example, singing is a common vocal behaviour that serves diverse functions including maintaining a territory, sustaining social relationships, and attracting a breeding partner (Catchpole and Slater 2008). A particularly conspicuous bout of avian song typically occurs in the early morning during the breeding season; this singing period is known as the “dawn chorus” (Staicer et al. 1996). The dawn chorus is nearly ubiquitous among bird species, yet it is less well-studied than daytime song (Staicer et al. 1996). Studies of dawn chorusing provide information regarding conservation and maintenance of the natural world, as changes in singing behaviours can have notable evolutionary consequences for bird species (e.g., Dalziell and Cockburn 2008). In this thesis, I explore the dawn singing behaviour of birds in a temperate community, to enhance our understanding of this interesting animal behaviour.

## Bird song

Bird song mediates fitness through both female choice and male competition. Intersexually, bird song functions in attracting breeding partners (Nowicki and Searcy 2004). A study of Swamp Sparrows (*Melospiza georgiana*), for example, revealed that female Swamp Sparrows respond sexually to males with high-quality songs more so than to males with low-quality songs (Ballentine et al. 2004; in this case, quality was measured by number of difficult-to-perform trills). Likewise, a study of Pied (*Ficedula* *hypoleuca*) and Collared Flycatchers (*Ficedula albicollis*) used speakers placed on top of nest-boxes, broadcasting either male song or silence, to demonstrate that female flycatchers choose nest-boxes of singing males significantly more often than those of males who do not sing (Eriksson and Wallin 1986).

Much research has supported the idea that bird song has a second important purpose in repelling other males from a defended space (Nowicki et al. 1998). This territorial defense function has often been demonstrated through playback studies. For example, a classic experiment revealed that after removing resident Great Tit (*Parus major*) males from their territories and replacing some with speakers playing tit songs, outside males were less likely to move into territories occupied by speakers (Krebs et al. 1978). More recently, a study showed that male Banded Wrens (*Thryophilus pleurostictus*) were less likely to challenge speakers playing high-quality wren songs than those playing low- or medium- quality songs, demonstrating that song can be used to ward off potential territory intruders (De Kort et al. 2009). Certainly, both the mate attraction and territory defense functions of bird song have been well-supported in the literature over time (Catchpole and Slater 2008).

### Dawn chorusing

Although many birds will sing at various times of the day, the period of song with the highest song rates occurs in the early morning during the breeding season; this phenomenon is known as the “dawn chorus” (Mace 1987). The dawn chorus is a daily episode of high vocal output (Mace 1987), beginning shortly before the sun rises and continuing until sometime around sunrise (Staicer et al. 1996). In the temperate zone, the dawn chorus is performed almost exclusively by males (Staicer et al. 1996). Importantly, avian dawn chorusing can have fitness consequences, as has been shown, for example, in Superb Fairywrens (*Malurus cyaneus*); male fairywrens that produced longer trills during their dawn choruses benefited from a greater number of extra-pair copulations (Dalziell and Cockburn 2008). Overall, dawn chorusing is less-thoroughly studied than daytime singing, possibly because it occurs exclusively during one time of day; this made it difficult to follow multiple individuals per day before new technological recording advances became available. Further research on avian dawn song is, therefore, necessary in order to determine more clearly the functions of this bout of singing, as well as to recognize influential factors that can alter dawn chorus behaviour.

In 1996, Cynthia Staicer and colleagues published a thorough and compelling review of existing literature on the dawn chorus. They suggested that the dawn chorus occurs as a result of multiple factors. Staicer et al. (1996) stressed that these factors are not mutually-exclusive and, even within a single avian species, multiple factors appear to explain dawn chorus performance. The review (Staicer et al. 1996) grouped the factors that explain dawn singing behaviour into intrinsic factors, environmental factors, and social factors.

### Intrinsic factors and the dawn chorus

Intrinsic factors may play a role in the function of dawn singing. Staicer et al. (1996) proposed the circadian cycles hypothesis, stating that male birds sing in the early morning due to increases in hormone levels. Some research has supported this idea. For example, Van Duyse et al. (2005) found that male Great Tits were less likely to sing a dawn chorus after being implanted with a hormone inhibiting testosterone secretion, demonstrating the influence of hormones on song. However, another study increased testosterone levels in some Blue Tits (*Cyanistes caeruleus*), but saw no differences between dawn chorus characteristics of treated and untreated birds (Kunc et al. 2006).

A second intrinsic factor presented by Staicer et al. (1996) is the self-stimulation hypothesis. This idea suggests that male birds are able to stimulate their own hormone production by singing a dawn chorus (Staicer et al. 1996). Some research has demonstrated that hearing recordings of a bird's own vocalizations can stimulate development of their gonads (Cheng 1992). This hypothesis has received little attention, and more work is required to understand the interplay of hormone levels and dawn song performance.

### Environmental factors and the dawn chorus

Some research has shed light on the environmental influences on dawn singing. One environmental explanation for dawn song is the inefficient foraging hypothesis, suggesting that birds sing in the early morning because light levels at this time are not sufficient for foraging, but are appropriate for social interactions through singing (Staicer et al. 1996). This hypothesis has been supported by research on the relationship between chorus start times and eye size. Birds with larger eyes relative to body size tend to begin dawn chorusing and foraging earlier than those with smaller eyes, presumably because they are able to perceive low levels of light sooner (Thomas et al. 2002, Berg et al. 2006).

Staicer et al. (1996) also discussed the possibility that atmospheric conditions in the early morning could be more ideal for vocal transmission compared to other times of the day, an idea known as the acoustic transmission hypothesis (Henwood and Fabrick 1979). This idea is intuitively compelling, because the still conditions at dawn appear to be appropriate for long-range sound transmission. However, careful investigation has not supported this hypothesis, with some studies finding that the early morning may even be a less efficient time for song propagation (e.g., Dabelsteen and Mathevon 2002).

An alternate idea, known as the energy storage stochasticity hypothesis, suggests that the purpose of dawn song is to exhaust excessive overnight energy reserves (Barnett and Briskie 2007). One study of Silvereyes (*Zosterops lateralis*) demonstrated that male birds produced longer dawn choruses if they had received excess food the night before (Barnett and Briskie 2007). Similarly, another study found that male Zebra Finches (*Taeniopygia guttata*) on restricted diets tended to start dawn chorusing later than those receiving normal amounts of food (Ritschard and Blumm 2012). Notably, this hypothesis does not account for the fact that flight would be a much more efficient method of dispelling excess energy (Gill 2007).

### Social factors and the dawn chorus

The influences of social factors on bird song have been well established for daytime singing, but less clearly quantified for dawn singing. Social functions of avian vocalizations can include both inter-sexual (male-female) and intra-sexual (male-male) components, as explained above. Inter-sexual explanations for dawn chorusing include the mate attraction hypothesis, the mate guarding hypothesis, and the mate stimulation hypothesis. Intra-sexual explanations for dawn chorusing include the territory defense hypothesis and the social dynamics hypothesis.

The mate attraction hypothesis proposes that singing in the early morning functions in attracting female social mates and extra-pair mates (Staicer et al. 1996). One study found that male Eastern Kingbirds (*Tyrannus tyrannus*) that began singing their dawn choruses earlier tended to have larger body sizes and longer flight feathers (Murphy et al. 2008), demonstrating that dawn chorus characteristics can provide honest cues of male quality to female birds. Additionally, Poesel et al. (2006) found that earlier-singing male Blue Tits participated in a greater number of extra-pair copulations. Consequently, dawn chorusing does appear to honestly reflect quality and function in mate attraction for some species.

The mate guarding hypothesis suggests that male birds sing a dawn chorus to prevent their female mates from participating in extra-pair copulations (Staicer et al. 1996). Notable evidence comes from a study of Great Tits; males were found to end their dawn choruses once their female breeding partner emerged from their nest-box (Mace 1986). One explanation for this behaviour is that males were singing in an attempt to prevent extra-pair copulations by their social mate, a behaviour that typically occurs at dawn (Mennill et al. 2004).

A final inter-sexual explanation for dawn chorusing is the mate stimulation hypothesis, which suggests that singing a dawn chorus assists males in stimulating their female mate’s reproductive development and reproductive investment (Staicer et al. 1996). A recent study on Zebra Finches demonstrated that males with the highest song rates tended to have female partners that produced more highly-nutritious eggs (Bolund et al. 2012). However, this research focused on daytime singing; it has yet to be considered for dawn song exclusively.

Intra-sexually, the territory defense hypothesis suggests that male birds sing a dawn chorus to prevent intrusion of their territories by other males (Staicer et al. 1996). One study on Black-capped Chickadees (*Poecile atricapillus*) found that, after territorial intrusions were simulated through playback, males began dawn chorusing an average of

4.3 minutes earlier (Foote et al. 2011). This outcome suggested that the dawn chorus does play a role in territory defense; similar results have been found in other species, including a compelling example from Chipping Sparrows (*Spizella passerina*) where birds who had all of their territorial neighbours removed showed a significant decrease in their dawn chorus output (Liu 2004). Additional evidence for this hypothesis was provided by a study on Common Nightingales (*Luscinia megarhynchos)*. Researchers found that unmated male nightingales moved around to visit different territories most often during the early morning, assessing habitat availability and singing activities of rivals (Amrhein et al. 2004). This suggested that the dawn chorus does function in maintaining territorial boundaries between male birds.

Another intra-sexual explanation for dawn chorusing is the social dynamics hypothesis, which states that singing a dawn chorus allows males to maintain social relationships with nearby birds (Staicer et al. 1996). Microphone array analysis of the dawn chorus activities of Banded Wrens showed that males match song types interactively at dawn (Burt and Vehrencamp 2005). Song type matching is known to be important in establishing and maintaining social relationships in many species (Vehrencamp 2001). Support for this hypothesis also comes from research on Black-capped Chickadees; males tended to frequency-match neighbouring birds' vocalizations significantly more often than would be expected by chance (Foote et al. 2010a), showing that dawn chorus characteristics can function socially.

Overall, much research has focused on avian dawn chorusing since Staicer and colleagues' review was published in 1996, yet the functions of dawn song and factors that influence avian chorusing behaviour remain nebulous. Evaluating the current literature reveals variable levels of support for almost all of the hypotheses proposed by Staicer et al. (1996) for why birds sing dawn choruses. Furthermore, dawn singing appears to serve different functions for different avian species. It is important to continue studying the dawn choruses of many different bird species, using integrative approaches in order to understand relationships between different functions of the dawn chorus.

## Anthropogenic influences on the dawn chorus

Recently, studies have suggested that anthropogenic factors can also influence avian vocal behaviour, including dawn chorusing. This type of research has implications for conservation biology because increased urbanization adds both noise and light pollution to bird habitats (Troy et al. 2011). Some research has demonstrated that birds may modify song timing, frequency, and amplitude in response to artificial noise (Warren et al. 2006). One recent study found that, for Spotless Starlings (*Sturnus unicolor*) and House Sparrows (*Passer domesticus*), experimental exposure to artificial noise correlated with earlier dawn chorus start times (Arroyo-Solis et al. 2013). Additionally, Kempenaers et al. (2010) explored the effect of artificial lighting on the dawn chorus and found that four of five focal European bird species began dawn chorusing significantly earlier if their territory was near streetlights. Certainly, it is often difficult in urban environments to disentangle the effects of different anthropogenic factors, such as the relative contribution of anthropogenic noise pollution and light pollution. Further research should focus on determining how these different anthropogenic factors can alter dawn chorusing, as changes in song can lead to changes in fitness (e.g., Kempenaers et al. 2010).

## Dawn chorus dynamics

An interesting attribute of the dawn chorus is that different species in the same area begin their songs at different times, often in a predictable and characteristic order (Thomas et al. 2002). As early as 1930, Harry Allard recognized that birds within a certain range do not begin chorusing synchronously. In fact, Thomas et al. (2002) found that species in the same general area could differ in the timing of their first songs by over 1.5 hours. Some research has suggested that the ability to perceive light strongly affects what time birds begin dawn chorusing (e.g., Berg et al. 2006). However, differences in species start times are not yet well understood and further research is required to determine what factors are governing this phenomenon. In particular, by studying variation in dawn chorus start times among multiple species, we may gain significant insight into the intrinsic, environmental, and social factors that influence this dynamic animal behaviour.

## Study species

In this thesis, I focus on eight temperate songbird species and study their dawn chorus dynamics. I studied six of the species within Chapter 2 and four of the species within Chapter 3 of this thesis. I chose these particular species because they are common and well-recognized in North America, and they typically have only one or two song types that are readily distinguishable in spectrograms of recordings. I expect that this group of focal species is representative of northern temperate bird communities, and that this group will demonstrate a range of chorus behaviours, given their taxonomic diversity and diversity of life histories. I provide a brief background of the natural history and bioacoustics of each species below.

### *Eastern Phoebe*

The Eastern Phoebe (*Sayornis phoebe*) is a suboscine tyrant flycatcher that breeds throughout eastern Canada and the United States and winters in Mexico (Weeks 2011). Phoebes will often nest on human-built structures such as cottages and bridges, and their nests are easily distinguishable because of their characteristic inclusion of moss (Weeks 2011). Adult Eastern Phoebes are a grayish-brown colour on top, with a slightly darker head and tail (Figure 1.1; Sibley 2003). The Eastern Phoebe is typically a double-brooded species, producing two clutches per season, each consisting of between three and six eggs (Weeks 2011). Population numbers of aerial insectivores, including Eastern Phoebes, have been recently declining (McCracken 2008).

The Eastern Phoebe has a simple vocal array (Weeks 2011). It has two types of songs, *phee-bee* and *phee-b-be-bee*, and bouts are comprised of a combination of both types, often in alternation (Figure 1.1; Kroodsma 1985). Phoebes do not exhibit song learning; even without hearing adult songs, juvenile phoebes develop normal vocalizations (Kroodsma 1985). Additionally, Eastern Phoebes have been found to have individually distinctive songs (Foote et al. 2013).

### *Alder Flycatcher*

The Alder Flycatcher (*Empidonax alnorum*) is a suboscine tyrant flycatcher. The Alder Flycatcher typically migrates to its breeding grounds in late spring, and returns to its non-breeding territory in early fall (Lowther 1999). Alder Flycatchers have greenish-olive coloured plumage on top and white underneath with a characteristic narrow white eye-ring (Figure 1.1; Lowther 1999). Usually, Alder Flycatcher females will lay three to four eggs in a single brood of nestlings per season (Stein 1958). Like Eastern Phoebes, the overall abundance of Alder Flycatchers has lately been declining (McCracken 2008).

Alder Flycatchers produce a simple *fee-bee-o* song (Figure 1.1; Lowther 1999). Young birds begin singing a similar song immediately after fledging, and develop a more adult-like song within two months (Lowther 1999). The *fee-bee-o* song is not learned; Kroodsma (1984) found that Alder Flycatcher fledglings played only Willow Flycatcher (*Empidonax traillii*) songs still produced normal *fee-bee-o* songs.

### *Black-capped Chickadee*

The Black-capped Chickadee is a non-migratory species that is found throughout North America (Foote et al. 2010b). Generally, Black-capped Chickadees are more common near edges of wooded areas, including both deciduous and mixed woodlands (Foote et al. 2010b). Chickadees have black caps and throats, white cheeks, and grey, black, and white back, wing, and tail feathers (Figure 1.1). Males tend to be slightly larger than females in this species (Desrocher 1990). Chickadees usually produce one brood per breeding season; a brood can consist of up to twelve eggs (Smith 1991, Foote et al. 2010b).

Black-capped Chickadees produce a *fee- bee-ee* song that consists of two clear notes; the first note is of higher frequency than the second (Weisman et al. 1990). The second note also has a brief amplitude break in the middle, distinguishable in a spectrogram (Figure 1.1; Foote et al. 2010b). The total duration of this song is approximately one second (Weisman et al. 1990**.**).

### *American Robin*

The American Robin (*Turdus migratorius*) is the largest and most abundant thrush in Canada (Sallabanks and James 1999). The robin's breeding range extends throughout most of North America, while it typically winters anywhere between southern Canada and northern Mexico (Sallabanks and James 1999). The size of the American Robin's breeding range has increased with the development of suburban parklands, suggesting that urbanization may offer certain benefits to this particular species (Sallabanks and James 1999). Its plumage is deep-gray to dark-brown on top, with a black head and red belly (Figure 1.1; Ridgway 1907). Female robins lay three to four eggs per brood, and robin pairs will often produce two broods per breeding season (Sallabanks and James 1999).

The song of American Robins is composed of a collection of distinctive syllables (Sallabanks and James 1999). The robin's song is described as clear whistles resembling the phrase *cheerily, cheer up, cheerio, cheerily, cheer up* (Figure 1.1; Sallabanks and James 1999). Robin song frequency is greatest for males during the breeding season, typically lessening or stopping after eggs hatch (Howell 1942, Wauer 1999).

### *Ovenbird*

The Ovenbird (*Seiurus aurocapilla*) is found prevalently in deciduous forests within North America (Porneluzi et al. 2011). The Ovenbird is a migratory species that spends the breeding season in eastern North America and the winters in Central America (Porneluzi et al. 2011). Ovenbirds tend to be olive-brown coloured on top and white underneath. A white ring around the eyes also helps with identification (Figure 1.2; Porneluzi et al. 2011). Typically, Ovenbirds will produce between three and six eggs twice per season, using nests built on the ground in deciduous forests (Porneluzi et al. 2011)

Ovenbird songs are conspicuous due to being very loud and ringing (Hann 1937). Each song phrase is composed of between three and five separate notes, together generating a sound similar to *teacher…teacher…teacher* (Figure 1.2; Hann 1937).

### *Chipping Sparrow*

The Chipping Sparrow is one of the most common songbirds in North America (Middleton 1998). The breeding territory for this species extends from northern Mexico to central Yukon Territories (Godfrey 1986). During the breeding season, adult Chipping Sparrows display a red-coloured cap, with grey under-parts and a mix of brown, orange and white on the back and wings (Figure 1.2). Chipping Sparrows typically produce two broods per season, with approximately four eggs in each brood (Middleton 1998).

Although Chipping Sparrows nest in shrubs or trees, they typically forage on the ground (Middleton 1998).

The Chipping Sparrow’s song is composed of a trill of rapidly repeated *tssips* sounds (Figure 1.2; Marler and Isaac 1960). The song begins softly and continuously becomes louder (Marler and Isaac 1960). Song frequency and duration remain fairly consistent between different Chipping Sparrow individuals (Middleton 1998).

### *Song Sparrow*

The range of the Song Sparrow (*Melospiza melodia*) extends from northern Canada to southern Mexico (Arcese et al. 2002). The Song Sparrow’s plumage features a streaked brown and white pattern on the breast and mantle, and a brown spot is often noticeable in the centre of the breast area. (Figure 1.1; Arcese et al. 2002). Song Sparrows will often produce two broods of fledglings per breeding season, each consisting of three to five eggs in nests that are typically near the ground (Nice 1943).

The Song Sparrow’s song is a varied series of two to six phrases, represented by the mnemonic *maids-maids-maids put on your tea kettle-kettle-kettle* (Figure 1.1; Arcese et al. 2002). Song Sparrows develop their songs through four distinct stages, until the song eventually assumes a crystallized adult form (Nice 1943). Notably, there is considerable individual and geographic variation in the songs of this species (Arcese et al. 2002).

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*White-throated Sparrow*

The White-throated Sparrow (*Zonotrichia albicollis*) is a widespread North American songbird (Falls and Kopachena 2010). The breeding range of the White-throated Sparrow occurs throughout Canada, but usually east of the Rocky Mountains, while its wintering range primarily includes the southeastern United States (Falls and Kopachena 2010). It has a characteristic white throat patch with a gray lower throat and breast. It also exhibits sharply contrasting black and white stripes on the crown, with yellow patches above its beak (Figure 1.1; Falls and Kopachena 2010). White-throated Sparrows may produce one or two broods in a breeding season; the female typically lays approximately four eggs per clutch (Peck and James 1987). Like Chipping Sparrows and Song Sparrows, White-throated Sparrows tend to nest either on or just above the ground (Falls and Kopechena 2010).

The White-throated Sparrow's song includes a number of pure-tone whistled notes with at least one major pitch change usually occurring after the first or second note, resembling the expression *oh, sweet Canada, Canada, Canada* (Figure 1.1; Borror and Gunn 1965). The length and amplitude of the songs exhibit great variation (Falls 1969).

## Thesis goal

In this thesis, I explore variation in dawn chorus start times within a community of North American birds. Specifically, I focus on the effects of weather variables and natural and artificial lighting on the dawn chorus singing behaviour of the eight temperate songbird species summarized above. I was motivated by an interest in expanding our understanding of North American avian dawn chorusing. Relative to daytime song, there is much to learn about dawn chorus vocal behaviour. Additionally, the few studies that exist on chorus start time variation have mostly focused on tropical or European species.

In Chapter 2 of my thesis, I investigate the influence of Julian day, moon brightness, cloud cover, precipitation, and temperature on the dawn chorus start times of six North American bird species. This provides a more complete understanding of chorus dynamics for different temperate species, as it enables recognition of seasonal changes in dawn chorus behaviour and evaluates the repeatability of dawn chorus timing. Chapter 2 is written for submission to The Wilson Journal of Ornithology.

In Chapter 3 of my thesis, I consider whether changes in timing of exposure to short-term artificial lighting can alter dawn chorus start times for four temperate avian species. This represents a novel opportunity that provides valuable information regarding anthropogenic influence on ecological processes. Chapter 3 is written as a Short Communication for submission to the journal Avian Conservation and Ecology.

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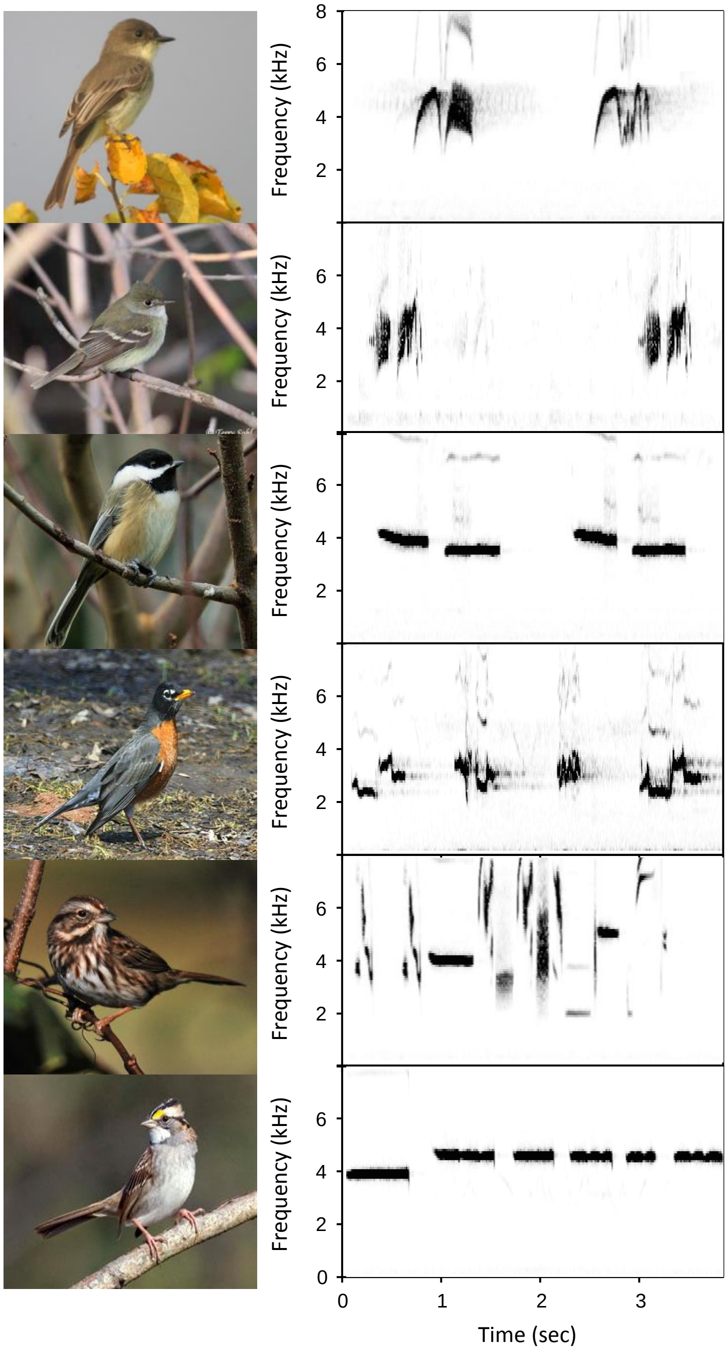

**Figure 1.1.** Chapter 2 study species beside spectrograms of songs (top to bottom: Eastern Phoebe, Alder Flycatcher, Black-capped Chickadee, American Robin, Song Sparrow, and White-throated Sparrow).

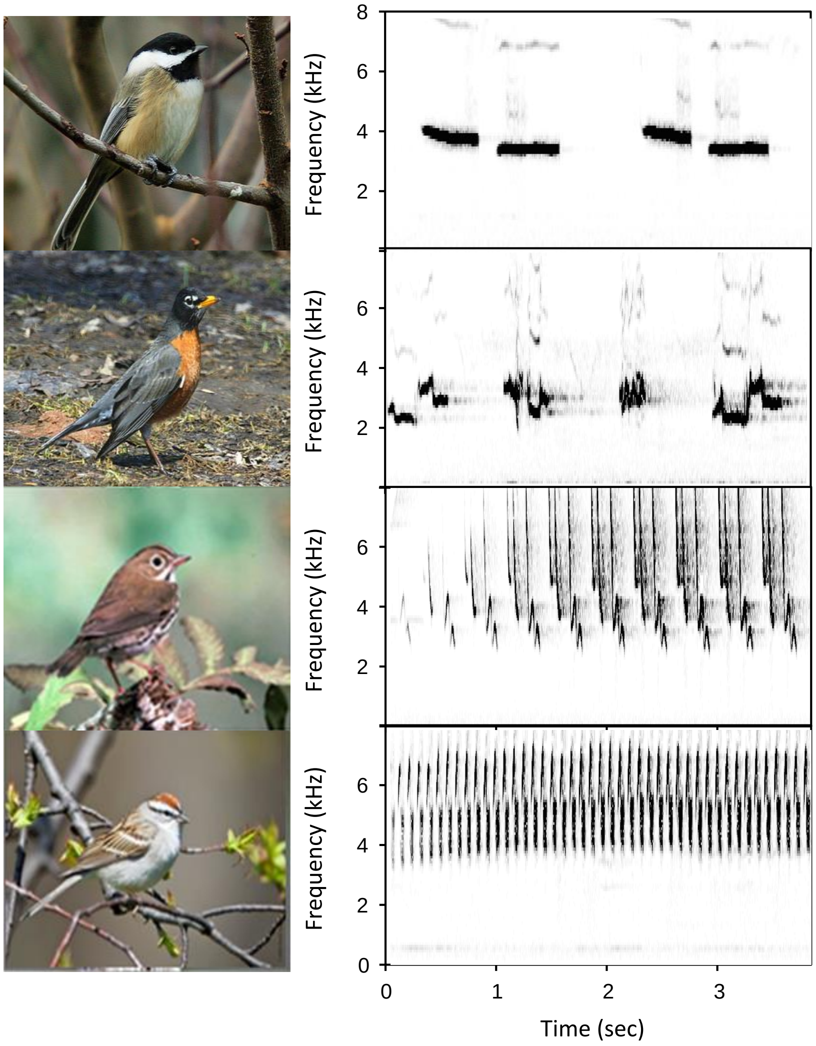

**Figure 1.2.** Chapter 3 study species beside spectrograms of songs (top to bottom: Black-capped Chickadee, American Robin, Ovenbird, and Chipping Sparrow).

# Chapter 2

# Dawn chorus start time variation in a northern bird community: relationships with seasonality, weather, and ambient light

## Chapter summary

The avian dawn chorus is a daily period of high song output performed predominantly during the breeding season. Dawn chorus performance can vary between individuals and between species. The many extrinsic factors that may relate to dawn chorus start times for different North American bird species have received little attention. In this study, we consider relationships between dawn chorus start times and time of year, moon brightness, cloud cover, precipitation, and ambient temperature for six common bird species living in a northern temperate rural area. Our results indicate that extrinsic variables related to different species in different ways; overall, we saw that birds typically start singing earlier with increasing moon brightness and with increasing temperature at nautical twilight, and that birds start singing later with presence of cloud cover and precipitation. Based on mean start times, we also found that Alder Flycatchers begin singing earliest in this group of birds, followed respectively by Song Sparrows, White-throated Sparrows, American Robins, Eastern Phoebes, and Black-capped Chickadees. This represents the first comprehensive study of dawn chorus start time variation in North American birds.

## Introduction

The most prominent period of bird song occurs prior to sunrise during the breeding season, and is known as the “dawn chorus” (Staicer et al. 1996). An interesting, yet perplexing, feature of avian dawn chorusing is that different species often begin singing at very different times (Allard 1930). In fact, the difference between dawn chorus start times of birds living within the same area can be over 100 minutes (Thomas et al. 2002). Notably, the species within a given bird community begin dawn chorusing in a predictable sequence, often following a specific order (McNeil et al. 2005). This attribute of the dawn chorus has been recognized by scientists and nature enthusiasts alike for many decades (Allen 1913), although the reasons for its occurrence are enigmatic. Many of the hypothesized benefits to singing in the early morning should be applicable to all species that sing a dawn chorus (Berg et al. 2006). For example, if acoustic transmission is better at dawn (Staicer et al. 1996), it would be beneficial for all avian species to begin dawn chorusing as early as possible. Likewise, if dawn chorus plays a role in attracting females (Staicer et al. 1996), beginning to sing as early as possible would have fitness benefits for members of every species. Therefore, other factors must influence these differences in dawn chorus initiation. A number of additional variables may influence dawn chorus start times. These include intrinsic factors such as reproductive stage and eye size (Mace 1987, Berg et al. 2006), but also extrinsic factors such as time of year, time of sunrise, moon brightness, cloud cover, precipitation, and ambient temperature (Allen 1913, Davis 1958, Slagsvold 1977, Thomas 1999, Thomas et al. 2002, Miller 2006).

Prior investigations have demonstrated that sunrise time plays a strong role in influencing dawn chorus start time. A study of Eastern Towhees (*Pipilo erythrophthalmus*) showed that dawn chorus start times correlated strongly with time of civil twilight and sunrise throughout the breeding season (Davis 1958). Early work on Willow Warblers (*Phylloscopus trochilus*) revealed that during the first half of the breeding season, as sunrise becomes progressively earlier, birds begin dawn chorusing earlier as well (Brown 1962). Another study found that dawn chorus onset of Golden-crowned Sparrows (*Zonotrichia atricapilla*) mirrored sunrise time for the duration of the breeding season (Holmes and Dirks 1978). Certainly, solar radiation is widely understood to be an important cue for initiating the avian dawn chorus, though other factors are recognized to play a role as well.

Although sunlight is widely considered the proximate cue that initiates the dawn chorus (Thomas et al. 2002), moon brightness may also affect dawn chorus onset. Moon brightness depends on moon stage; a full moon is approximately ten times brighter than a quarter moon (Russell 1916). Leopold and Eynon (1961) suggested, many years ago, that bright moonlight might lead to earlier dawn chorusing in birds. Their observational research demonstrated that brightly moonlit nights correlated with earlier singing of American Robins (*Turdus migratorius*) during March, April, and May, but did not correlate with earlier dawn song during June (Leopold and Eynon 1961). A more recent study on American Robins did not find any correlation between these two factors in the field (Miller 2006). Studies on overnight artificial light exposure reveal that higher ambient light levels alter start times (Miller 2006), further suggesting that birds are sensitive to light sources other than the sun when it comes to initiating the dawn chorus.

In order to determine whether a relationship between moon brightness and dawn song exists, it will be necessary to compare moon brightness to dawn chorus start time for a number of different species and over a longer period of time that encompasses several lunar cycles.

Recognizing the strong influence of sunlight on dawn chorus initiation times (Thomas et al. 2002), weather variables that limit the amount of sunlight perceived by birds may also be expected to alter dawn chorus start time. One variable relating to dawn chorus initiation may be the amount of cloud cover. When cloud cover is extensive, birds may perceive light later and, therefore, begin their dawn chorus performance later. This phenomenon was noticed anecdotally in Tree Swallows (*Tachycineta bicolor*) and American Robins (Allen 1913). Alternatively, if there is relatively little cloud cover, birds may perceive light earlier and, therefore, begin singing earlier. In an urban environment, this relationship might be reversed, because cloud cover can actually trap and amplify artificial light near the Earth's surface (Miller 2006). However, in non-urban environments where anthropogenic lighting is sparse, increased cloud cover is expected to correlate with later dawn chorus start times.

Along with cloud cover, precipitation could also influence the start time of the dawn chorus. If rain is present in the early morning, birds may be expected to wait until it stops before commencing their dawn chorus performance. Although this seems intuitive, an empirical study found no relationship between daily song output and precipitation for more than 20 bird species in Norway (Slagsvold 1977). However, in a more recent study, occurrence of wind and rain significantly correlated with later onset of singing in Common Bulbuls (*Pycnonotus barbatus*) and Common Blackbirds (*Turdus merula*;

Hasan 2010). Presence of precipitation has not yet been studied in relation to dawn chorus start time for North American birds.

Finally, ambient temperature is a factor that affects metabolic expenditure, and may thereby influence dawn chorus performance (Thomas 1999). The energy storage stochasticity hypothesis suggests that birds must store fat reserves in order to ensure overnight survival (Staicer et al. 1996). However, the unpredictability of overnight conditions may leave birds with an energy surplus, making possible high dawn chorus output in the early morning (Staicer et al. 1996, Thomas 1999). Although a bird cannot allow its fat reserves to diminish completely, storing excess fat is disadvantageous due to increased risk of predation and higher metabolic expenditure (Cuthill and Houston 1997). An inherent issue with this hypothesis, however, is that flight is a more energetically-expensive activity than song (Gill 2007) and, consequently, should be a more efficient method of using stored energy.  Nevertheless, previous research has demonstrated a strong positive correlation between minimum overnight temperature and duration of dawn chorus in both Great Tits (*Parus major*) and Eurasian Wrens (*Troglodytes troglodytes*; Garson and Hunter 1979). A similar result was observed in American Robins (Thomas 1999). These studies have focused on song output, but whether there is a relationship between temperature and dawn chorus start time has yet to be studied.

In this study, we examine the relationships between dawn chorus start times and Julian day, moon brightness, cloud cover, precipitation, and ambient temperature within a community of northern temperate birds. Given that ambient light exposure is understood to play a role in initiating dawn chorusing (Thomas et al. 2002, McNeil et al. 2005, Miller 2006), we predicted that birds would begin singing earlier when the moon cast more light before dawn. Based on our expectation that cloud cover would alter the amount of ambient light perceived by birds, we predicted that increasing cloud cover would correlate with later onset of dawn chorusing (Miller 2006). Based on our expectation that birds might not engage in long range acoustic signaling in the rain (Hasan 2010), we predicted that the presence of precipitation would correspond with later onset of the dawn chorus. Based on the energy storage stochasticity hypothesis, which posits that unpredictable overnight temperature conditions may leave birds with a surplus of energy to devote to song in the early morning (Staicer et al. 1996), we predicted that an increase in temperature at nautical twilight would correlate with earlier dawn chorus start times. Overall, this research represents the first comprehensive study of dawn chorus start time variation in North American birds.

## Methods

### *Field methods*

We recorded the dawn chorus at 13 different sites in Echo Bay, Ontario (46° 29'N, 84° 4'W) between April and July 2012. The site is a rural area dominated by eastern white pine (*Pinus strobus*) and tamarack (*Larix laricina*), and also including many agricultural fields. Echo Bay provides habitat for diverse species of breeding birds. We used automated digital recorders (model: Song Meter SM2, Wildlife Acoustics) programmed to start recording at nautical twilight (the point at which the horizon becomes visible) and continue for six hours each morning. Nautical twilight and sunrise times were acquired using the National Research Council Canada’s sunrise/sunset calculator (http://www.nrccnrc.gc.ca/eng/services/sunrise/ advanced.html). Each recorder was equipped with two omni-directional microphones, and sounds were recorded in WAV format with a sampling rate of 22,050 Hz and 16-bit accuracy. Recorders were placed in locations in which our six target species were known to occur: Eastern Phoebes (*Sayornis phoebe*), Alder Flycatchers (*Empidonax alnorum*), Black-capped Chickadees (*Poecile atricapillus*), American Robins, Song Sparrows (*Melospiza melodia*), and White-throated Sparrows (*Zonotrichia albicollis*). Adjacent recorders were placed at least 200 m apart to ensure that there was no overlap between individuals recorded at neighbouring sites. We downloaded recordings every four to ten days and archived them at Algoma University.

### *Data collection*

We visualized recordings using Syrinx-PC sound analysis software (J. Burt, Seattle Washington), which allowed us to scan spectrograms of recordings to identify the songs of our six target species. We used the time and frequency cursors in Syrinx-PC to annotate the first song of each of the six focal species each day. We annotated the start time of all six focal species on every possible calendar day between 3 April 2012 and 15 July 2012 for thirteen recorders; we skipped days only when strong winds or rain made it too difficult to detect the six species' songs in spectrograms (approximately eight days per recorder were not annotated because the amplitude of rain and/or wind in the recordings completely obscured any singing). After 15 July 2012, singing became much less frequent, so we stopped annotating after that date. We used the same recording level on all of the song meters and the same spectral gain settings in Syrinx-PC, so that the darkness of spectrograms was standardized across sites. Some diurnal bird species are known to sing sporadically at night (La 2012); in our annotations, we checked that each bird began singing continuously within five minutes of their first song to ensure that we were annotating the beginning of the dawn chorus and not an errant nocturnal song.

We standardized times of first song by calculating start times relative to daily sunrise; we acquired sunrise times from the National Research Council of Canada for Sault Ste. Marie, ON, Canada. We compared the six species' dawn chorus start times against weather data and Julian day. Moon stage information was collected from the Moon Phase Calculator (http://www.timeanddate.com/calendar/aboutmoonphases.html); we numerically ranked days between new moon and full moon as progressively brighter, then gradually duller as days cycled from full moon back to new moon. This is in accordance with similar methodology used in other studies of moonlight's influence on animal behaviour (e.g. Julien-Laferrière 1997). The cloud cover information was acquired using data collected at the Sault Ste. Marie Airport by Environment Canada (http://climate.weatheroffice.gc.ca/climateData/canada_e.html). We used weather data recorded between 0200 hours and 0600 hours daily and categorically designated the sky each day as either cloudy or clear. We also used Environment Canada data to record the presence or absence of precipitation and to determine the daily temperature. We selected the temperature during the hour in which the start of nautical twilight occurred; this is the time just before most species began to sing.

### *Data analysis*

The relationship between Julian day on dawn chorus start time was not linear and because it strongly contributed to many models, we determined which type of curve (linear or polynomial curves ranging from quadratic to quintic) provided the best fit to the data before building the models. To test for the effects of date, weather, and natural variation in light level on dawn chorus start time we used linear mixed effects models with recorder location as a random effect and Julian day (and its square or cube if the relationship between date and start time was not linear), moon brightness, presence/absence of cloud cover, presence/absence of precipitation, and temperature at nautical twilight as fixed effects. We also included all two-way interactions among fixed effects. We determined the best model for each of the six species using backward step-wise regression guided by AIC (Akaike information criterion). The residuals of the models were inspected for deviation from the assumptions of normality and homoscedasticity. We consider results significant at $p<0.05$. For all statistical analyses, we used JMP10 (SAS Institute Inc., Cary, NC, USA).

## Results

Recordings of the dawn chorus of six different species in a north temperate bird community reveal that extrinsic factors significantly influence dawn chorus start times. Our results demonstrate that different variables explain dawn chorus timing in different species. Based on the mean start times of each species, Alder Flycatchers began dawn chorusing the earliest, followed by Song Sparrows, White-throated Sparrows, American Robins, Eastern Phoebes, and Black-capped Chickadees respectively (Figure 2.7). We present results in order from earliest to latest singing species.

### *Alder Flycatcher*

Using linear mixed effects models, the best model explained 28.9% of variation in dawn chorus start time of Alder Flycatchers ($p<0.0001$; $N=352$). Differences between males at different recording sites accounted for 29.2% of the model's variation in chorus start time for this species while the remaining fixed effects accounted for 70.8% of the model variation (Figure 2.1a). None of the extrinsic variables had a significant influence on chorus start times in the best model for this species (Table 2.1; Figures 2.3a-2.6a). There was no relationship between Julian day and dawn chorus start time for Alder Flycatchers (Figure 2.2a; $r^2$=0.004, N=352, p=0.25 for linear model).

### *Song Sparrow*

The best model explained 25.1% of variation in dawn chorus start time of Song Sparrows (p<0.0001; N=688). Differences between males at different recording sites accounted for 14.75% of the model's variation in chorus start time for this species (Figure 2.1b). Song Sparrows began dawn chorusing significantly earlier with increasing moon brightness (Table 2.1; Figure 2.3b), and they began singing significantly later when precipitation was present (Table 2.1; Figure 2.5b). Song Sparrow dawn chorus start time was not significantly influenced by cloud cover (Figure 2.4b). Although temperature was not significant alone, Song Sparrows displayed a tendency for earlier song with increasing temperature, and song start time was significantly related to an interaction between temperature and moon brightness (Table 2.1). Both linear and squared Julian day terms contributed significantly to the model (Table 2.1). Dawn chorus start time of Song Sparrows was significantly related to Julian day both linearly ($r^2$=0.075, N=688, p<0.0001; Min before sunrise = 50.001907 + 0.144676*Julian Day) and quadratically, which was a better fit (Figure 2.2b; $r^2$=0.106, N=688, p<0.0001; Min before sunrise = 55.033106 + 0.127715*Julian day - 0.003865*(Julian day-146.359)$^2$).

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### *White-throated Sparrow*

The best model explained 50.2% of variation in dawn chorus start time of White-throated Sparrows ($p<0.0001$; $N=574$). Differences between males at different recording sites accounted for 41.6% of the model's variation in chorus start time for this species (Figure 2.1c). White-throated Sparrows sang significantly later when precipitation was present (Table 2.1; Figure 2.5c) and displayed a non-significant tendency for later singing when cloud cover was present (Table 2.1; Figure 2.4c). Additionally, White-throated Sparrows began singing significantly earlier dawn choruses with increasing temperature at nautical twilight (Table 2.1; Figure 2.6c). Moon brightness did not relate to dawn chorus start time for White-throated Sparrows (Table 2.1; Figure 2.3c). Linear, squared, and cubed Julian day terms contributed to the model for White-throated Sparrows (Table 2.1). Julian day was significantly related to dawn chorus start time of White-throated Sparrows both linearly ($r^2=0.077$, $N=574$, $p<0.0001$; Min before sunrise = 95.978882 - 0.2272522*Julian Day) and quadratically (r2=0.146, $N=574$, $p<0.0001$; Min before sunrise = 105.40843 - 0.2567555*Julian Day - 0.0103946*(Julian Day-151.355)$^2$), but was best described by a cubic curve (Figure 2.2c; $r^2=0.210$, $N=574$, $p<0.0001$; Min before sunrise = 167.216790 - 0.669191*Julian day - 0.007808*(Julian day-151.355)$^2$ + 0.000457*(Julian day-151.355)$^3$).

### *American Robin*

The best model explained 56.7% of variation in dawn chorus start time of American Robins ($p<0.0001$; $N=685$). Differences between males at different recording sites accounted for 36.6% of the model's variation in chorus start time for this species

(Figure 2.1d). American Robins sang significantly earlier with increasing levels of moon brightness (Table 2.1; Figure 2.3d) However, robins began singing significantly later with both presence of cloud cover (Table 2.1; Figure 2.4d) and precipitation (Table 2.1; Figure 2.5d). Temperature at nautical twilight did not significantly relate to American Robin dawn chorus start time (Table 2.1; Figure 2.6d), although an interaction between temperature at nautical twilight and presence of precipitation did (Table 2.1). Additionally, both linear and squared Julian day terms contributed significantly to the model (Table 2.1). Julian day was significantly related to dawn chorus start time for American Robins linearly ($r^2$=0.234, N=685, p<0.0001; Min before sunrise = 27.877036 + 0.2028983*Julian Day), but was best described by a quadratic curve (Figure 2.2d; $r^2$=0.275, N=685, p<0.0001; Min before sunrise = 32.691995 + 0.1861132*Julian Day - 0.0035244*(Julian Day-146.642)$^2$)).

### *Eastern Phoebe*

The best model explained 39.8% of variation in start times of Eastern Phoebes (p<0.0001; N=561). Differences between males at different recording sites accounted for 24.4% of the model's variation in chorus start time for this species (Figure 2.1e). Eastern Phoebes began singing their dawn choruses significantly earlier with increasing temperature at nautical twilight (Table 2.1; Figure 2.6e), but began singing significantly later when precipitation was present (Table 2.1; Figure 2.5e). Phoebes also displayed a non-significant tendency for later dawn chorusing with presence of cloud cover (Table 2.1; Figure 2.4e). There was no relationship between dawn chorus start time and moon brightness for this species (Figure 2.3e). For Eastern Phoebes, both linear and squared Julian day terms contributed significantly to the model (Table 2.1). There was a significant relationship between Julian day and dawn chorus start time linearly ($r^2$=0.071, N=561, p<0.0001; Min before sunrise = 16.311553 + 0.1540746*Julian Day), but the relationship was better described by a quadratic curve (Figure 2.2e; $r^2$=0.152, N=561 p<0.0001; Min before sunrise = 22.675231 + 0.139574*Julian day - 0.006903*(Julian day -143.597)$^2$).

### *Black-capped Chickadee*

The best model explained 46.2% of variation in dawn chorus start time in Black-capped Chickadees (p<0.0001; N=333). Differences between males at different recording sites accounted for 41.7% of the model's variation in chorus start time for this species (Figure 2.1f). Black-capped Chickadees began singing significantly earlier with brighter moon (Table 2.1; Figure 2.3f), whereas they began singing significantly later when there was precipitation in the early morning (Table 2.1; Figure 2.5f). Although the results of fixed-effects tests were not significant for temperature, it still contributed to the best model (Figure 2.6f), and was significant when interacting with precipitation (Table 2.1). There was no relationship between dawn chorus start time and presence of cloud cover (Figure 2.4f). Again, both linear and squared Julian day terms contributed significantly to the model for Black-capped Chickadees (Table 2.1). Although the relationship between Julian day and dawn chorus start time was significant linearly ($r^2$=0.003, N=333, p<0.0001; Min before sunrise = 34.301949 - 0.026117*Julian Day), it was best described by a quadratic curve (Figure 2.2f; $r^2$=0.276, N=333, p<0.0001; Min before sunrise = 21.831382 + 0.1029694*Julian Day - 0.0108909*(Julian Day-127.508)$^2$).

## Discussion

Our analysis of the dawn chorus start times of six north temperate bird species reveals that dawn chorus start time varies significantly with extrinsic factors such as weather and ambient light. Generally, we found that birds in a non-urban habitat begin their dawn chorus performance earlier with increasing moon brightness and with increasing temperature at nautical twilight. They typically begin their dawn chorus performance later with presence of cloud cover and with presence of precipitation. Further, dawn chorus initiation varied with Julian day. The factors that significantly influence start time varied from species to species, yet the relationships were in the same direction for all species, demonstrating that these extrinsic features shape dawn chorus performance in similar ways, but with different intensities, across species. These data reveal that the dawn chorus performance of birds in a temperate bird community varies with extrinsic factors.

For each of our six focal species, we found that individual variation in dawn chorus start times contributed significantly to the models. There are a number of reasons why birds of the same species at different recording locations might exhibit differences in daily song onset. For some species, such as Black-capped Chickadees, dominance hierarchies may play a role in influencing start times. High-ranking males tend to begin their dawn chorus performance significantly earlier than low-ranking males (Otter et al. 1992). In other species, age influences individual dawn chorus start times. For example, older Blue Tits (*Cyanistes caeruleus*) begin their dawn choruses significantly earlier than younger birds (Poesel et al. 2006). Whether a male is mated or unmated may also influence certain chorus characteristics within species (Burt and Vehrencamp 2005).

Additionally, a study of the breeding phenology of Willow Tits (*Parus montanus*) revealed that chorus onset was earliest during the fertile period of the singer's partner (Welling et al. 1995), suggesting that differences in breeding stage could also contribute to individual variation in start times. The birds in our study area were not individually marked or monitored for rank, age, or breeding stage; these factors, and others, are likely sources of individual variation in dawn chorus start time that influenced the models for all six of our focal species.

Five of the six focal species showed significant variation in dawn chorus start time with date. The sole exception, the Alder Flycatcher, returned from migration more than a month later than the other five species (see Fig. 2.2); this late arrival meant that Alder Flycatchers were sampled over a shorter period, which likely explains the lack of a significant effect in the model explaining variation in this species. For the remaining five species, variation in sunrise time with Julian day, as well as variation in the breeding stage of the singing animals, best explains variation in chorus start time.  None of these five focal species showed linear relationships as the strongest relationship between Julian day and dawn chorus start times. We found a cubic relationship between date and song onset fit best for White-throated Sparrows, and quadratic relationships between date and song onset fit best for Song Sparrows, American Robins, Eastern Phoebes, and Black-capped Chickadees. Interestingly, most species displayed mid-season peaks in earliness of dawn chorus start time. This reinforces a pattern seen in earlier research (e.g., Davis 1958, Nolan 1978) and suggests that breeding stage likely is an influential factor on dawn chorus start times (Staicer et al. 1996); we estimate that most birds were at the egg-laying stage, when female choice for male song performance is most intense, at the time of these mid-season peaks.

We found that moon brightness affected dawn chorus start time for half of our focal species, demonstrating a prominent lunar relationship with the early morning behaviour of these diurnal animals. Prior studies have provided similar insight; an early investigation of American Robins found that they sing earlier on brightly moonlit nights between March and May (Leopold and Eynon 1961), and several recent investigations have revealed that overnight lighting can influence chorus start time (e.g. Miller 2006). Our results showed that Song Sparrows, American Robins, and Black-capped Chickadees all began dawn chorusing significantly earlier when the moon was brighter. Conversely, Alder Flycatchers, White-throated Sparrows, and Eastern Phoebes did not demonstrate significant relationships between dawn chorus start time and moon brightness, suggesting that these species may be less thoroughly influenced by natural overnight lighting.

Our results demonstrated that cloud cover was significantly related to dawn chorus start time for only one of six focal species. Presence of cloud cover can alter ambient light conditions in the early morning (Graham et al. 2003) and, therefore, has the potential to cause variation in avian singing behaviour. Red-legged Partridges (*Alectoris rufa*), for example, produce fewer vocalizations with increasing cloud cover (Pépin and Fouquet 1992). Yet cloud cover may have complex effects on dawn chorus start time in urban environments, where anthropogenic light can be trapped and amplified by clouds and thereby advance dawn chorus start time (Miller 2006). However, our study site in Echo Bay is a rural area with few anthropogenic light sources. Consequently, we expected that the presence of clouds in the early morning would delay dawn chorus start time. Our predictions were supported solely for American Robins. However, both White-throated Sparrows and Eastern Phoebes displayed non-significant trends in the same direction. We found no relationship between dawn chorus start time and cloud cover for Alder Flycatchers, Song Sparrows, or Black-capped Chickadees. More of the focal species were significantly influenced by moon brightness than cloud cover; it is possible that overnight lighting may be more critical for dawn chorus timing than lighting experienced in the early morning. Interestingly, American Robins were the only species for which dawn chorus start times were related to both moon brightness and cloud cover, suggesting that robins may be the most sensitive to light variation. Indeed, previous research has demonstrated that American Robins alter song start times in response to exposure to light pollution (e.g., Miller 2006, Kempenaers et al. 2010). Our research provides evidence that natural lighting also strongly influences robin dawn chorus initiation.

We also found that precipitation significantly altered dawn chorus onset for five of the focal species. Previous research on bird communities in Australia (Keast 1994) and Jordan (Hasan 2010) documented delays in dawn chorus onset as a result of rain; the influence of rain on dawn chorus start time for North American birds has not been studied previously, as far as we are aware. We expected that bird species would begin dawn chorusing later than usual when precipitation was present in the early morning, in part because rain would be accompanied by cloud cover, and in part because rain is expected to lead to an overall decrease in the activity of wild animals (Link et al. 2011). This prediction held true for Song Sparrows, White-throated Sparrows, American Robins, Eastern Phoebes, and Black-capped Chickadees, which all began singing significantly later when precipitation was present.  In contrast, Alder Flycatchers did not appear to vary their chorus start time with precipitation. As the earliest starting species, Alder Flycatchers may have begun dawn chorusing prior to precipitation beginning on some mornings, and could be unaffected by its presence as a result. Overall, presence of precipitation does appear to strongly influence temperate bird dawn chorusing because it was significant for almost all of the focal species in this study.

Our analyses revealed that dawn chorus start times of two of our six focal species were significantly related to ambient temperature. Relationships between ambient temperature and avian singing behaviour are well recognized (e.g., Slagsvold 1977, Garson and Hunter Jr. 1979, Gottlander 1987). The relationship between temperature and onset of dawn song, however, has not been well-studied (Astrom 1976). Nevertheless, we found that temperature at nautical twilight does relate to significantly earlier dawn chorus onset for White-throated Sparrows and Eastern Phoebes. Alder Flycatchers, Song Sparrows, American Robins, and Black-capped Chickadees did not show significant relationships between dawn chorus start times and temperature at nautical twilight. However, temperature did show a significant relationship with Song Sparrow dawn chorus start time when considered as an interaction with moon brightness. Analysis of a large global data set did find that moon stage can slightly, but noticeably, influence temperatures in the lower troposphere (Balling Jr. and Cerveny 1995). Consequently, Song Sparrows may be more thoroughly influenced by overnight lighting, and the resulting difference in temperature between new and full moon (Balling Jr. and Cerveny 1995) could explain why this particular interaction is significant for Song Sparrows. Additionally, temperature showed a significant relationship with dawn chorus start times for American Robins and Black-capped Chickadees when considered as an interaction with precipitation. This suggests that, for these species, temperature is only important while it rains. A combination of cold temperatures and precipitation related to later dawn chorus start times than warm temperatures and precipitation; this suggests that, although precipitation alone may not delay dawn chorusing for robins and chickadees, cold weather and precipitation together may produce overly challenging conditions through which to sing. For White-throated Sparrows and Eastern Phoebes, temperature was significant when considered alone. Clouds have a net cooling effect on the atmosphere (Ramanathan et al. 1989, Witze 1998), so a possible explanation for these results would be that it is warmer at nautical twilight on days with more sun exposure and, because some light is visible at this time, these species' songs could be more affected by light exposure than temperature. Another potential explanation for earlier singing on warmer mornings might relate to activity of prey sources for insectivores. Higher temperatures provide more thermal energy required for growth and reproduction (Bale et al. 2002), and if insects are more active earlier on warmer mornings, insectivorous avian species might benefit from completing their dawn choruses earlier in order to begin foraging as soon as possible. The energy storage stochasticity hypothesis predicts that dawn chorus performance is influenced by surplus energy stored by birds to ensure survival through variable nighttime temperatures (Barnett and Briskie 2007). This hypothesis could be an alternative explanation for the relationship between dawn chorus onset and temperature, although it is controversial, given that locomotion may be a much more efficient method of eliminating surplus energy than singing (Gill 2007). Certainly, the total length of the dawn chorus would be an important consideration in determining whether birds are truly singing to expel energy. A next step may be to consider chorus length in addition to chorus start time, and then compare both factors to temperature at nautical twilight.

Previous research has demonstrated that avian species with larger eyes relative to body size can perceive low levels of light earlier in the morning and, consequently, begin singing their dawn choruses earlier than species with relatively smaller eyes (e.g., Thomas et al. 2002, Berg et al. 2006). The inefficient foraging hypothesis suggests that the timing of dawn chorusing is related to light availability, stating that birds sing a dawn chorus because the early morning is an appropriate time for social communication but not for foraging (Staicer et al. 1996). Consequently, interspecific variation in dawn chorus start time could result from differences in species' abilities to see at low light levels (Thomas et al. 2002). Kacelnik (1979) found that foraging efficiency is light-limited for approximately two hours after morning activity begins for Great Tits. We did not measure eye size because we had no affiliation with nearby banding stations at which to capture and measure our focal species. Also, eye size is measured at a species level (Berg et al. 2006), and we recognized that we could not attain a significant correlation using data for only six species. Despite this, previous research (e.g., Thomas et al. 2002) allows us to assume that the species in our study that began singing earliest have larger eyes than those that began singing later. Our results demonstrate that Alder Flycatchers and Song Sparrows begin singing earliest, indicating that they likely have the largest eyes relative to their body mass. White-throated Sparrows and American Robins began singing the next earliest, suggesting that they have moderately-large eyes in relation to their body masses. Finally, Eastern Phoebes and Black-capped Chickadees began singing the latest overall, suggesting that these two species likely have the smallest eyes relative to their body masses. Future research should consider the relationship of both dawn chorus onset and foraging strategy to eye size and eye quality.

We know that different species begin dawn chorusing at very different times (e.g., Allard 1930), so it can be expected that weather and lighting variables influence these species in different ways (Staicer et al. 1996). There also exist certain inherent differences between the study species that may have contributed to interspecific variation in our results. For example, all species are migratory (Lowther 1999, Sallabanks and James 1999, Arcese et al. 2002, Falls and Kopechena 2010, Weeks 2011) except the Black-capped Chickadee, which is a non-migratory bird (Smith 1991). Alder Flycatchers and Eastern Phoebes are suboscine species, while American Robins, Black-capped Chickadees, Song Sparrows, and White-throated Sparrows are oscine species (Gill 2007). Additionally, these six species have some differences in diet preferences, which could alter the time in the morning at which foraging becomes efficient (Thomas et al. 2002). The focal species also vary markedly in body size; American Robins are the largest (77 - 85 g; Sallabanks and James 1999) and Black-capped Chickadees the smallest (9 -14 g; Foote et al. 2010). Important inherent differences between the six focal species can likely help explain why extrinsic factors demonstrate unique relationships with each.

Overall, our research provides novel insight on avian dawn chorusing behaviour, serving as the first comprehensive study of dawn chorus start time variation in North American passerines. In accordance with previous research on tropical and temperate European bird species, we discovered that northern temperate birds begin dawn chorusing in a non-random, predictable order. Alder Flycatchers begin singing the earliest, followed respectively by Song Sparrows, White-throated Sparrows, American Robins, Eastern

Phoebes, and Black-capped Chickadees. Julian day was also significantly related to dawn chorus start time for all species except the Alder Flycatcher. Although the four weather and lighting variables we considered did not significantly relate to start times for all of the focal species, each was important for at least a subset of species and relationships always occurred in the same direction for those that were influenced. Overall, we found earlier dawn chorus start times with increasing level of moon brightness as well as with increasing temperature at nautical twilight. We found later dawn chorus start times with presence of cloud cover and with presence of precipitation in the early morning. Our results suggest that extrinsic variables such as Julian day, temperature, moon brightness, cloud cover and precipitation relate to dawn chorus start time in North American passerines. Our results yield insight into dawn chorus start time dynamics of six species of temperate songbird.

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**Table 2.1**. Results of linear mixed effects models for extrinsic factors influencing dawn chorus start time for six temperate bird species, showing the parameters for the models of best fit.

| **Species**<br>***Predictor Variables*** | **F** | **DF** | **P** | **Earlier song** |
|---|---|---|---|---|
| Alder Flycatcher | | | | |
| Song Sparrow | | | | |
| *Julian day* | 24.77 | 674.2 | <0.0001* | Later in season |
| *Julian day*$^2$ | 20.26 | 673.3 | <0.0001* | |
| *Moon brightness* | 16.64 | 670.5 | <0.0001* | When brighter |
| *Precipitation* | 3.97 | 671.1 | 0.0468* | When absent |
| *Temperature* | 0.64 | 670.7 | 0.4232 | |
| *Temp*Moon brightness* | 12.69 | 671.1 | 0.0004* | |
| White-throated Sparrow | | | | |
| *Julian day* | 72.49 | 556.2 | <0.0001* | Later in season |
| *Julian day*$^2$ | 65.50 | 556.3 | <0.0001* | |
| *Julian day*$^3$ | 57.82 | 556.5 | <0.0001* | |
| *Cloud cover* | 3.38 | 554.8 | 0.0667 | |
| *Precipitation* | 8.52 | 555.2 | 0.0037* | When absent |
| *Temperature* | 6.39 | 555.0 | 0.0117* | When warmer |
| American Robin | | | | |
| *Julian day* | 156.38 | 667.1 | <0.0001* | Later in season |
| *Julian day*$^2$ | 112.28 | 666.8 | <0.0001* | |
| *Moon brightness* | 22.39 | 665.7 | <0.0001* | When brighter |
| *Cloud cover* | 37.25 | 664.8 | <0.0001* | When absent |
| *Precipitation* | 28.48 | 664.8 | <0.0001* | When absent |
| *Temperature* | 2.34 | 665.0 | 0.1268 | |
| *Temp*Precipitation* | 8.49 | 664.6 | 0.0037* | |
| Eastern Phoebe | | | | |
| *Julian day* | 79.11 | 548.7 | <0.0001* | Later in season |
| *Julian day*$^2$ | 73.11 | 549.4 | <0.0001* | |
| *Cloud cover* | 3.32 | 544.1 | 0.0688 | |
| *Precipitation* | 9.18 | 544.8 | 0.0026* | When absent |
| *Temperature* | 13.87 | 545.1 | 0.0002* | When warmer |
| Black-capped Chickadee | | | | |
| *Julian day* | 76.06 | 325.7 | <0.0001* | Later in season |
| *Julian day*$^2$ | 68.04 | 326.0 | <0.0001* | |
| *Moon brightness* | 9.61 | 313.3 | 0.0021* | When brighter |
| *Precipitation* | 8.86 | 312.1 | 0.0031* | When absent |
| *Temperature* | 0.16 | 312.1 | .6895 | |
| *Temp*precipitation* | 10.19 | 312.1 | .0016* | |

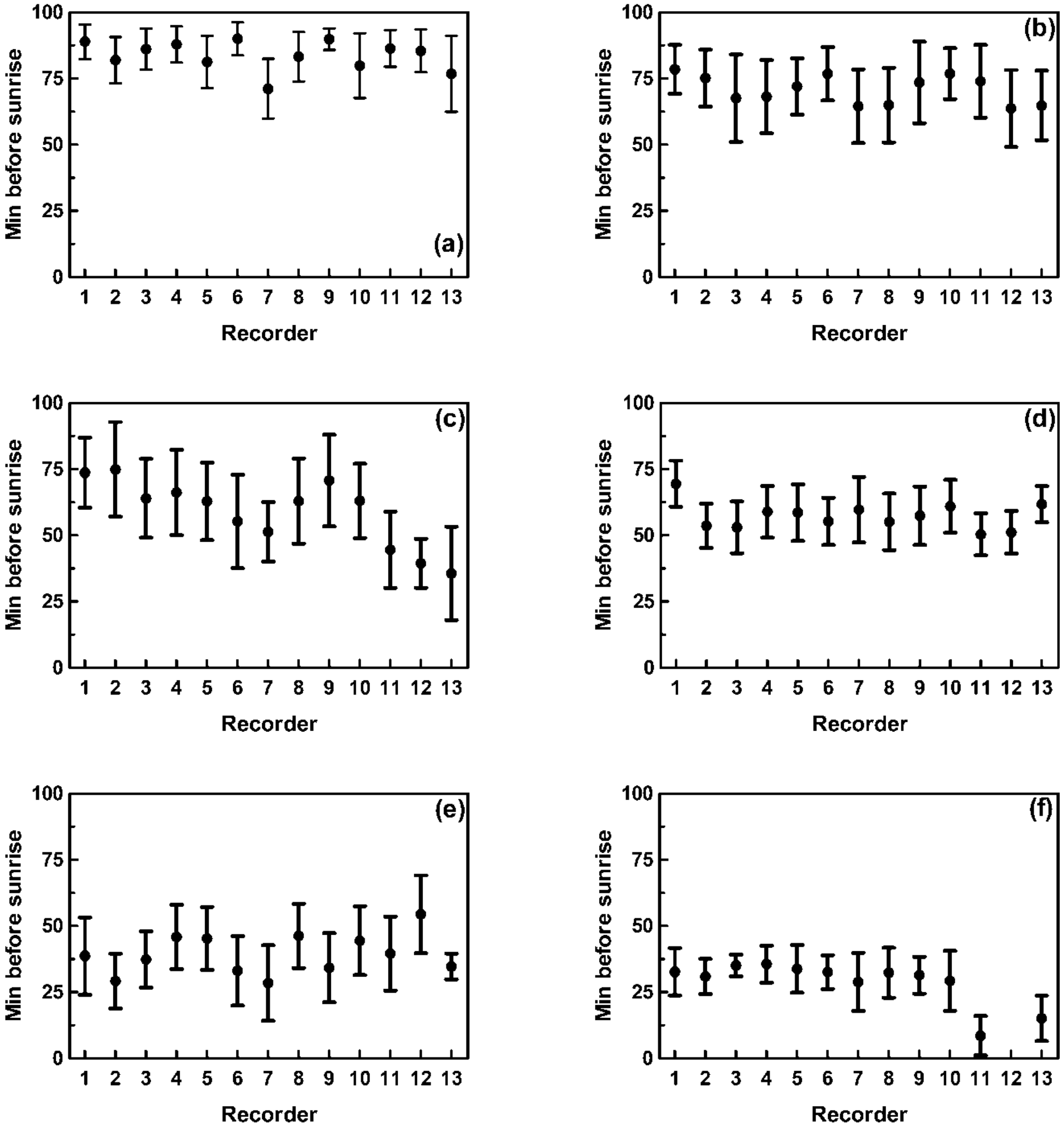

**Figure 2.1.** Within species, birds at 13 different recording locations exhibit substantial variation in dawn chorus start time. Dawn chorus start times are shown for (a) Alder Flycatchers, (b) Song Sparrows, (c) White-throated Sparrows, (d) American Robins, (e) Eastern Phoebes, and (f) Black-capped Chickadees. Error bars represent standard deviation.

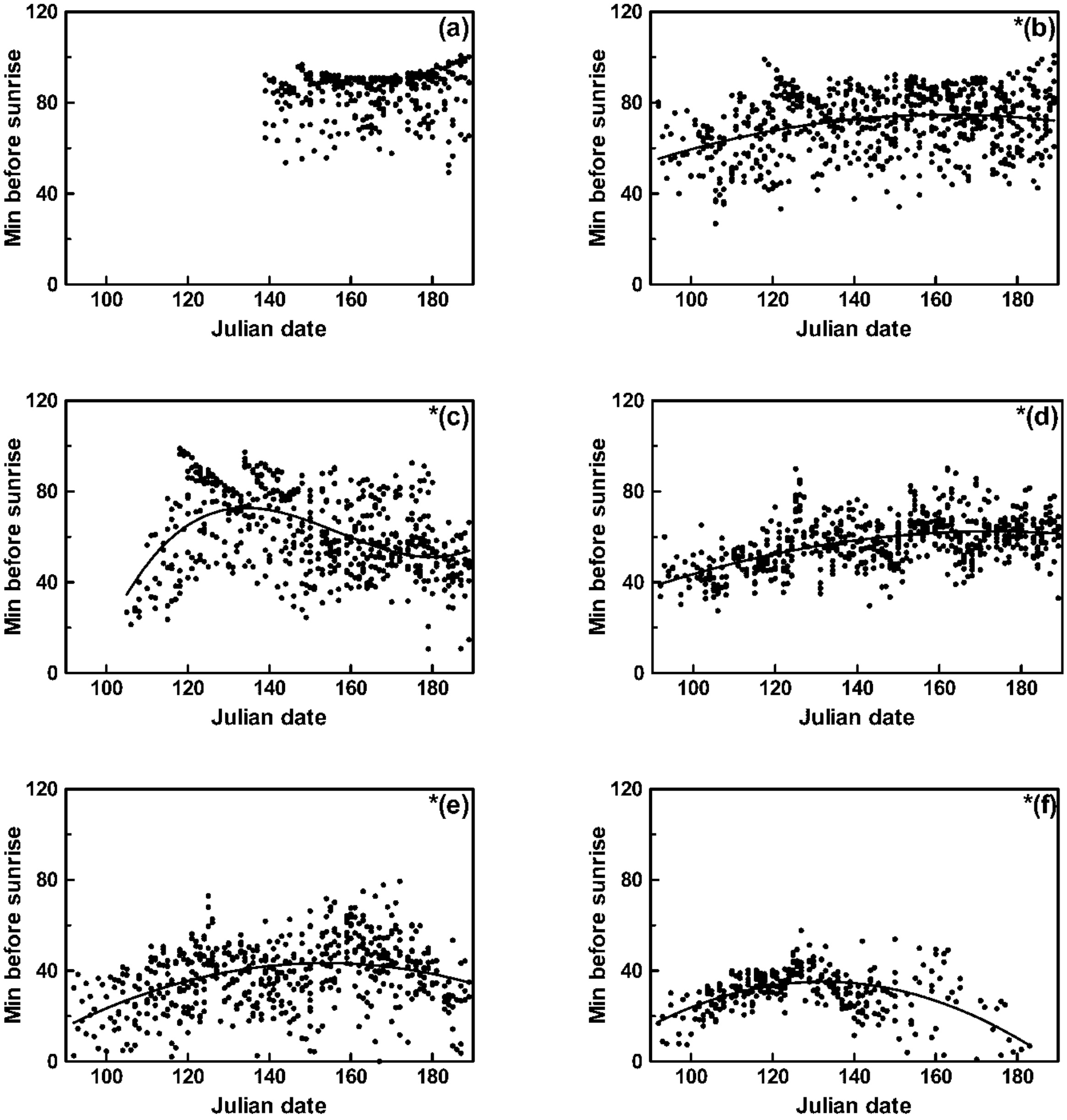

**Figure 2.2.** Six species of temperate songbird show variation in dawn chorus start time over the course of the breeding season. Each dot represents an annotated day at one recorder location for (a) Alder Flycatchers, (b) Song Sparrows, (c) White-throated Sparrows, (d) American Robins, (e) Eastern Phoebes, and (f) Black-capped Chickadees. The line of best fit is also shown.

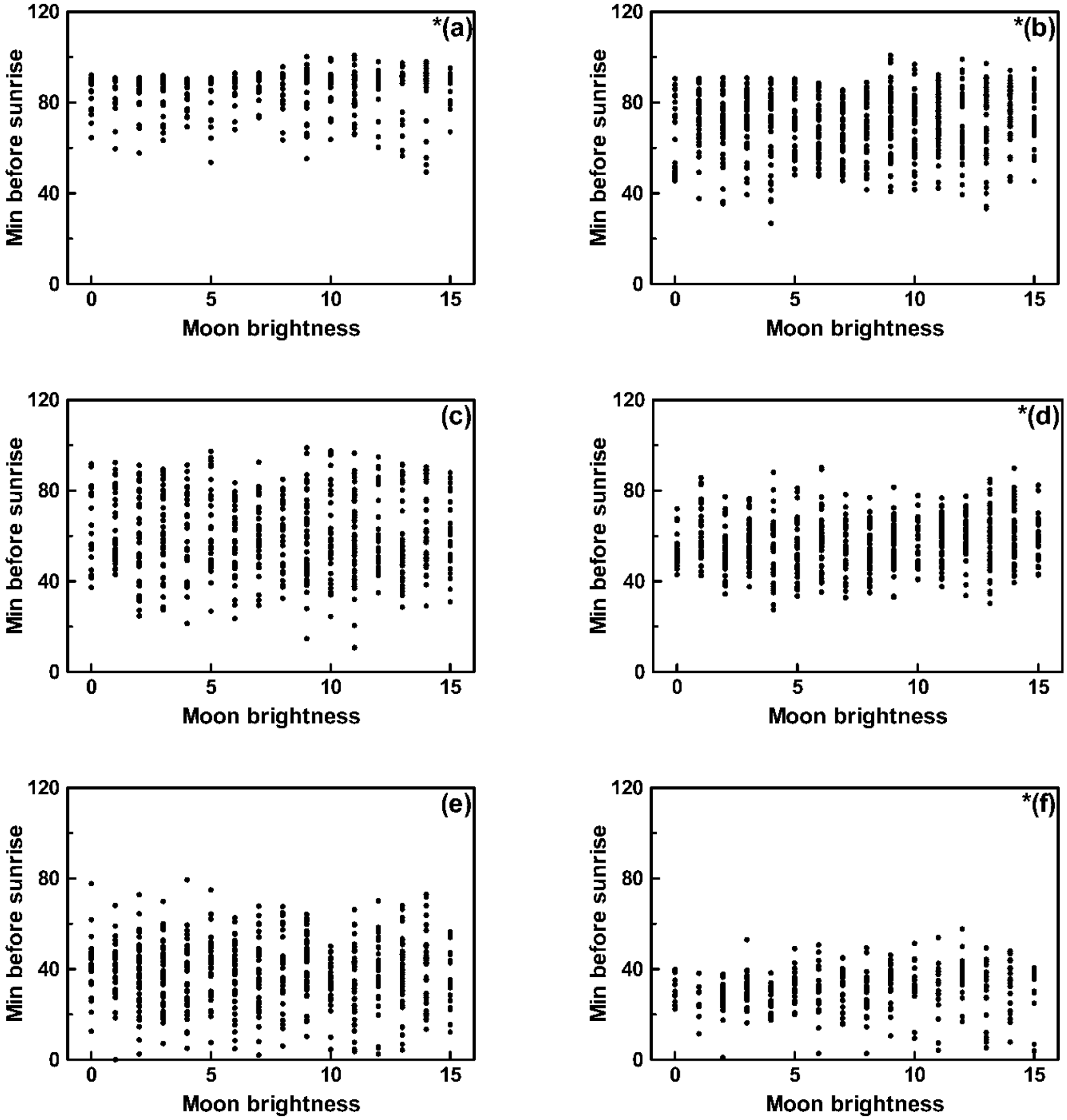

**Figure 2.3.** Temperate birds show variation in dawn chorus start time according to moon brightness. Here, moon brightness ranges from 0 (new moon) to 15 (full moon). Each dot represents an annotated day at one recorder location. Significant relationships were seen for (b) Song Sparrows, (d) American Robins, and (f) Black-capped Chickadees. No significant relationships existed for (a) Alder Flycatchers, (c) White-throated Sparrows, or (e) Eastern Phoebes.

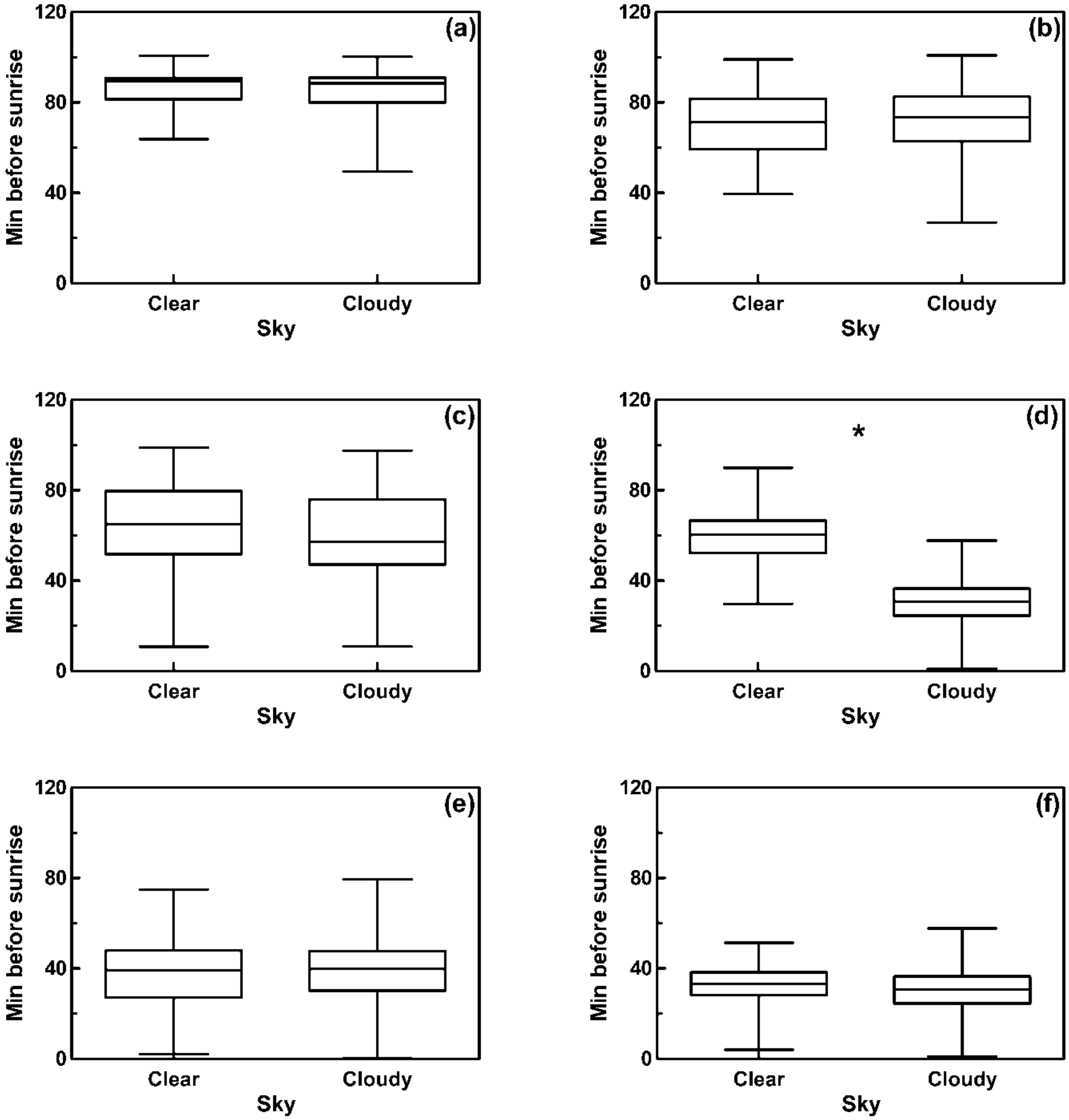

**Figure 2.4.** Temperate birds show variation in dawn chorus start time according to presence of cloud cover. Boxes represent 25th, 50th, and 75th percentile, and whiskers show the full range of data. Significant relationships were seen for (c) White-throated Sparrows, (d) American Robins, (e) Eastern Phoebes, and (f) Black-capped Chickadees. No significant relationships existed for (a) Alder Flycatchers or (b) Song Sparrows.

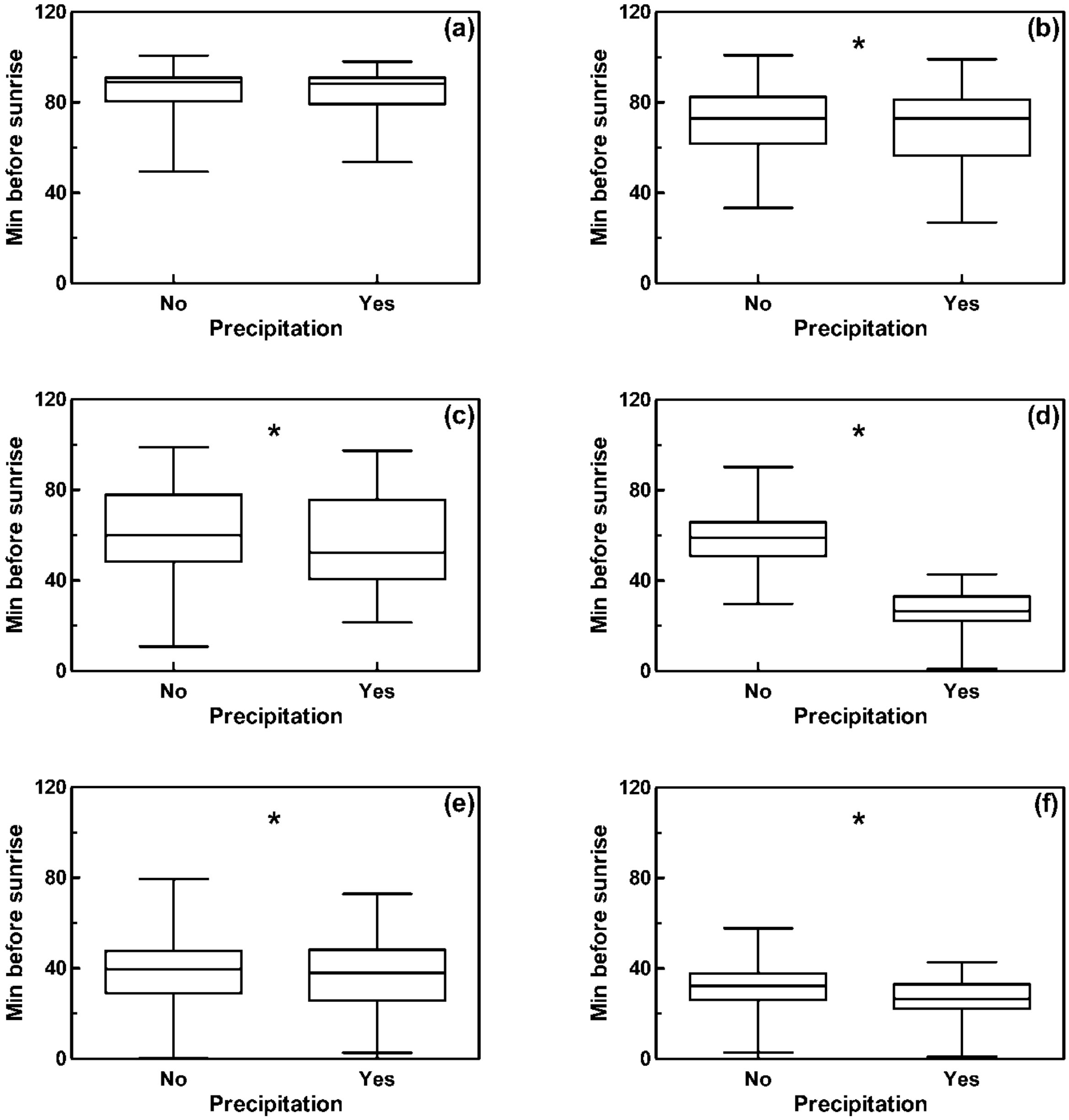

**Figure 2.5.** Temperate birds show variation in dawn chorus start time according to presence of precipitation. Boxes represent 25th, 50th, and 75th percentile, and whiskers show the full range of data. Significant relationships were seen for (b) Song Sparrows, (d) American Robins, and (e) Eastern Phoebes. No significant relationships existed for (a) Alder Flycatchers, (c) White-throated Sparrows, or (f) Black-capped Chickadees.

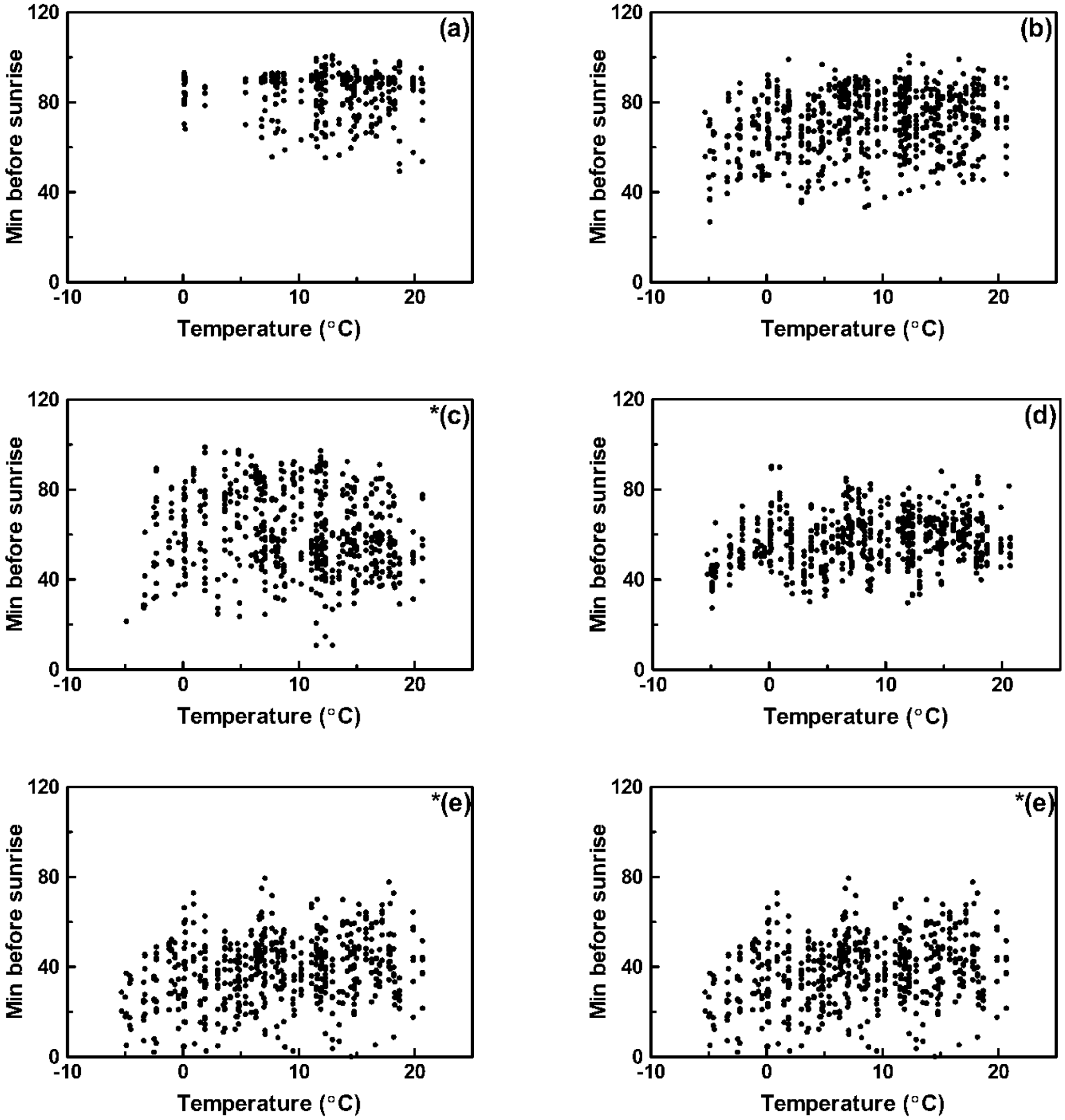

**Figure 2.6.** Temperate birds show variation in dawn chorus start time according to temperature at nautical twilight. Each dot represents an annotated day at one recorder location. Significant relationships existed for (b) Song Sparrows, (d) American Robins, and (e) Eastern Phoebes. No significant relationships existed for (a) Alder Flycatchers, (c) White-throated Sparrows, or (f) Black-capped Chickadees.

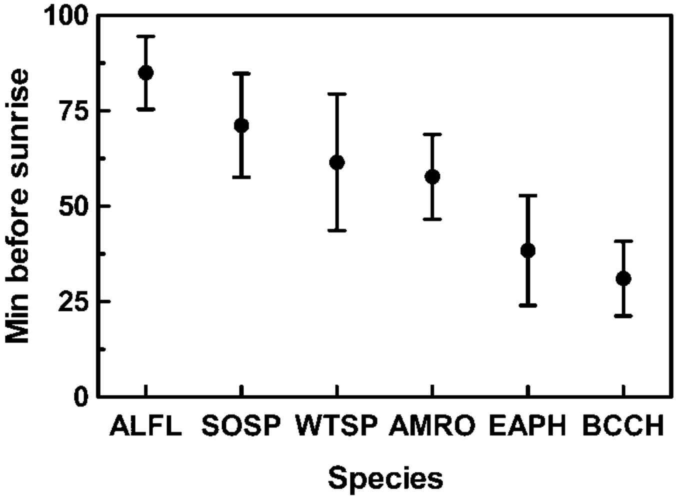

**Figure 2.7.** Variation in dawn chorus start times is exhibited by different north temperate bird species living in the same area. Alder Flycatchers (ALFL) begin dawn chorusing earliest in relation to sunrise, followed respectively by Song Sparrows (SOSP), White-throated Sparrows (WTSP), American Robins (AMRO), Eastern Phoebes (EAPH), and Black-capped Chickadees (BCCH). Error bars represent standard deviation.

# Chapter 3

## Anthropogenic lighting and the avian dawn chorus: short-term light exposure does not influence chorus start times

## Chapter summary

With an increase in global urbanization, anthropogenic activities have a growing influence on the ecology and behaviour of wildlife. Previous research has demonstrated that both noise and light pollution influence vocal behaviour of wild birds. Past studies have been challenged by an inability to differentiate the effects of noise pollution and light pollution, and have been limited to comparing the behaviour of birds in different areas (e.g., areas exposed to anthropogenic light versus pristine sites). In this study, we experimentally manipulated lighting along a cross country ski trail in a wilderness area near Sault Ste. Marie, Ontario, to determine whether short-term changes in light exposure can alter dawn chorus start times for four species of temperate songbirds. We compare the dawn chorus start times of birds before and after an artificial light manipulation, and we compare birds on the experimental trail to birds in an unlit control area. None of the four species showed a significant difference in dawn chorus start time on the experimental trail before and after the lights were turned on. American Robins on the lit trail began dawn chorusing earlier than robins on the unlit trail; however, there were no significant differences between dawn chorus start times on the lit versus unlit trails for Black-capped Chickadees, Chipping Sparrows, or Ovenbirds. These results suggest that short-term anthropogenic lighting in the absence of noise pollution does not disrupt the normal circadian schedule of dawn chorusing for north temperate birds. This research has important conservation implications, suggesting that short-term light pollution does not necessarily lead to disturbances to wildlife.

## Introduction

Anthropogenic activities have the potential to influence animal behaviour. As global urbanization expands, human activities introduce increasingly significant changes into natural animal habitats (Ditchkoff et al. 2006). Anthropogenic noise and light are considered environmental pollutants (Hasan 2010) that have the potential to interfere with animals' circadian cycles, because they can alter distinctions between night and day (Longcore and Rich 2004, Dominoni et al. 2013). Many animal populations now live within or nearby urban areas where noise and light pollution may have a significant influence on their behaviour (Ditchkoff et al. 2006, Fuller et al. 2007). Consequently, successful conservation efforts will benefit from an expanded understanding of wildlife behaviour in urban settings (Ditchkoff et al. 2006).

Birds provide a compelling model for studying the effects of anthropogenic factors on animal behaviour, given their diversity and their abundance in habitats that are influenced by anthropogenic effects. Bird song, in particular, is an important and widespread avian behaviour that may show a pronounced effect of anthropogenic noise and light (Fuller et al. 2007). The dawn chorus, a predictable period of prolonged bird song produced prior to sunrise each day (Staicer et al. 1996), is of particular interest for studying urbanization's influence on avian behaviour given that anthropogenic light pollution overnight or in the early morning might alter dawn chorus timing. Notably, disruption of the dawn chorus can influence avian fitness and breeding patterns (e.g., Dalziell and Cockburn 2008, Kempenaers et al. 2010).

Recently, several investigations have focused on the effects of artificial light exposure on avian behaviour, and particularly on singing activities of birds. A study of

European songbirds found that four of five focal species began dawn chorusing significantly earlier if their territory was near streetlights, compared to distant birds with territories far from streetlights (Kempenaers et al. 2010). Another study found that American Robins (*Turdus migratorius*) living in areas with greater intensities of artificial light began singing their dawn choruses during true nighttime hours (Miller 2006). Similarly, European Robins (*Erithacus rubecula*) began singing and foraging significantly earlier when they were housed in artificially-lit aviaries (Thomas et al. 2004). These investigations indicate that artificial light does appear to adjust the circadian singing rhythms across a diversity of songbird species.

The consequences of artificial light exposure are expected to be complex, and may or may not be detrimental to the fitness of wild birds. Singing earlier could be beneficial to birds by providing more opportunities for extra-pair copulations (e.g., Kempenaers et al. 2010). However, earlier song could be disadvantageous to birds because birds that sing earlier are known to breed earlier; the resulting time of greatest nestling food requirement may not correspond with time of greatest food availability for birds with artificially adjusted breeding times (Lambrechts et al. 1997). Further research is required to determine whether light pollution presents serious conservation issues for wild birds. Unfortunately, it is often difficult in urban environments to distinguish between the effects of artificial noise and artificial light. For this reason, studies in low-noise environments are needed. In addition, research on this topic to date has been limited to comparing song start times of birds nesting near lights to birds nesting at different sites, far from lights (e.g., Miller 2006, Kempenaers et al. 2010). These studies are unable to control for the possibility that earlier-singing birds might be more likely to nest near light sources. Studies that experimentally alter light exposure after birds have settled into their breeding territories are, therefore, an important next step.

In this investigation, we experimentally altered short-term artificial light exposure in the field using lights along a cross country ski trail. We sought to determine whether changes in anthropogenic light levels influence avian dawn chorus start times, focusing on four species of temperate songbirds: American Robins, Black-capped Chickadees (*Poecile atricapillus*), Chipping Sparrows (*Spizella passerina*), and Ovenbirds (*Seiurus aurocapillus*). The central hypothesis of this study is that short-term exposure to artificial light can influence dawn chorus start times for avian species in a non-urban area. We predicted that upon exposure to short-term overnight artificial light on a ski trail, birds would begin their dawn chorus performance earlier in the morning. This is the first study to investigate the influence of light pollution on bird song in the absence of noise pollution, and the first to manipulate artificial lighting in the field. Uniquely, our experimental design allowed us to wait until birds established their breeding territories before beginning to manipulate light exposure.

## Methods

### *Field methods*

We studied wild, free-living songbirds around the Kinsmen Cross Country Ski Trail in Sault Ste. Marie, Ontario, throughout May of 2013. In early May, we observed the area for seven days in order to determine which bird species were most common and to ensure that birds were settled into their breeding territories before we began experimentally altering light exposure. We chose to focus on American Robins, Black-capped Chickadees, Chipping Sparrows, and Ovenbirds, because multiple territory-holding males of each of these species were abundant enough at both the experimental and control sites.

To record the birds holding territories in the forest surrounding the ski trail, we used an array of 44 microphones (Figure 3.1a). The array consisted of 22 autonomous digital recorders (Wildlife Acoustics model: SM2+GPS) recording in stereo (22,050 Hz, 16 bit, WAC format). Recorders were placed approximately four meters from the ground strapped to light posts along the central portion of the ski trail (Figure 3.2). The left channel of each recorder was fixed at the recorder location, while the right channel was placed 40-50 m away using an extension cable. Each recorder was equipped with a Global Positioning System (GPS) unit that eliminated clock drift and allowed us to synchronize the recordings later, in the laboratory. This configuration created a 44 microphone acoustic location system that covered a 300 m x 650 m area and encompassed the entire ski trail loop (Figure 3.1a).

We also placed twelve recorders on trees within a section of the ski trail that did not have lights (Figure 3.1b); these recorders were placed at least 170 meters from adjacent recorders ($\bar{x}$ = 210.75 ± 38.3 m) so that individual birds would be picked up by only a single recorder. These recorders allowed us to collect a reference dataset in a control area that was not subject to any experimental light manipulation.

We set the song meters to record from two hours prior to nautical twilight until two hours after sunrise, encompassing the time period when birds perform their dawn chorus at both sites. We focused our analyses on a two day period. (1) On 2013 May 21 we collected dawn chorus recordings for a morning when the ski trail lights were off. The lights had not been turned on since the end of the ski season almost two months earlier, on 2013 March 29. (2) On 2013 May 22, the following day, we turned on the lights along the ski trail throughout the night, from dusk (2115 hours) to dawn (0554 hours), and collected dawn chorus recordings. Meanwhile, the twelve recorders in the non-lit section of the ski trail recorded dawn choruses on both days using the same recording schedule. At the conclusion of the experiment, we collected the memory cards from the recorders and archived the recordings at Algoma University.

To confirm that the experimental manipulation increased light levels along the ski trail, we used a light level meter (Extech Instruments model: Easyview 33) to take light intensity measurements at locations within the array. For recorders along the lit trail, these measurements were taken both when ski trail lights were off and when ski trail lights were on. The measurements were taken within five minutes of civil twilight. We took light level readings directly under the lamppost, and at distances of 10 m, 25 m, 50 m, and 75 m from the lamppost.

### *Analysis*

Using Syrinx-PC (J. Burt, Seattle, WA), we visualized spectrograms of the recordings. We identified the start of the dawn chorus for each unique individual of the four target species, distinguishing between different individuals on the basis of their position within the microphone array. We used the time and frequency cursors in Syrinx-PC to annotate the first song of each focal species on the morning prior to turning on the lights and the morning following light exposure, both for animals in the lit and non-lit sites. While annotating, we confirmed that each bird began singing continuously within five minutes of their first song to make sure that we were annotating the beginning of the dawn chorus rather than an errant nocturnal song. We then used these annotations to calculate dawn chorus start times relative to sunrise each day. We acquired astronomical twilight, nautical twilight, civil twilight and sunrise times from the National Research Council Canada sunrise/sunset calculator (http://www.nrccnrc.gc.ca/eng/services/sunrise/advanced.html).

### *Statistics*

We compared the experimental sites before and after the light manipulation using paired t-tests. We compared the experimental sites to the control site using an unpaired t-test. All data were normally distributed. Statistical analyses were conducted in JMP10 (SAS Institute Inc., Cary, NC, USA).

## Results

Light level measurements demonstrated that the experimental manipulation significantly increased the light intensity in the area immediately surrounding the lampposts (Figure 3.3).

Within the experimentally lit area, none of the four focal species showed a significant effect of short-term overnight light exposure. At the experimental site, American Robins did not sing significantly earlier after the light manipulation (paired t-test: t=1.5, p=0.19, n=7; Figure 3.4a). Similarly, Black-capped Chickadees did not sing significantly earlier after the light manipulation (t=0.8, p=0.44, n=13; Figure 3.4b). Chipping Sparrows showed no difference in dawn chorus start time after the light manipulation (t=1.0, p=0.36, n=11; Figure 3.4c). Likewise, Ovenbirds showed no difference in chorus start time after the light manipulation (t=1.1, p=0.34, n=6; Figure 3.4d).

Comparison to our control site, where no light manipulation took place, reveals that birds in the experimentally lit area began singing significantly earlier for only one of our focal species. American Robins began singing significantly earlier before sunrise in the experimental site following the light manipulation compared to the control site (unpaired t-test: t=2.4, p=0.04, n=7 experimental birds, 9 control birds). In contrast, the other three species showed no significant difference. Black-capped Chickadees showed no difference between the experimental and control site (t=0.2, p=0.82, n=13 experimental birds, 11 control birds). Likewise, Chipping Sparrows showed no difference between the experimental and control site (t=1.4, p=0.17, n=11 experimental birds, 6 control birds). Finally, Ovenbirds showed no difference between the experimental and control site (t=0.6, p=0.55, n=6 experimental birds, 11 control birds).

## Discussion

Our experimental manipulation of artificial light exposure did not produce compelling evidence that birds alter their dawn chorus start time in response to short-term changes in anthropogenic light levels. Although one of our four focal species showed an earlier start time following experimental light manipulation compared to a different control site, none of our four focal species showed an earlier dawn chorus start time in paired comparisons within the experimental area. These findings match the results of a study of European Robins, which found artificial light levels to be unimportant in dawn chorus song timing (Fuller et al. 2007). However, our results stand in contrast to previous findings that American Robins living in proximity to artificial light sources begin singing significantly earlier in the morning (Miller 2006). Additionally, more recent findings have demonstrated that overnight exposure to streetlights advanced dawn chorus start times for four European temperate species (Kempenaers et al. 2010). Taken together, the research on artificial light pollution has yielded mixed results on the anthropogenic effects of light pollution, with our findings demonstrating no substantial effect of artificial light.

There are several potential explanations for the results of our experiment. Firstly, it is possible that natural lighting variables are more important than artificial lighting characteristics in influencing animal behaviour. Research has demonstrated that factors such as moon brightness and cloud cover can affect dawn chorus start times for birds (e.g. Leopold and Eynon 1961, Pépin and Fouquet 1992, Chapter 2). Natural lighting regulates avian circadian rhythms (Dominoni et al. 2013). It is possible that artificial light is not sufficiently similar to natural light in quality, spectrum, dispersion, or intensity to influence singing behaviours of north temperate birds. Notably, natural lighting conditions appeared similar between the two days of study; on both days, cloud cover was dominant and light levels of precipitation occurred. Studies that measure levels of both natural and artificial lighting will be important in determining the relative biological importance of each.

Alternatively, our results could be attributed to the fact that light pollution is only important when occurring in conjunction with noise pollution. Anthropogenic noise can interfere with the propagation of the vocalizations of wildlife species (Fuller et al. 2007), and prior research has shown that noise pollution can be an important factor in song timing for some bird species. One study of Common Nightingales (*Luscinia* *megarhynchos*) found that male birds in noisier locations sang at relatively greater sound levels, suggesting that environmental background noise can influence energy expenditure and quality of avian song (Brumm 2004). Research on European Robins determined that artificial noise was a more influential factor than artificial light on timing of song (Fuller et al. 2007). Recently, another study demonstrated that House Sparrows (*Passer domesticus*) and Spotless Starlings (*Sturnus unicolor*) living near noisier streets began their dawn choruses significantly earlier than those living near quieter streets (Arroyo-Solis et al. 2013). Our study site is an area of very low noise pollution and, hence, this research provided the unique opportunity to study artificial light in the absence of artificial noise. We did not find evidence that dawn chorus start times of temperate birds are advanced in the presence of artificial light exposure in the field. It is possible that previous research suggesting otherwise could have been complicated by a simultaneous presence of artificial noise.

In contrast to our investigation, the results of previous studies may have been influenced by a propensity for earlier-singing migratory birds to be more likely to settle near sources of artificial light. Past studies have only been able to compare the dawn chorus start times of birds singing near light sources to those singing away from light sources (e.g., Kempenaers et al. 2010). In our study, we waited until birds were settled into unlit breeding territories before beginning the lighting manipulation. Our results demonstrated no significant differences in singing before and after lights were turned on, suggesting that this could have been a confounding factor in previous research on the influence of artificial light on dawn chorusing.

Our study also had some limitations that may have affected our results. We only assessed dawn chorus start times on the day immediately prior to light exposure, and on the morning following overnight artificial light exposure. If exposure to artificial lighting gradually alters dawn chorusing over a period of time, our experiment would have been unable to capture these changes due to our limited sampling window. Future investigations in this system will involve leaving the lights on for several consecutive days to determine whether length of time exposed to anthropogenic light might induce a response.

Additionally, measurements taken with a light level meter indicated that the ski trail lights greatly increased ambient light levels directly around the light posts and at a distance of 10 m from the posts. However, measurements taken at 25, 50, and 75 m from the light posts were similar whether the artificial lights were turned on or off. In a study using streetlights, light levels continued to be recognizable up to 50 m from the light sources (Kempenaers et al. 2010). For this reason, birds may have only had the opportunity to be influenced by the lights if they were in the immediate proximity of the lampposts. Future research in this system will triangulate exact positions of each singing bird, and allow an assessment of whether distance from the artificial light source may explain variation in response.

Furthermore, we assumed that ski trail lights were an appropriate proxy for city lights. If the ski trail lights emit lower intensities of artificial light than city streetlights, this could indicate that there is a certain threshold level of light pollution required to alter avian vocalization behaviour. This could account for the fact that significant influences of artificial light have been found in previous investigations involving city streetlights, but were not seen in our experiment when considering ski trail lights. If this threshold level exists, city planners could aim to stay below a certain degree of light when urbanizing previously natural animal habitats in order to avoid disrupting local wildlife.

Although we found no significant changes in our four focal species in pairwise analyses before and after the light manipulation, one of the four focal species, American Robins, showed an earlier dawn chorus start time in the artificially lit area compared to the off-site control area. This difference may have arisen because different individuals show a propensity to initiate the dawn chorus at different times according to factors such as breeding stage, microhabitat differences, or bird density (Leopold and Eynon 1961, Mace 1987, Thomas et al. 2002). Past research on the influence of light pollution on bird song has found differences in robin chorus start times (Miller 2006), suggesting that this species might be more sensitive than others to the influence of anthropogenic light. Additional research regarding the influence of lighting variables, such as moonlight and cloud cover, on American Robin dawn chorusing has demonstrated that this species is affected by natural lighting as well (Leopold and Eynon 1961, Chapter 2). However, results of our key comparison of American Robins in the lit area before and after the experiment suggest that the effect of artificial light on dawn chorus timing for this species is not an overwhelming one.

Overall, although we did not find an appreciable effect of short-term experimental light manipulation, our study provided unique opportunities to study artificial light in the absence of artificial noise, and to manipulate light exposure in the field once birds were already settled into their breeding territories. This study has conservation implications because, with increasing global urbanization, it is important for us to understand the influence of anthropogenic noise and light on animal behaviour. Animal communication is crucial for fitness, so continuing to research the effects of noise and light pollution on vocalization patterns is important for the well-being of wild animals found in proximity to anthropogenically-modified habitats.

## Acknowledgements

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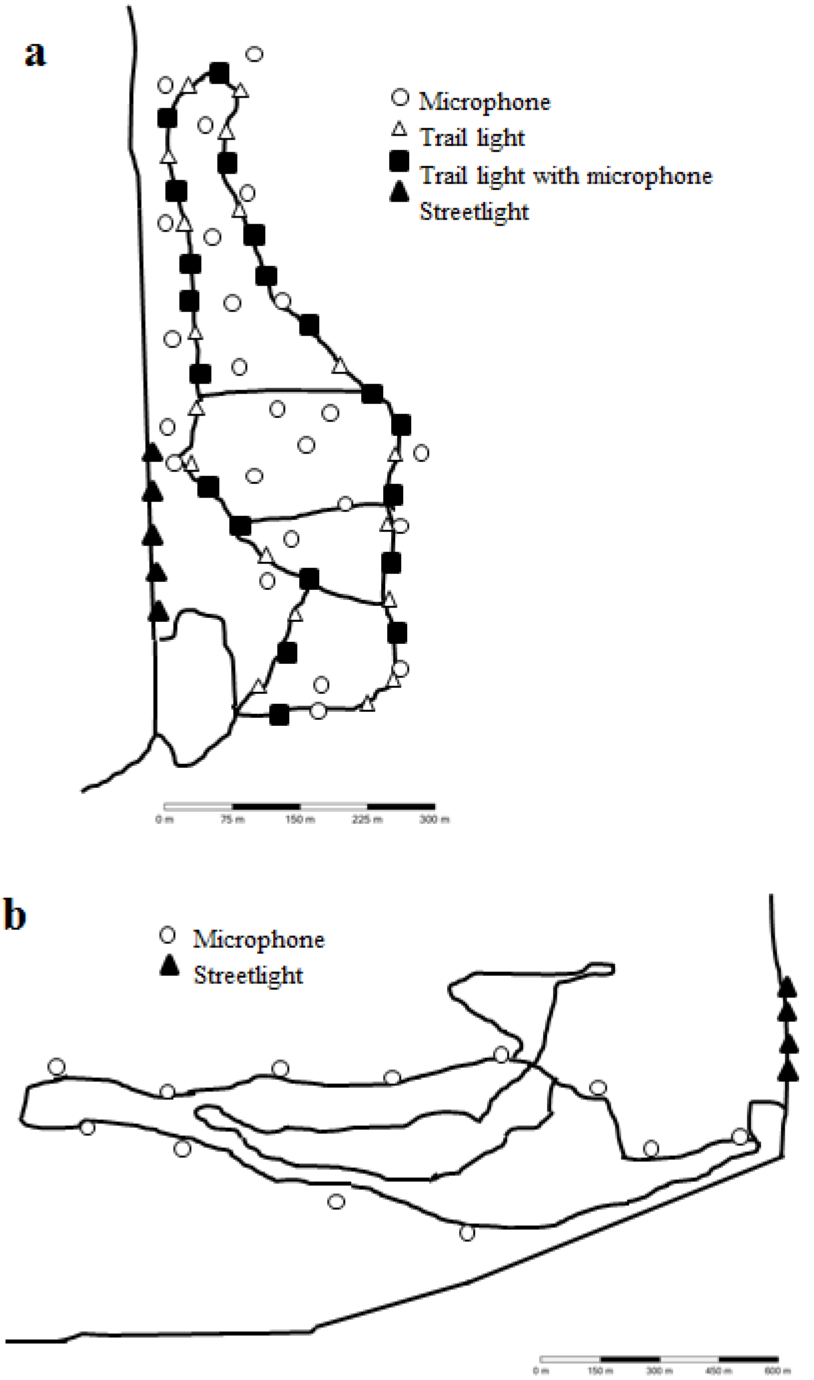

**Figure 3.1.** Maps of (a) array set-up on the Kinsmen Cross Country Ski trail, our experimental site and (b) recorder locations on the adjacent non-lit trail, our control site, both in Sault Ste. Marie, Ontario.

**Figure 3.2.** Photo of automated digital recorder mounted on a ski trail light. Recorders were secured to posts at a height of approximately 4.0 m along the Kinsmen Cross Country Ski trail in Sault Ste. Marie, Ontario. A white arrow points to the recorder.

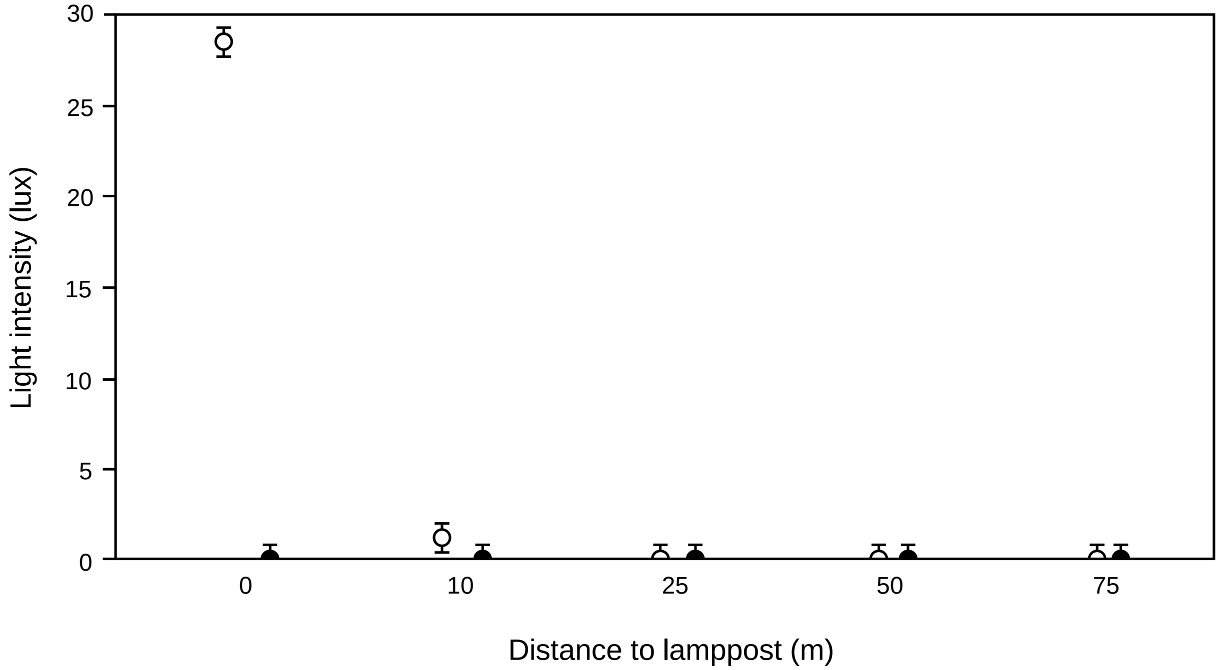

**Figure 3.3.** Light intensity on the trail was significantly higher when the lights were on at zero and ten m from the lights. This graph shows light intensity measurements taken with a light level meter while the ski trail lights were on (white circles) and off (black circles) at civil twilight.

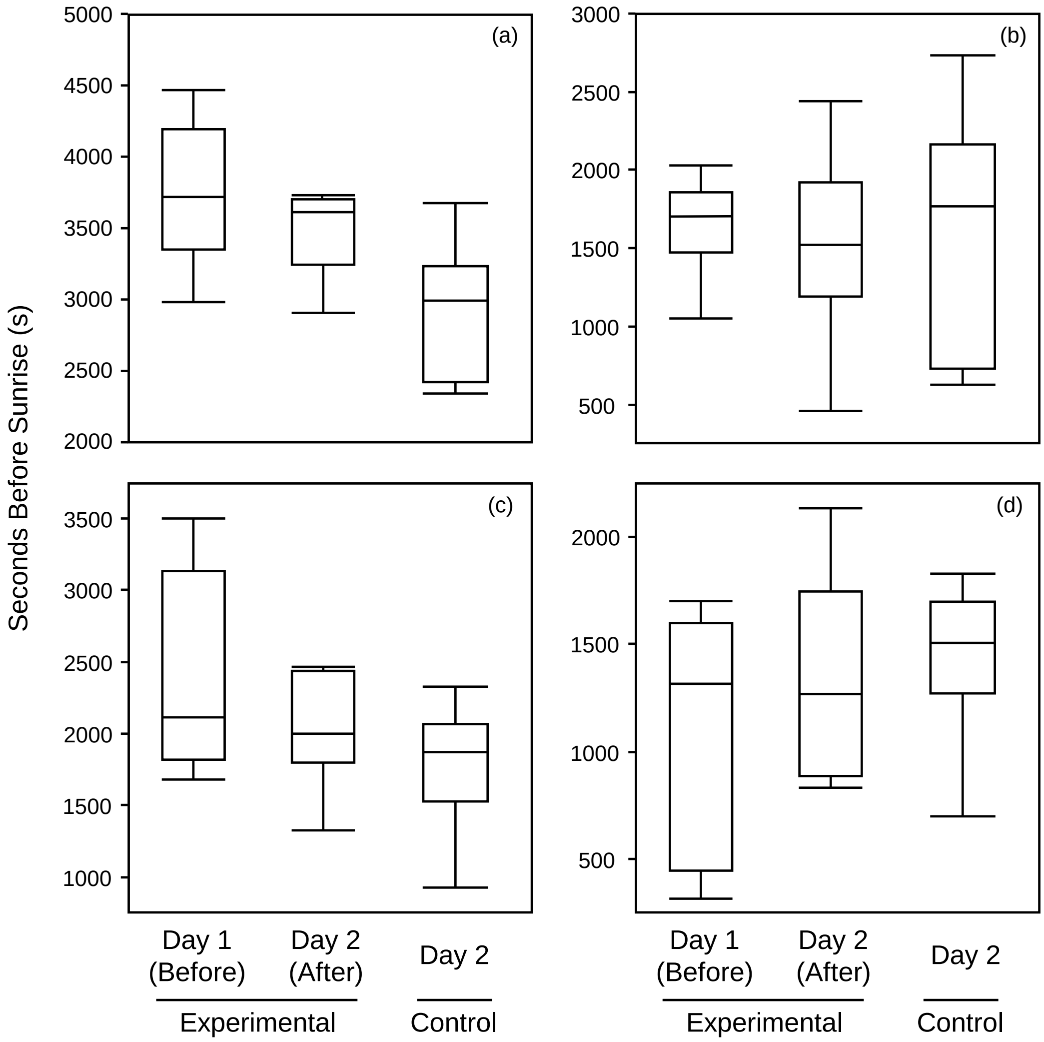

**Figure 3.4.** We found no significant differences between dawn chorus start time before and after the ski trail lights were turned on for (a) American Robins (N=7 experimental birds, 9 control birds), (b) Black-capped Chickadees (N=13 experimental birds, 11 control birds), (c) Chipping Sparrows (N=11 experimental birds, 6 control birds), or (d) Ovenbirds (N=6 experimental birds, 11 control birds.. American Robins begin singing significantly earlier on the lit trail when the lights were on compared to on the unlit trail, but this was not the case for the other three species. Boxes represent 25th, 50th, and 75th percentile, and whiskers show the full range of data.

# Chapter 4

# General Discussion

Vocal communication has important fitness consequences for many animals (McGregor 2005). Bird song is a well-recognized example of a vocal communication behaviour that has been studied extensively across many avian species (Bradbury and Vehrencamp 1998). Several decades of research has determined that bird song primarily functions in mate attraction and territory defense (Catchpole and Slater 2008). More enigmatic are the specific functions of the avian dawn chorus (Staicer et al. 1996), a daily period of high song output performed by birds prior to sunrise during the breeding season (Mace 1987). A review by Cynthia Staicer et al. (1996) suggested that the dawn chorus occurs for a combination of non-mutually exclusive intrinsic, environmental, and social purposes. Continuing to study the avian dawn chorus is important because changes in chorus characteristics have been shown to have fitness consequences (Dalziell and Cockburn 2008, Kempenaers et al. 2010).

An interesting feature of the avian dawn chorus is that different species living within a similar area begin singing in a non-random order (Thomas et al. 2002). These fascinating chorus dynamics are not yet well-understood. Although intrinsic factors such as reproductive stage and eye size may influence dawn chorus timing (Mace 1987, Thomas et al. 2002), a number of extrinsic factors have also been suggested to influence dawn chorus start time for bird species, and these have not yet been studied in detail in North American songbirds. These extrinsic factors include time of year, time of sunrise, moon brightness, cloud cover, precipitation, and ambient temperature (Allen 1913, Davis 1958, Slagsvold 1977, Thomas 1999, Miller 2006). In Chapter 2 of my thesis, I considered these extrinsic variables in relation to dawn chorus start times for six north temperate bird species. My results demonstrated that different extrinsic factors are important in affecting dawn chorus onset for different species. Typically, birds began singing earlier when the moon was brighter and when ambient temperature at nautical twilight was higher. Birds tended to begin singing significantly later when cloud cover and precipitation were present in the early morning. Based on the mean start times of each species, I found that Alder Flycatchers (*Empidonax alnorum*) began singing their dawn choruses earliest, followed in order by Song Sparrows (*Melospiza melodia*), White-throated Sparrows (*Zonotrichia albicollis*), American Robins (*Turdus migratorius*), Eastern Phoebes (*Sayornis phoebe*), and Black-capped Chickadees (*Poecile atricapillus*). These findings on dawn chorus onset provide us with a more comprehensive understanding of the effects of extrinsic environmental factors on the behaviour of birds in a north temperate avian community.

Other extrinsic factors that have the potential to influence avian dawn chorus timing include anthropogenic noise and light (Ditchkoff et al. 2006). However, previous research has been challenged with a difficultly in separating the effects of artificial noise and artificial light. Additionally, most past studies have been limited to comparing the chorus timing of birds that had either previously settled near noise or light sources or far away from them. In Chapter 3 of my thesis, I experimentally manipulated artificial light in the absence of artificial noise by using lights along a cross country ski trail in Sault Ste. Marie, Ontario. I recorded dawn choruses on a day while the trail lights were turned off, and on the following day when the trail lights were turned on to simulate the light pollution that would typically be experienced by birds living near human development. My results revealed no significant differences between dawn chorus start times at the experimental site before and after the lights were turned on for any of the four focal species. In comparison to a nearby control site, American Robins at the experimental site began singing significantly earlier, but this was not the case for the other three species. Overall, the results of this experiment suggest that, in the absence of noise pollution, short-term exposure to artificial light does not alter dawn chorus start times for four north temperate songbird species.

Taken together, my two data chapters provide valuable information regarding the influences of natural and artificial extrinsic variables on the start time of the avian dawn chorus. My results confirm that different bird species are affected by different extrinsic factors, and these factors may help to explain the established interspecific differences in dawn chorus onset. In addition, my results suggest that, for north temperate bird species, natural lighting appears to be a greater influence on dawn chorus onset than artificial lighting. The descriptive study in Chapter 2 is unique because it represents the first comprehensive study of dawn chorus start time variation in North American birds. The size of the data set used in Chapter 2 also makes the research unique, as I annotated songs of six species recorded at 13 different locations over the course of an entire breeding season; dawn chorus research typically involves short-term monitoring (e.g., Welling et al. 1995, Berg et al. 2006) with a single site covered each morning (e.g. Thomas et al. 2002). The experimental study in Chapter 3 is unique because it is the first study to manipulate artificial light in the field in relation to avian dawn chorusing. Additionally, this study allowed me to study the influence of anthropogenic light in the absence of anthropogenic noise. Further, it enabled me to eliminate the possibility that earlier-singing birds are more likely to settle near light sources, given that the experimental manipulation did not occur until birds had already settled into their breeding territories.

The results in my thesis raise many questions for future investigations. In Chapter 2 I showed that different species, even within the same area, are influenced by different extrinsic factors. Similar research using different groups of bird species would be an important next step towards understanding whether closely related bird species are influenced by similar extrinsic factors. Additionally, looking at both extrinsic and intrinsic factors would be interesting in the future, to explore the relative importance of the extrinsic factors I investigated here versus other, intrinsic features. For example, incorporating data on eye size and breeding stage into research on dawn chorus start time would provide an increasingly comprehensive picture of interspecific chorus dynamics, although such research will necessarily be challenging and time consuming. In Chapter 3, I found that short-term artificial light exposure did not alter dawn chorus start times for four species when considering the day before and the day after overnight experimental light treatment. There is much room for expanding this research approach in future investigations. (1) Future research should analyze the effect of leaving lights on for a longer period of time, because the effect of anthropogenic light pollution on dawn chorus start time might occur more gradually than on the first day after treatment. (2) Future studies should also consider whether proximity to artificial light sources has an influence on presence of a response; animals that are closest to light sources are the most likely candidates for showing an effect of anthropogenic light. (3) Instead of turning the lights on overnight, turning lights on only one or two hours prior to sunrise would represent a different way to manipulate light exposure. This approach might simulate an earlier-than-normal sunrise instead of overnight anthropogenic light pollution, and might thereby provide insight into how much light is critical for initiating the dawn chorus. Importantly, this unique experimental design, involving cross country ski trail lights, opens the doors for many future investigations.

Research on the dawn chorus is important for understanding the behavioural rhythms of wild animals. Furthermore, wildlife habitats are being modified and developed for human use; consequently, understanding patterns of animal behaviour, and the variables that influence it, will help enable us to quantify and possibly mitigate the effects of human development. The dawn chorus has fitness implications for avian species (e.g., Dalziell and Cockburn 2008) and, therefore, it is an important area of research in evolutionary ecology. My thesis research sheds new light on the extrinsic factors, both natural and artificial, that affect dawn chorus start times of temperate songbirds.

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