

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

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Abstract The avian dawn chorus is a daily period of high song output performed predominantly during the breeding season. Dawn chorus performance varies at both the individual and species level. 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 ambient temperature, precipitation, cloud cover, lunar phase, and Julian date for six common bird species living in a northern temperate rural area. Overall, birds began singing earlier with full or third quarter moon (when moonlight is present at dawn) and with increasing temperature at nautical twilight, and birds began singing later with the presence of cloud cover and precipitation. Our results indicate that a different suite of environmental factors influenced the chorus start times of different species and to different degrees. Alder flycatchers begin singing earliest in this group of birds, followed by Song Sparrows, White-throated Sparrows, American Robins, Eastern Phoebe, and Black-capped Chickadees. This investigation reveals that extrinsic abiotic factors have a significant effect on the dawn chorus start times of north temperate

birds, and represents the first comprehensive study of dawn chorus start time variation in North American birds.

Keywords Ambient light · Animal behaviour · Dawn chorus · Phenology of song · Temperate birds · Weather

Zusammenfassung

Variation im Beginn des Morgengesangs in einer Brutvogelgemeinschaft gemäßigter Zonen: Beziehungen mit Saisonalität, Wetter und Umgebungslicht

Der Morgengesang von Vögeln ist täglich eine Periode hoher Gesangsaktivität vorwiegend während der Brutzeit. Die Darbietung des Morgengesangs variiert sowohl auf dem Individuen- als auch auf dem Artniveau. Den vielen extrinsischen Faktoren, mit denen der Beginn des morgendlichen Gesangs verschiedener nordamerikanischer Vogelarten zusammenhängt, wurde wenig Beachtung geschenkt. In dieser Studie betrachten wir die Zusammenhänge zwischen dem Beginn des Morgengesangs und der Umgebungstemperatur, Niederschlag, Bewölkung, Mondphase und Julianisches Datum für sechs verbreitete Vogelarten in einem nördlichen gemäßigten ländlichen Gebiet. Insgesamt begannen die Vögel früher zu singen bei Voll- oder Dreiviertelmond (Mondlicht noch in der Dämmerung) und mit ansteigender Temperatur während der nautischen Dämmerung. Die Vögel begannen später zu singen bei Bewölkung und Niederschlag. Unsere Ergebnisse deuten darauf hin, dass unterschiedliche Umweltfaktoren den Gesangsbeginn verschiedener Arten in unterschiedlicher Weise beeinflussen. Erdtrollen beginnen am frühestens mit dem Gesang, gefolgt von Singammer, Weißkehlammer, Wanderdrossel, Weißbauch-Phoebetryann und Schwarzkopfmeise. Die Untersuchung zeigte, dass extrinsische abiotische Faktoren einen

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signifikanten Effekt auf den Beginn des Morgengesangs von Vögeln nördlicher gemäßigter Zonen haben. Diese Studie ist zudem die erste Umfassende zu Variationen im Beginn des Morgengesangs nordamerikanischer Vögel.

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). The timing of the dawn chorus is likely the result of a number of social, environmental, and intrinsic factors (Staicer et al. 1996). Many of the hypothesized social benefits to singing in the early morning may be applicable to all species that sing a dawn chorus (Staicer et al. 1996). Intrinsic factors such as reproductive stage and eye size may influence the timing of the dawn chorus within and among species (e.g. Mace 1987; Berg et al. 2006). Environmental factors such as time of year, time of sunrise, moon brightness, cloud cover, precipitation, and ambient temperature could also affect the timing of the dawn chorus (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. Early work on Willow Warblers (*Phylloscopus trochilus*) revealed that during the first half of the breeding season, birds begin the dawn chorus earlier as sunrise becomes progressively earlier (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.

Although sunlight is widely considered the proximate cue that initiates the dawn chorus (Thomas et al. 2002), moonlight may also affect dawn chorus onset (Leopold and Eynon 1961). Moon brightness depends on moon stage; a full moon is approximately ten times brighter than a quarter moon (Russell 1916). A recent study of White-browed Sparrow Weavers (*Plocepasser mahali*) found males sing earlier when the moon is full and above the horizon at dawn (York et al. 2014) while a recent study of American Robins (*Turdus migratorius*) did not find any correlation between moonlight and chorus start time in the field (Miller 2006). Studies of overnight artificial light exposure reveal that higher ambient light levels alter dawn chorus 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. Additional studies that encompasses several lunar cycles will be an important next

step in understanding the influence of moonlight on dawn song.

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. Cloud may result in a later start of dawn chorus performance if extensive cloud cover delays the increase in light level associated with twilight. In an urban environment, this relationship might be reversed, because cloud cover can 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 they begin their dawn chorus performance. Although this seems intuitive, one empirical study found no relationship between daily song output and precipitation for more than 20 bird species in Norway (Slagsvold 1977). In a more recent study, however, the 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 the evening, to ensure overnight survival in the face of unpredictable overnight conditions; when they find themselves with an energy surplus at dawn, an extended bout of song may facilitate metabolism of the excess fat (Staicer et al. 1996). An inherent problem with this hypothesis, however, is that flight is a more energetically-expensive activity than song (Gil and Gahr 2002) and should, therefore, be a more efficient method of quickly 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 European Robins (*Erithacus rubecula*; 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.

Here, we examine the relationships between dawn chorus start times and Julian date, lunar stage, 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 the dawn chorus (Thomas et al. 2002; McNeil et al. 2005; Miller 2006), we predicted that birds would begin singing earlier when the moon was above the horizon at 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 dawn chorus onset (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. This investigation 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 the rural community of Echo Bay, Ontario (46°29'N, 84°4'W) between April and July 2012. We used automated digital recorders (model: Song Meter SM2, Wildlife Acoustics) programmed to start recording from 0 to 25 min before twilight and continue for six hours each morning. Recording start time was adjusted to ensure we picked up the earliest singing throughout the season. 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 deployed in the field beginning on 3 April 2012 (mean deployment date 26 April 2012; range 3 April 2012–25 May 2012; 55.6 ± 22.6 days recorded/recorder). Recorders were placed in locations where our six target species were known to occur: Eastern Phoebes (*Sayornis phoebe*), Alder Flycatchers (*Empidonax alnorum*), Black-capped Chickadees (*Poecile atricapillus*), American Robins (*Turdus migratorius*), Song Sparrows (*Melospiza melodia*), and White-throated Sparrows (*Zonotrichia albicollis*). All species were recorded at all 13 sites, except Black-capped Chickadees which were recorded at 12 of 13 sites. Adjacent recorders were placed at

least 200 m apart to ensure that there was no overlap between individuals recorded at neighbouring sites (mean distance to the nearest recorder: 350 ± 12.6 m; range 200–450 m). 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 (see Figure S1 for example sound spectrograms). We annotated the start time of all six focal species on every possible calendar day between 3 April 2012 and 10 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). However, because recorder location varied in exposure to prevailing wind and rain, no songs were recorded at any recorder on only two days (10 April and 24 June 2012). After 10 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 assume the same birds singing in the same areas were the resident animals. We standardized times of first song by calculating start times relative to nautical twilight; we acquired twilight times from the National Research Council of Canada for Sault Ste. Marie, ON, Canada. Moon stage information was collected from the Moon Phase Calculator (<http://www.timeanddate.com/calendar/aboutmoonphases.html>). We divided the lunar cycle into four periods: new moon, first quarter, full moon and third quarter. We began each stage at the midpoint between that stage and the previous stage (e.g., new moon began half way between third quarter and new moon and ended half way between new moon and first quarter). This is in accordance with similar methodology used in other studies of moonlight's influence on animal behaviour (e.g., Julien-Laferrière 1997). We compared the six species' dawn chorus start times against weather 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 and 0600 h daily and categorically designated the sky each as either cloudy or clear at dawn. We also used Environment Canada data to record the presence or absence of precipitation and to determine the 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

To test for the effects of Julian date, weather, and variation in lunar stage on dawn chorus start time we used linear mixed effects models with recorder location as a random effect and Julian date, cloud cover (present or absent), precipitation (present or absent), temperature, moon stage (new, first quarter, full, second quarter) 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. In these models, the sample size reflects the total number of dawn chorus recordings where a focal species was recorded. Table S2 shows correlation estimates among fixed effects. Date and temperature were significantly correlated; however, the effects of the two variables were often had opposite effects and for species where species where both factors were important, we included both terms in the model. Because the data for all six species were from the same recording data set, we consider results significant at the Bonferonni corrected alpha level of $p < 0.0083$. For all statistical analyses, we used JMP11 (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 our six focal species, Alder Flycatchers begin their dawn choruses the earliest, followed by Song Sparrows, White-throated Sparrows, American Robins, Eastern Phoebes, and Black-capped Chickadees (Figure S2). We present results in order from earliest- to latest-singing species.

Alder Flycatcher

Based on linear mixed effects models, the best model explained 33.5 % of variation in dawn chorus start time of

Alder Flycatchers ($p < 0.0001$; $n = 352$). Differences between males at different recording sites accounted for 32.0 % of the model's chorus start time variance for this species. No fixed effects significantly related to Alder Flycatcher dawn chorus start time (Table 1; Figs. 1a, 2, 3, 4, 5a). However, moon stage contributed significantly to the best model for this species. Males tended to begin singing earlier when the moon was closer to full or in the third quarter (Fig. 4a).

Song Sparrow

The best model explained 24.7 % of variation in dawn chorus start time of Song Sparrows ($p < 0.0001$; $n = 688$). Differences between males at different recording sites accounted for 15.4 % of the model's chorus start time variance for this species (Fig. 2b). Song Sparrows began their dawn chorus significantly earlier when the moon was full (Table 1, S2; Figs. 4b). Song sparrows began singing significantly later when precipitation was present and when it was warmer (Table 1, S2; Figs. 1b, 2b). There was a significant interaction between temperature and precipitation such that the effect of precipitation was most apparent at cold temperatures. Julian date also contributed significantly to the model with dawn chorus start time becoming later relative to twilight as the season progressed (Table 1; Fig. 5b). Song Sparrow dawn chorus start time was not significantly influenced by cloud cover (Fig. 3b).

White-throated Sparrow

The best model explained 57.2 % 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 38.8 % of the model's chorus start time variance for this species. White-throated Sparrows began singing significantly later when cloud cover was present (Table 1, S2; Fig. 3c). Dawn chorus onset was earlier when it was warmer or when there was precipitation, although not significantly so (Table 1, S2; Figs. 1c, 2c). White-throated Sparrows sang earlier when the moon was in the third quarter (Fig. 4c), however, there were significant interactions between moon stage and both temperature and precipitation; birds sang earlier when there was a full moon and no precipitation, and under a third-quarter moon when temperatures were colder (Table 1, S2; Fig. 4c). Julian date was significantly related to dawn chorus start time of White-throated Sparrows (Table 1; Fig. 5c).

American Robin

The best model explained 45.0 % of variation in dawn chorus start time of American Robins ($p < 0.0001$;

Table 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	Effect	Estimate of effect (\pm SE)	<i>F</i>	<i>DF</i>	<i>P</i>	Dawn chorus begins earlier
Alder Flycatcher	Moon stage	2.14 \pm 0.75	-1.56	338.6	0.015	
		-1.8 \pm 0.79				
		-0.71 \pm 0.73				
Song Sparrow	Julian date	0.18 \pm 0.03	43.53	674.9	<0.0001*	Earlier in the season
	Temperature	-0.43 \pm 0.13	11.59	668.1	0.0007*	With warmer temperature
	Precipitation	-3.01 \pm 0.81	13.86	669	0.0002*	With no precipitation
	Moon stage		8.48	670.1	<0.0001*	During full moon
	New to 3rd quarter	1.62 \pm 0.79				
	3rd quarter to full	-0.77 \pm 0.83				
	Full to 1st quarter	-3.46 \pm 0.81				
	Temperature \times precipitation	0.44 \pm 0.10	18.45	667.6	<0.0001*	With warm or cold and no precipitation
White-throated Sparrow	Julian date	0.50 \pm 0.04	159.19	546.1	<0.0001*	Earlier in season
	Temperature	-0.22 \pm 0.15	2.17	545.2	0.1415	
	Precipitation	-2.46 \pm 1.10	4.99	545.2	0.0259	
	Cloud cover	-1.95 \pm 0.71	7.48	545	0.0065*	With clear sky
	Moon stage		5.35	544.9	0.0012*	During third quarter
	New to 3rd quarter	0.311 \pm 1.51				
	3rd quarter to full	-7.48 \pm 1.88				
	Full to 1st quarter	4.49 \pm 2.46				
	Moon stage \times temperature		13.22	545.5	<0.0001*	During full moon/third quarter when it is colder
	New to 3rd quarter	-0.87 \pm 0.17				
	3rd quarter to full	0.47 \pm 0.20				
	Full to 1st quarter	0.81 \pm 0.20				
	Moon stage \times precipitation		7.86	545.2	<0.0001*	During full moon with no precipitation and when precipitation in third quarter
	New to 3rd quarter	-0.72 \pm 1.49				
	3rd quarter to full	9.01 \pm 1.87				
	Full to 1st quarter	-6.54 \pm 2.33				
Moon stage \times cloud		3.22	544.7	0.0224		
New to 3rd quarter	-3.38 \pm 1.24					
3rd quarter to full	-0.32 \pm 1.22					
Full to 1st quarter	0.68 \pm 1.18					
American Robin	Temperature	0.15 \pm 0.06	5.92	668.7	0.0152	
	Precipitation	-2.98 \pm 0.51	34.34	666.9	<0.0001*	With no precipitation
	Cloud cover	-1.79 \pm 0.34	28.17	666.6	<0.0001*	With clear sky
	Moon stage		12.16	668	<0.0001*	During third quarter
	New to 3rd quarter	1.42 \pm 0.49				
	3rd quarter to full	-0.83 \pm 0.51				
	Full to 1st quarter	-2.42 \pm 0.50				
	Temperature \times precipitation	0.24 \pm 0.06	14.53	666.4	0.0002*	With cold temperature and no precipitation

Table 1 continued

Species	Effect	Estimate of effect (\pm SE)	<i>F</i>	<i>DF</i>	<i>P</i>	Dawn chorus begins earlier
Eastern Phoebe	Julian date	0.20 \pm 0.03	45.49	547.7	<0.0001*	Earlier in season
	Temperature	-0.32 \pm 0.12	7.78	543.2	0.0055*	With warmer temperature
	Precipitation	-3.59 \pm 0.96	14	541.8	0.0002*	With no precipitation
	Moon stage		2.44	543.2	0.064	
	New to 3rd quarter	-2.69 \pm 1.25				
	3rd quarter to full	-1.95 \pm 1.64				
	Full to 1st quarter	3.39 \pm 1.97				
	Temperature \times julian	0.01 \pm 0.003	8.42	544.9	0.0039*	When warm earlier in the season
	Moon stage \times precipitation		2.45	541.9	0.062	
	New to 3rd quarter	2.22 \pm 1.22				
	3rd quarter to full	0.91 \pm 1.64				
	Full to 1st quarter	-4.97 \pm 1.96				
	Black-capped Chickadee	Julian date	0.27 \pm 0.03	87.22	326.1	<0.0001*
Precipitation		-3.88 \pm 0.88	19.5	315.3	<0.0001*	With no precipitation
Cloud cover		-0.98 \pm 0.52	3.58	315.3	0.059	
Moon stage			8.27	315.6	<0.0001*	During first and third quarter
New to 3rd quarter		-0.21 \pm 1.13				
3rd quarter to full		-3.91 \pm 1.50				
Full to 1st quarter		8.17 \pm 1.73				
Moon stage \times precipitation			11.88	315.2	<0.0001*	During full moon and no precipitation
New to 3rd quarter		2.55 \pm 1.12				
3rd quarter to full		3.60 \pm 1.50				
Full to 1st quarter	-10.29 \pm 1.73					

*Indicates a significant fixed effect at the Bonferroni corrected level of $p < 0.0083$

$n = 687$). Differences between males at different recording sites accounted for 37.9 % of the variance for this species. American Robins sang significantly earlier when the moon was full or in the third quarter (Table 1, S2; Fig. 4d). American robins began singing significantly later with both presence of cloud cover (Table 1, S2; Fig. 3d) and precipitation (Table 1, S2; Fig. 2d). They sang earlier when temperature at nautical twilight was colder, though not significantly (Table 1, S2; Fig. 1d). A significant interaction between temperature and precipitation was found (Table 1, S2); robins began singing earlier when it was colder when it was not raining. There was less variation in start time at warm temperatures whether or not it was raining. Julian date did not relate to dawn chorus start time in American Robins (Fig. 5d).

Eastern Phoebe

The best model explained 36.1 % of variation in start times of Eastern Phoebes ($p < 0.0001$; $n = 563$). Differences

between males at different recording sites accounted for 23.9 % of the model's chorus start time variance for this species. Eastern Phoebes began singing their dawn choruses significantly earlier with increasing temperature at nautical twilight (Table 1; Fig. 1e), but began singing significantly later when precipitation was present (Table 1, S2; Fig. 2e). For Eastern Phoebes, the date contributed significantly to the model both independently and through an interaction with temperature (Table 1; Fig. 5e); phoebes began singing later as the season progressed and earlier when it was warmer. Their interaction between Julian date and temperature reflected a stronger influence of temperature on dawn chorus start time earlier in the season (Table 1; Figs. 1e, 5e). Eastern Phoebe dawn chorus start time was not significantly influenced by moon stage. However, both moon stage and a moon stage by precipitation interaction contributed to the best model for this species (Table 1, S2; Fig. 4e). Males tended to sing later in the third quarter compared to other stages when precipitation was absent.

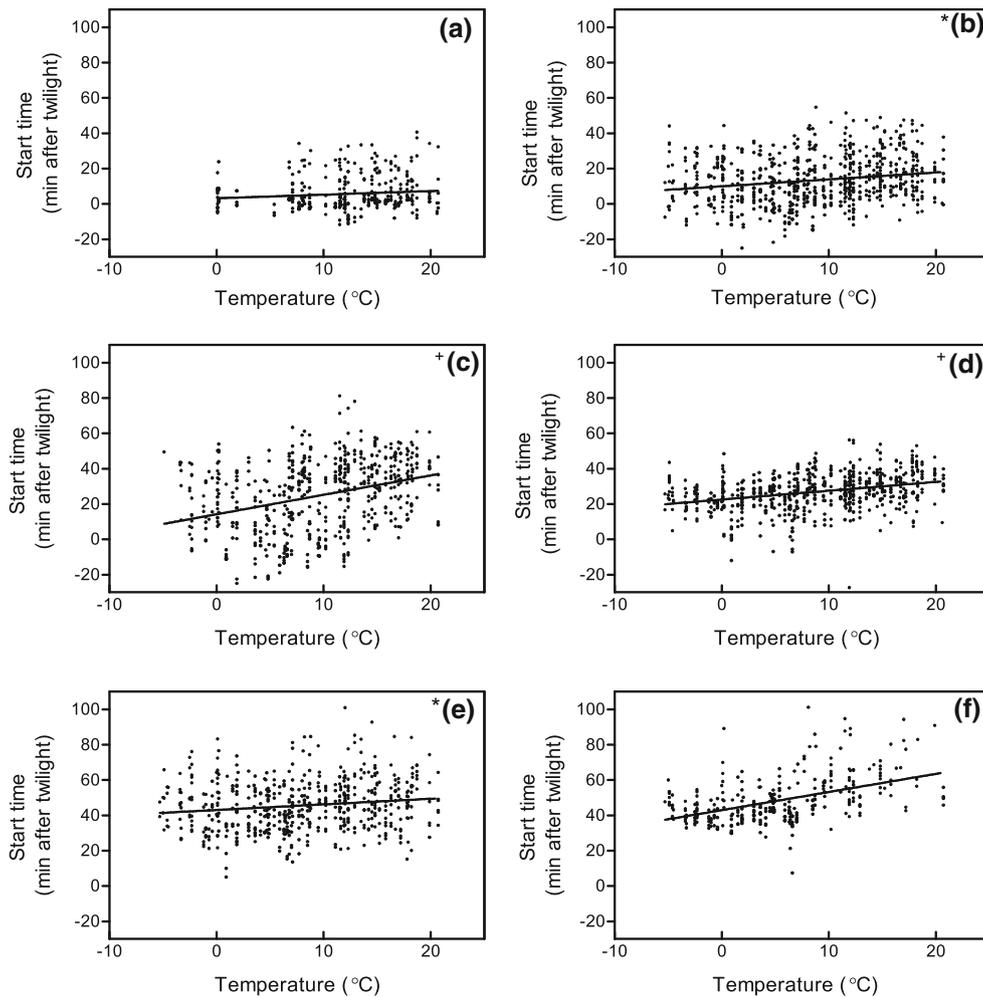


Fig. 1 Relationship between dawn chorus start time and temperature at nautical twilight for six north temperate bird species: **a** Alder Flycatcher, **b** Song Sparrow, **c** White-throated Sparrow, **d** American

Robin, **e** Eastern Phoebe, and **f** Black-capped Chickadee. A line of best fit is plotted to show direction of the relationship and *each dot* represents an annotated day at one recorder location

Black-capped Chickadee

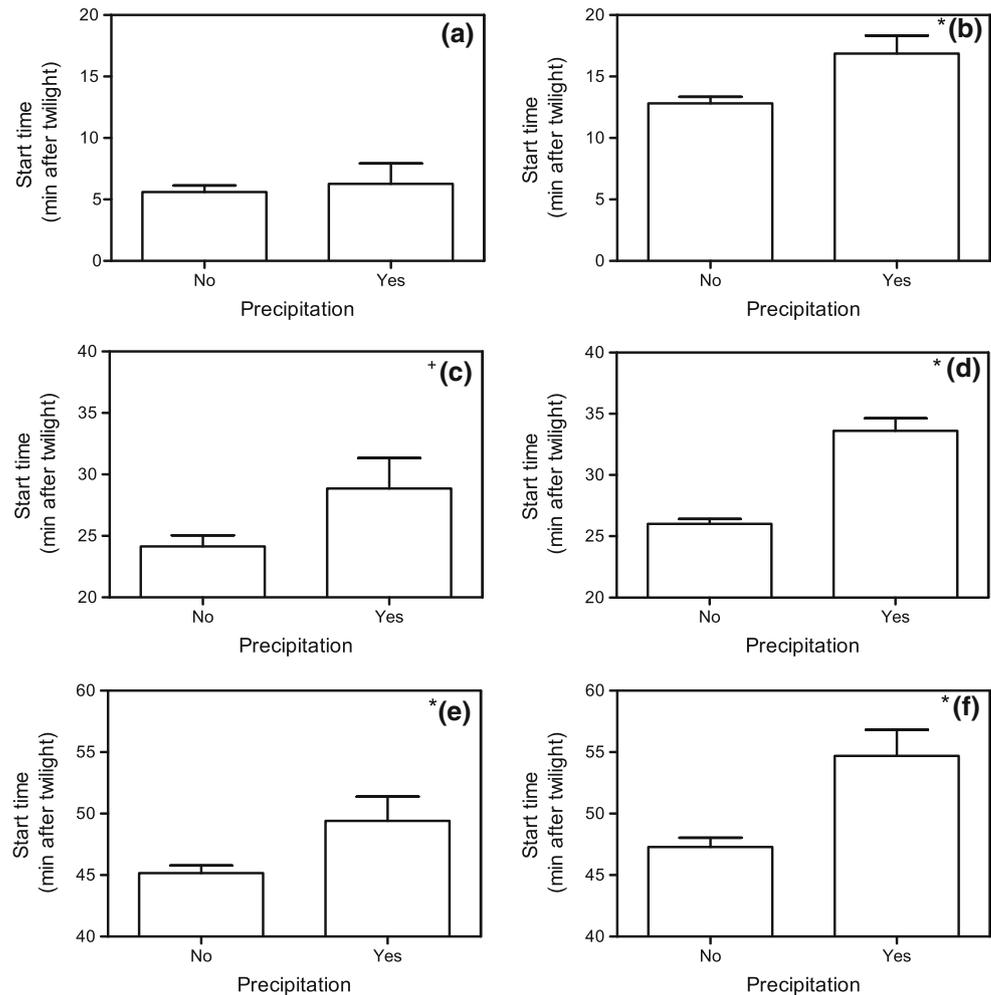
The best model explained 62.8 % of variation in dawn chorus start time in Black-capped Chickadees ($p < 0.0001$; $n = 337$). Differences between males at different recording sites accounted for 59.1 % of the model’s chorus start time variance for this species. Black-capped Chickadees began singing significantly later with precipitation in the early morning (Table 1, S2; Fig. 2f). Surprisingly, moon stage had a significant effect where Black-capped Chickadees sang later under a full moon. However, a significant interaction between moon stage and precipitation revealed the earliest singing was at full moon when there was no precipitation (Table 1, S2; Fig. 4f). Black-capped Chickadees tended to sing earlier when the sky was clear, though the relationship was not significant (Fig. 3f). Black-capped chickadee dawn choruses start time was significantly

influenced by date with song being earliest in the middle of the recording period (Table 1; Fig. 5f).

Discussion

Our analysis of the dawn chorus singing behaviour of six north temperate bird species reveals that dawn chorus start time varies significantly with extrinsic factors including weather, date, and lunar phase. Temperate songbirds living in a non-urban habitat commence their dawn chorus performance earlier when the moon is above the horizon at dawn (four of six species), and with increasing temperature at nautical twilight (two species). Birds begin their dawn chorus performance later when it is raining (four of six species) or when there is increasing cloud cover (two of six species). Dawn chorus initiation times vary with date (four

Fig. 2 Mean (\pm standard error) dawn chorus start time relative to nautical twilight when precipitation was present or absent at twilight for six north temperate bird species: **a** Alder Flycatcher, **b** Song Sparrow, **c** White-throated Sparrow, **d** American Robin, **e** Eastern Phoebe, and **f** Black-capped Chickadee. Values are in minutes after nautical twilight and thus lower values represent earlier singing. All y-axes are standardized to 20 min intervals, though the interval differs among species



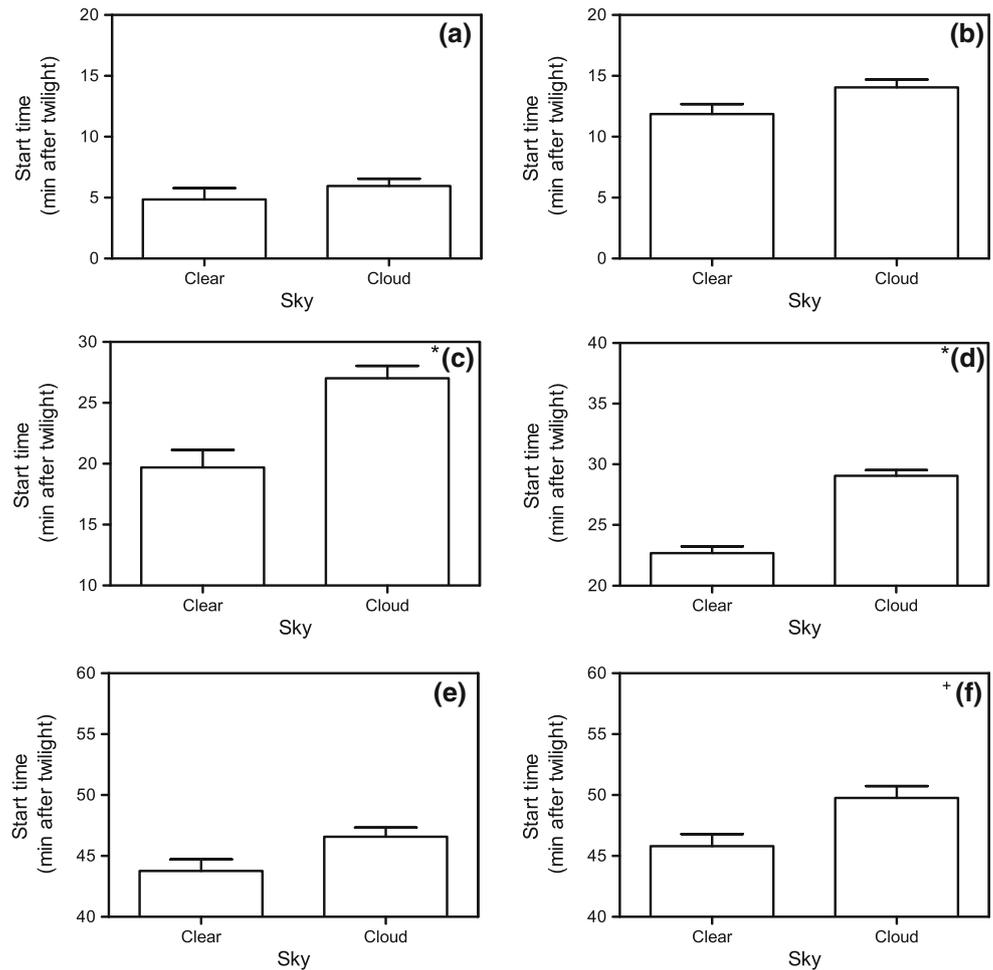
of six species) where three species birds start their dawn performance at later times as the season progresses, relative to nautical twilight. The factors that show significant relationships with chorus start time vary from species to species, yet the relationships are in the same direction (with the exception of temperature in one species); even non-significant terms show tendencies in the same direction across species, demonstrating that these extrinsic environmental features shape dawn chorus performance in similar ways across species. Taken together, these data reveal that the dawn chorus performance of birds in a temperate bird community varies with extrinsic abiotic factors.

For each of our six focal species, we found that variation in dawn chorus start times between sites contributed significantly to the models, accounting for 15–59 % of the models' variation. There are a number of reasons why birds of the same species at different recording sites might exhibit differences in daily song onset. Individual differences in quality may play a role in influencing start times. In Black-capped Chickadees, for example, 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). Social factors, such as the number of neighbours or changes in territorial boundaries can also influence the dawn chorus (e.g. Liu 2004; Burt and Vehrencamp 2005). Additionally, dawn chorus timing can vary among breeding stages. For example, a study of the breeding phenology of Willow Tits (*Parus montanus*) revealed that chorus onset is earliest during the fertile period of the singer's partner (Welling et al. 1995). The birds in our study area were not individually marked or monitored for rank, age, or breeding stage; these intrinsic 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.

Four of the six focal species showed significant variation in dawn chorus start time with Julian date. For Black-capped Chickadees, start time of the dawn chorus became progressively earlier, relative to nautical twilight, as the

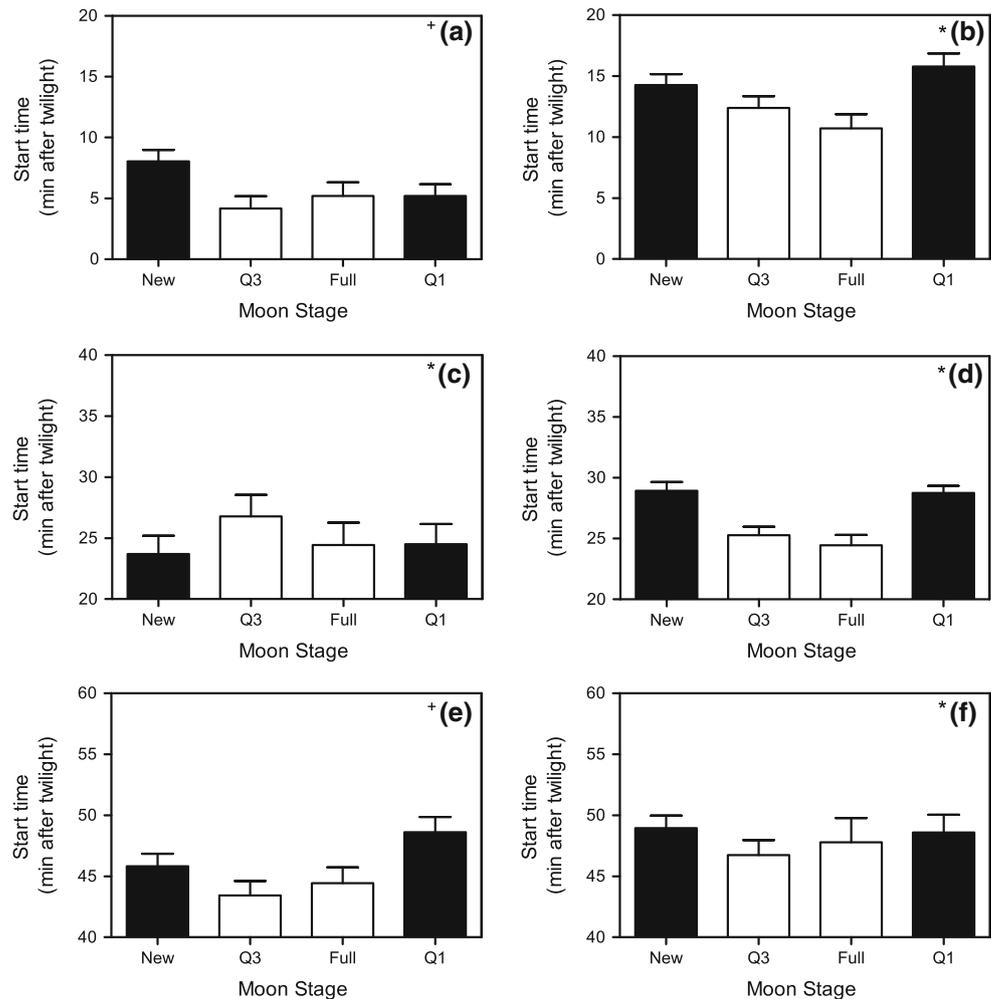
Fig. 3 Mean (\pm standard error) dawn chorus start time relative to nautical twilight when cloud was present or absent at twilight for six north temperate bird species: **a** Alder Flycatcher, **b** Song Sparrow, **c** White-throated Sparrow, **d** American Robin, **e** Eastern Phoebe, and **f** Black-capped Chickadee. Values are in minutes after nautical twilight and, thus, lower values represent earlier singing. All y-axes are standardized to 20 min intervals, though the interval differs among species



season progressed before reversing direction following a mid-season peak. Song Sparrows, White-throated Sparrows, and Eastern Phoebes showed later start times relative to morning twilight as the season progressed. Whereas the three latter species are typically multi-brooded (Arcese et al. 2002; Falls and Kopachena 2010; Weeks 2011), Black-capped Chickadees are single-brooded and rarely lay replacement clutches after nest loss (Foote et al. 2010), and, thus, the early decline in dawn song may reflect a decline in territoriality later in the season, or an earlier molt, in that species. Alder Flycatchers returned from migration more than a month later than the other five species (see Fig. 5a); this late arrival meant that Alder Flycatchers were sampled over a shorter period, which may explain the lack of a significant effect in the model explaining variation in this species. The recording end date falls within the laying and hatching dates of first broods for this species (Lowther 1999). Alternatively, Alder Flycatchers may differ from other species in other aspects of their ecology. The multi-brooded American Robin (Sallabanks and James 1999) did not show a significant pattern of variation in dawn chorus start time with Julian date.

Our results demonstrated that cloud cover alone did not strongly influence dawn chorus start time across species. Only American Robins and White-throated Sparrows showed significantly delayed choruses when the sky was cloudy. Presence of cloud cover can alter ambient light conditions in the early morning (Graham et al. 2003) and, therefore, clouds have the potential to lead to variation in avian singing behaviour. Red-legged Partridges (*Alectoris rufa*), for example, produce fewer vocalizations with increasing cloud cover (Pépin and Fouquet 1992). Perhaps White-throated Sparrows and American Robins—species with intermediate dawn chorus start times—are most sensitive to both moonlight and natural variation in early morning light from the rising sun. Indeed, previous research has demonstrated that American Robins alter song start times in response to exposure to light pollution (Miller 2006). More of the focal species were significantly influenced by moonlight than cloud cover; it is possible that overnight lighting may be more critical for dawn chorus timing than lighting experienced in the early morning from the rising sun for most species. We did not distinguish between light and heavy cloud cover, and it is

Fig. 4 Mean (\pm standard error) dawn chorus start time relative to nautical twilight with moon phase (new, 3rd quarter = Q3, Full, 1st quarter = Q1) for six north temperate bird species: **a** Alder Flycatcher, **b** Song Sparrow, **c** White-throated Sparrow, **d** American Robin, **e** Eastern Phoebe, and **f** Black-capped Chickadee. *Dark-shaded bars* indicate moon phases where the moon is below the horizon at dawn. Values are in minutes after nautical twilight and, thus, lower values represent earlier singing. All y-axes are standardized to 20 min intervals, though the interval differs among species

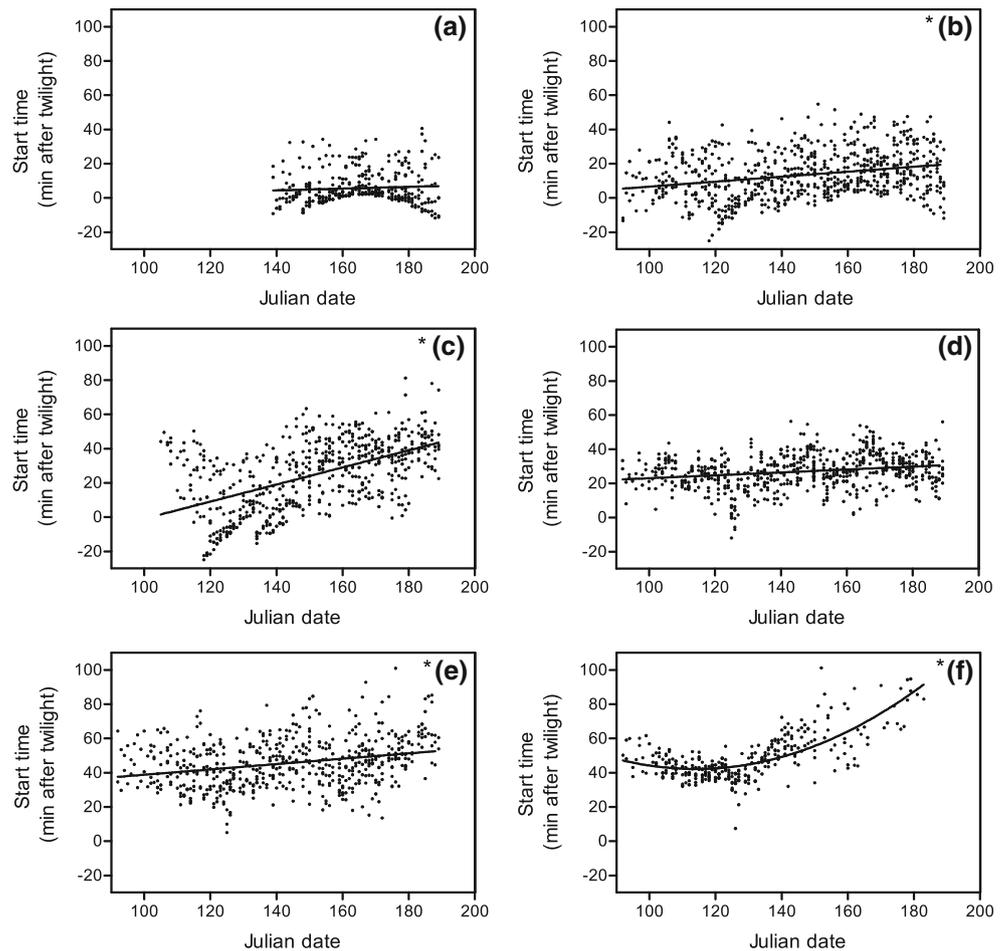


possible that not all days classified as cloudy may have been sufficiently cloudy to influence the apparent light level.

Dawn chorus onset varied with precipitation for all species except Alder Flycatchers (though not significantly for White-throated Sparrows). Previous investigations of bird communities in Australia (Keast 1994) and Jordan (Hasan 2010) also 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. Precipitation could delay activity in part because the masking effects of the sound of rain would decrease communication efficiency, and in part because rain is expected to lead to an overall decrease in the activity of wild animals (e.g., Link et al. 2011). As the earliest starting species, Alder Flycatchers may have begun their dawn chorus performance prior to precipitation beginning on some mornings. Overall, precipitation appears to strongly influence temperate bird dawn chorus start times. Precipitation also showed significant interactions with other variables, as we discuss below.

Dawn chorus start times in two of the six focal species showed a significant relationship with ambient temperature. Relationships between ambient temperature and avian singing behaviour are well recognized (e.g., Slagsvold 1977; Garson and Hunter 1979; Gottlander 1987). The relationship between temperature and onset of dawn song, however, has not been well-studied (Aström 1976). Nevertheless, we found that temperature at nautical twilight does relate to significantly earlier dawn chorus onset for Song Sparrows and Eastern Phoebes and contributed to the best model for White-throated Sparrows and American Robins. Prior studies show that White-throated Sparrows sing less during inclement weather or cold temperature (Falls and Kopachena 2010), and, thus perhaps cold temperature influences the length of the chorus more than the timing. The influence of temperature on chorus start time may be partly explained through an interaction with precipitation for both Song Sparrows and American Robins. American Robins tend to sing earlier when the temperature is cooler, yet the interaction between temperature and precipitation reveals that precipitation had a greater effect

Fig. 5 Relationship between dawn chorus start time and Julian date for six north temperate bird species: **a** Alder Flycatcher, **b** Song Sparrow, **c** White-throated Sparrow, **d** American Robin, **e** Eastern Phoebe, and **f** Black-capped Chickadee. A *line* of best fit is plotted to show direction of the relationship and *each dot* represents an annotated day at one recorder location



on onset of the dawn chorus when temperatures were colder. For Song Sparrows, the latest start times were observed when it was cold and precipitation was present; precipitation did not have as large an effect at warmer temperatures. These interactions suggest that combined cold temperature and precipitation may result in overly challenging conditions through which to sing. Alder Flycatchers were not present in the earlier, colder part of the season and so the temperature fluctuations experienced by that species may have been less than for others. Black-capped Chickadees are non-migratory residents in our study area (Foote et al. 2010) and may be better acclimated to cooler spring and summer temperatures than migrant species.

Unlike other species, American Robins sang earlier when it was colder and precipitation was absent (significant interaction between these factors). Perhaps sound transmission of American Robin songs is optimized at colder temperatures. The acoustic transmission hypothesis predicts that conditions at dawn are ideal for sound transmission and that certain song types should travel further with particular conditions (Henwood and Fabrick 1979).

Alternatively, if Song Sparrows and White-throated Sparrows sing later when it is colder, American Robins may benefit from reduced acoustic interference by singing earlier, whenever heterospecific acoustic interference is reduced.

One potential explanation for earlier singing on warmer mornings might be that insects have the potential to be more active earlier on warmer mornings (Bale et al. 2002), so insectivorous avian species might benefit from completing their dawn choruses earlier in order to begin foraging as soon as possible. Alder Flycatchers are aerial insectivores (Lowther 1999) and did not show a relationship between song start time and temperature. However, because they are the earliest to sing, they may complete their dawn chorus before insect activity commences regardless of temperature. 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 in Song Sparrows and Eastern Phoebes,

although it is controversial, given that locomotion may be a much more efficient method of eliminating surplus energy than singing (Gil and Gahr 2002). Given that only two species were significantly influenced by temperature alone, this hypothesis is not well supported by our data. 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.

We found that lunar stage affected dawn chorus start time for all six species, demonstrating a prominent lunar relationship with the early morning behaviour of these diurnal animals. For Alder Flycatchers and Eastern Phoebes, however, lunar stage contributed to the best model explaining start time but was not significant. Overall, song was earlier during third quarter or full moon (when the moon is above the horizon at dawn) at least during good weather. 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 a recent study by York et al. (2014) found that White-browed Sparrow Weavers sing earlier when the moon was full and above the horizon. White-throated Sparrows have previously been shown to be sensitive to moonlight variation and sing more nocturnal songs on bright moonlit nights (Falls and Kopachena 2010). Several recent investigations have revealed that overnight light from anthropogenic sources can influence chorus start time (e.g. Miller 2006; Kempnaers et al. 2010). Moonlight can also extend the evening activity level of diurnal birds at evening twilight when the moon is above the horizon (e.g. Alonso et al. 1985). It would be interesting to better understand how daytime activity period varies in diurnal birds across the lunar cycle by incorporating changes to both dawn and dusk activity with moonlight. Importantly, we found significant interactions between precipitation and moon stage revealing and song was earlier during full moon or 3rd quarter stages only when there was no precipitation (an effect that held true for three of six species). The interaction was also a contributor to the model for Eastern Phoebes, though was not significant. Precipitation delays start time alone but thick cloud associated with precipitation may block moonlight in the environment. Though cloud cover alone did not interact with moon stage (except non-significantly in White-throated Sparrows), perhaps heavier cloud associated with precipitation has a greater effect on moonlight transmission than cloud in general.

Not all recorders could be analysed on days of intense precipitation or strong wind due to acoustic interference. Thus, we may have missed some of the days on which the most extreme effects of weather of the dawn chorus would be evident. Nevertheless, we show that precipitation is an important factor. We did not include wind speed or

direction in this analysis because this factor causes the most acoustic interference and, thus, we could not reliably test for its effects. Future studies of examining the effects of weather on the dawn chorus could include direct observation when extreme weather events are forecast to ensure the complete spectrum of weather is included in the dataset.

We know that different species begin their dawn choruses at 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 Kopachena 2010; Weeks 2011) except the Black-capped Chickadee, which is a non-migratory bird (Foote et al. 2010). Interestingly, the Black-capped Chickadee is the latest species to begin chorusing. Alder Flycatchers and Eastern Phoebes are subsong species but are early and late singers, respectively, while American Robins, Black-capped Chickadees, Song Sparrows, and White-throated Sparrows are oscine species so broad taxonomic differences cannot explain the order of start time observed in this study. 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). All species, however, typically eat insects during the breeding season and the more flexible species that also eat seeds are both early (sparrows) and late singers (Black-capped Chickadee; Lowther 1999; Sallabanks and James 1999; Arcese et al. 2002; Falls and Kopachena 2010; Foote et al. 2010; Weeks 2011). 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).

Overall, our research provides novel insight on avian dawn chorus 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 (Thomas et al. 2002; Berg et al. 2006), we discovered that northern temperate birds begin their dawn choruses in a non-random, predictable order. Although the five 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. Our results yield insight into dawn chorus start time dynamics of six species of temperate songbird and suggest value in including extrinsic factors in studies of the timing of the dawn chorus.

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