

Factors Influencing Bioacoustically Derived Arrival Timing of Three Migrant Bird Species in the
Western Boreal Forest

by

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Abstract

Habitat alteration is the leading cause of bird population declines globally. Therefore, understanding the processes influencing habitat selection are important for the identification and protection of important areas for birds. Long-distance migrant birds are particularly vulnerable and are experiencing disproportionate declines relative to other avian groups. Preventing further declines requires a more thorough understanding of how quality habitat is assessed by birds and new measures for determining the potential productivity of a territory. Differences in territory settlement date (arrival) have been shown to reflect habitat quality on small spatial scales, thus differential arrival timing of migrant birds may help us address fundamental questions of habitat selection across landscapes. Despite widespread acceptance of arrival time as an indicator of habitat quality, a large-scale multi-species demonstration of this phenomenon is absent due to the logistical difficulty of collecting the appropriate data. I investigated the potential value of habitat assessment through measured differences in relative migrant arrival date estimated from provincial scale long term bioacoustic monitoring. I first assess the descriptive ability of two different operational arrival definitions used previously to justify the arrival date of three boreal migrants (first detection and first instance of three-day consecutive detection) and an additional novel definition (the detection-gap definition). The descriptive ability of each was assessed through the strength of an assumed positive latitudinal relationship. I found that all definitions performed similarly, producing the anticipated latitudinal relationship in 8 of 9 species-arrival definition combinations. Therefore, I adopted the first detection definition to describe arrival in this system as it provides similar descriptive ability with reduced sampling effort. I then address large-scale settlement patterns of three migrants: Ovenbirds (*Seiurus aurocapilla*), Tennessee Warblers (*Leiothlypis peregrina*), and Yellow-rumped Warblers (*Setophaga coronata*) across the boreal regions of Alberta. I also examined the local settlement patterns of Ovenbird by comparing both relative arrival timing and measured density changes between nearby territories. Using predicted density as a habitat quality proxy, I found increasingly early arrivals in higher quality sites both provincially and locally for species where habitat specificity has been reported. I also found that sites where higher densities of Ovenbird are predicted to occur locally are filled to higher densities before sites of lower density. Finally, I found that additional life history characteristics including habitat associations and migration distance may be measurable through arrival timing comparison. In

this study, I present the first landscape-scale examination of simultaneous multi-species migrant arrival time using bioacoustics. By correlating migrant arrival time and density, I demonstrate that density is a reasonable measure of habitat quality. Combined, density and arrival data provide a relatively low-cost way of assessing habitat quality and should be used to inform land management decisions in the boreal forest region.

Preface

This thesis is an original work by Justin Johnson. Data was collected by countless individuals working under the University of Alberta, the Alberta Biodiversity Monitoring Institute, and Environment and Climate Change Canada. The data was analysed by Justin Johnson with the assistance of Gihyun Yoo. Justin Johnson wrote the manuscript. Erin Bayne helped design the project, secured funding, and provided analytical advice and edits for the manuscript. No part of this thesis has been previously published.

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Chapter 1. Is arrival from migration correlated with density for birds in the Western Boreal forest?

Introduction

Habitat alteration through anthropogenic processes is cited as a primary cause of population declines across most North American birds (Johnson 2007; Rosenberg *et al.* 2019). In the boreal forest, habitat loss and fragmentation from agricultural conversion, oil development, and forest harvesting are cited as common threats (Brawn *et al.* 2001; Ball *et al.* 2016; Nixon *et al.* 2016; Van Wilgenburg *et al.* 2018). Boreal forest bird populations have changed considerably, with an average population decline across species of 33% since 1970 (Rosenberg *et al.* 2019). Migrants breeding in this region are particularly vulnerable: although data is limited, migratory populations are declining over five times faster than resident species (Van Wilgenburg *et al.* 2018; Rosenberg *et al.* 2019). Mitigating such population declines requires distribution and abundance data at a scale useful to management (Betts *et al.* 2006). Thus, understanding the habitat requirements of migrant birds across the entire life cycle of these animals is vital in conserving these species.

Our understanding of habitat selection in breeding areas comes primarily from point counts. Point counts are typically used to estimate density or relative abundance in a location (Marshall and Cooper 2004; Cornell and Donovan 2010; Yip *et al.* 2017). Higher relative abundance or density from point counts is regularly used as a metric of importance of a habitat type for birds. However, the utility of abundance or density as a measure of habitat quality has been questioned (Remés 2003). Density may accurately reflect habitat quality in localized study systems but may misrepresent habitat quality due to ecological traps (Vaughan and Ormerod 2003; Haché *et al.* 2013). This idea has led to several authors suggesting that studying habitat selection through density alone might be misleading (Van Horne 1983; Johnson 2007). Demographic studies are the gold standard for assessing ecological traps and population sinks but are spatially localized and include a limited sample of relatively few individuals. In studies where demography and density are examined together, there tends to be a positive correlation between density and reproductive success except in landscapes with high levels of anthropogenic disturbance (Bock and Jones 2004). However, linking density and reproductive success directly is very expensive and time consuming making it difficult to quantify the relationship between density and demography at large spatial extents (Vaughan and Ormerod 2003; Betts *et al.* 2006; Furnas and Callas 2015). Therefore, we should be evaluating other cost-effective methods of assessing

habitat importance over large areas through metrics other than density and demography (Chalfoun and Martin 2007).

Seasonal reproductive success is often related to the arrival timing of migrant birds (Smith and Moore 2005). Early arriving males tend to initiate clutches earlier and secure more extra pair copulations; ultimately producing more offspring (Arvidsson and Neergaard 1991; Currie *et al.* 2000; Choi *et al.* 2010). Additionally, individuals in good physical condition typically arrive earlier and may be more likely to have a second brood or successfully replaced a failed clutch (Kokko 1999; Gunnarsson *et al.* 2006). Competition for high-quality territories is intense at settlement and birds must arrive early to secure space from competitors. Therefore, earlier settlement typically identifies high quality territories and subsequent settlement patterns should provide insights into perceived habitat quality (Kokko 1999; Joos *et al.* 2014; Samplonius and Both 2017). Thus, population level patterns in habitat importance may be assessed by relative arrival timing as it describes habitat selection under varying population densities and can be used to identify and rank habitat preferences across the population annually. Combining this measure with a methodology facilitating landscape-scale data collection would be particularly advantageous. Tracking migrant landbirds and their arrival at large spatial scales is challenging; however, bioacoustic monitoring can provide the required arrival information (Buxton *et al.* 2016; Paxton and Moore 2017; Oliver *et al.* 2018). Estimating arrival is a relatively novel application of bioacoustics tested primarily through acoustic indices in remote northern songbird community soundscapes. We argue, species-level arrival can be measured from acoustic surveillance and provides arrival dates similar to traditional methods of migration monitoring, such as mist netting and human-based point count surveys (Oliver *et al.* 2018), but at larger spatial extents.

We explore spatial and temporal factors influencing the arrival timing of three boreal migrant bird species (see Study Species). Our first objective was to measure the arrival date of these species and determine if the assumption that arrival time and breeding densities from independent data are correlated. We predict that arrival timing should be earlier in areas of higher breeding densities if such areas provide higher quality territories (Currie *et al.* 2000; Gunnarsson *et al.* 2006; Chalfoun and Martin 2007). We also compare the strength of vegetation cover, forest age, latitude, and longitude as predictors of arrival time under the premise that it may inform which elements of a high-density site is most important to these species. We predict a negative latitude and positive longitude response as migrants are delayed

simply by the increased distance to more northern and western territories based on migratory patterns believed to exist in our north-western boreal study area.

While understanding regional patterns of arrival are important, there may be additional insights that can be gained from looking at arrival patterns locally. Local breeding density often is used as a proxy for territory quality if ecological traps do not occur. However, behavioural processes such as conspecific attraction and competition can be particularly important and more easily observed at smaller spatial scales (Remés 2003; Robertson and Hutto 2006). To assess if birds fill a local area first before subsequent arrivals move to lower density locations or whether high and low density sites in the same general area are settled simultaneously, we estimated the arrival of Ovenbird at four locations 600m apart within each site. Specifically, we evaluated the day at which the maximum local count occurred at each station. We hypothesize that due largely to the habitat specificity of Ovenbird, regional patterns in arrival timing will be generally reflected in local arrival timing and fine tuned in response to subsequent territory saturation following arrival.

Methods

Site Selection and Study Area

We conducted four years (2015-2018) of acoustic surveillance across the boreal forest region of Alberta (54°N-60°N; Figure 1.1, Panel A). Stations were selected from a pool of 626 acoustic sampling sites deployed by the Alberta Biodiversity Monitoring Institute (ABMI), Environment and Climate Change Canada, and the University of Alberta to monitor vocal activity in the boreal region. A site typically consists of four acoustic recording units (ARUs) spaced 600m apart with each recording unit defined as a station. To reduce effects of spatial autocorrelation, we randomly chose one station from each available site and assessed focal species presence through audiovisual scanning of spectrograms generated by Audacity® 2.1.3 (Audacity Team 2017). We examined two dawn recordings per sampling day with a ten-minute recording at dawn + 00:30 and a three-minute recording at dawn + 01:30. Recording began on 20 April, sampling every fifth day until 14 June. If the focal species was detected on any recording, the station was flagged and added to a pool of available listening data for further processing. Stations without focal species detection were removed from the analysis and randomly replaced with a new station from within the site. Sites without focal species detection were removed from the analysis.

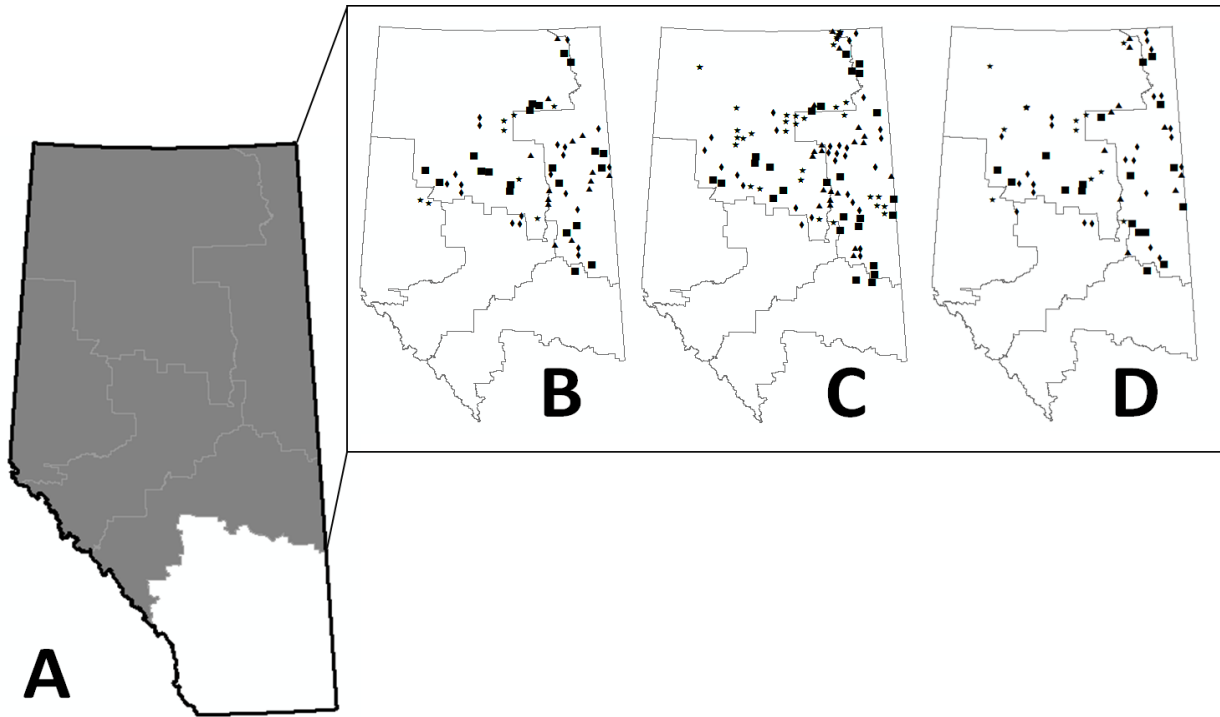


Figure 1.1. Survey area and sampling stations. *Panel A* - Survey area in grey within the province of Alberta covering most of the boreal forest region (54°N-60°N). Survey area consists of five LUFs representing Albertan watersheds. *Panels B-D* - Stations included in the analyses; *panel B* - Ovenbird, 70 stations; *panel C* - Tennessee Warbler, 129 stations; *panel D* - Yellow-rumped Warbler, 69 stations. Icons represent the approximate station location and sampling year (triangles - 2015; squares - 2016; diamonds - 2017; stars - 2018).

Study Species

We chose three boreal migrant warblers for this analysis: Ovenbird (OVEN; *Seiurus aurocapilla*), Tennessee Warbler (TEWA; *Leiothlypis peregrina*), and Yellow-rumped Warbler (YRWA; *Setophaga coronata*). These species represent a sample of boreal migrant life histories with special consideration of breeding habitat specificity, migration distance, and species distribution in the study area (Flockhart 2010). Additionally, these species vocalize conspicuously and are thus suited for acoustic monitoring of migrant phenology (Gordo *et al.* 2008). The Ovenbird is a short-to-long range neotropical migrant with individuals breeding in Alberta wintering in Mexico and Central America (Moore and Kerlinger 1987; MacMynowski and Root 2007; Porneluzi *et al.* 2011; Haché *et al.* 2017). This species is considered a breeding habitat specialist, nesting primarily in mid-age deciduous and mixedwood stands (Machtans

and Latour 2003; Mahon *et al.* 2016; Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project 2019a). Tennessee Warblers are long-range migrants wintering as far south as Ecuador (Moore and Kerlinger 1987; MacMynowski and Root 2007; Rimmer and MacFarland 2012). Tennessee Warbler breeding territories vary in vegetation structure and are typically found in mature forests; however, habitat preference varies annually and seems to be driven by availability of spruce budworm (*Choristoneura fumiferana*) (Machtans and Latour 2003; Vernier and Holmes 2010; Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project 2019b). The Yellow-rumped Warbler is a short-range migrant with individuals breeding in Alberta wintering in the southern United States and northern Mexico (Hunt and Flaspohler 1998; Leston *et al.* 2018). Considered a breeding habitat generalist, this species exhibits a weak preference for pine and other mature conifer stands (Machtans and Latour 2003; Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project 2019c). All focal species are found throughout the study area and sing during migration.

Recorders and Recoding Schedule

Our acoustic recordings were generated using Wildlife Acoustics® Songmeter SM2, SM2+, SM3, and SM4 acoustic recorders (Wildlife Acoustics, Inc., Maynard, Massachusetts, USA). The ARU model deployed often varied between and within sites. All ARUs were deployed before migrants return to breeding territory in spring with deployment typically occurring during the previous autumn. Acoustic monitoring began in March of the survey year and continued until recorder collection in late July. Recordings were stored on the unit as .wav or .wac format but were all converted to .wav files for processing. Recordings were processed manually by visual scanning and listening to the audio. Spectrograms were created using Audacity® 2.1.3 (Audacity Team 2017) software. Spectrograms were visualized using a 2048 FFT Hanning window and a sampling rate of 44,100Hz. To estimate the arrival of songbirds, we examined recordings taken during the dawn chorus as territorial birds are most vocal at this time during territory settlement (Wilson and Bart 1985; Arvidsson and Neergaard 1991). Two recordings were processed per sampling day, the first at dawn +00:30 and the second at dawn +01:30. Detection of the focal species on either recording was considered as a detection for the day. Recordings were examined daily from 20 April to 15 June representing the range of arrival for most boreal migrants. Three percent of recordings were disrupted by acute noise (*i.e.*, wind, rain, periodic anthropogenic noise) and subsequently eliminated from further analysis as they prevented accurate and standardized detection of focal species.

Arrival Estimation

We defined the first detection date of the focal species as the arrival date for the station. First detection is commonly used to measure migrant arrival (Both and Visser 2001; Gordo *et al.* 2008; Janiszewski *et al.* 2013; Joos *et al.* 2014) and acoustically derived first detections have been shown to correlate to arrival estimates provided by direct monitoring (Oliver *et al.* 2018). Although first detection has been criticized as error prone, within our study system alternative measures of arrival offered very similar accuracy with more effort required (Appendix One). Additionally, arrival windows of migratory warblers in northern Alberta are locally narrow with settlement often completed within 2-5 days potentially limiting the importance of any inaccuracy in the arrival estimate (Flockhart 2010). First detection provides an estimate of arrival date that is relatively precise and adaptable across a large area. Raw first detection dates were converted to ordinal date (1 January = 1) in Rstudio before inclusion in analysis (R package 'lubridate' version 1.7.4; Spinu *et al.* 2018, R Core Team 2019). Arrival distributions were tested for normality using Shapiro-Wilk's tests for all focal species.

Covariate Data Sources

Vegetation

Vegetation covariates were extracted from the Alberta Vegetation Inventory (AVI). We created circular buffers around each station and extracted all vegetation data within a 150m radius. Station locations were measured using a GPS and are accurate to within ~ten metres. The AVI provides fine scale vegetation classification with 74 distinct vegetation categories. These categories were reclassified into six generalized vegetation types: white spruce, black spruce, deciduous, mixedwood, shrub, and pine (ABMI 2015). We calculated the dominant stand type for each station as the generalized vegetation type with the greatest proportional coverage within the buffer (Ball *et al.* 2016). An estimate of vegetation age was provided by the AVI and was measured at the station as the average age of the dominant stand type within the buffer. We grouped vegetation age extracted from the AVI into nine groups following the methods of the ABMI (2015): 0-10 years, 10-20 years, 20-40 years, 40-60 years, 60-80 years, 80-100 years, 100-120 years, 120-140 years, and 140+ years. Although forest type was available for all stations, vegetation age estimates were unavailable for a small portion of stations as the AVI did not estimate age for every polygon. When the dominant stand age was unavailable, we used the average age of all vegetation types within the buffer. If the buffer lacked age data altogether, the average age of the dominant stand type across the watershed containing the buffer was used.

Latitude and longitude values used in analysis are approximate (within 5km of the station) as actual locations are confidential property of the ABMI. All spatial data processing was performed using ArcMap 10.7.1 (ESRI 2019).

Predicted Density

We extracted station level density predictions using the *cure4insect* package in Rstudio (Solymos *et al.* 2020, RStudio Team 2019). This package used over 60,000 point counts to create a model that predicts density for the focal species across Alberta. The original model includes variables such as anthropogenic disturbance, climatic conditions, spatial location, and landcover characteristics. To use the *cure4insect* model we input the generalized vegetation types, age group, and station coordinates as described above (latitude and longitude) which *cure4insect* then used to estimate an estimated density for each station we visited. Density values were transformed into a proportion of maximum density predicted for our stations to interpret and standardize effect size across species more easily.

Local Arrival Estimation

We also assessed the local arrival of Ovenbirds across 116 recording stations within 29 sites. In this situation, a maximum of four different places where territories could be settled within a site. Ovenbirds have territory sizes between 0.5 and 1.5 hectares in size (Bayne *et al.* 2005) so it is very unlikely the same individuals were being counted at each station. After an Ovenbird arrival was determined at the first station to be settled, we determined the arrival time of Ovenbirds at the other three stations. To assess how the space around an ARU station was filled, we estimated the number of Ovenbirds heard on each recording at each station (*i.e.*, did multiple individuals arrive at high density sites before a single individual arrived at low density sites). We monitored the station level count of Ovenbirds following arrival at the first station and continuing until one week after the final (*i.e.*, fourth) station was settled. We calculated the maximum count of Ovenbirds found at each station over this period and defined the first date that this value was reached as the “Maximum Date” (“MaxDate”).

Exploration of Arrival Covariates

We assessed how density, spatial coordinates and vegetation conditions influenced arrival data by fitting generalized linear models (GLMs) in RStudio with day of year as the continuous response variable (RStudio Team 2019). We assumed a Gaussian error family and identity link. Two model sets were created, the first using raw values from the AVI (vegetation model set) and

the second with density values calculated using the `cure4insect` package (Predicted Density Model set; predicted density models). For each model set, we prepared a list of candidate models by combining spatial and temporal predictors while considering and removing models that include correlated parameters (Table A2.1). We selected the top models from each model set through comparison of Akaike information criterion (AIC) values.

We conducted a separate analysis of Ovenbird density dependent local arrival patterns. First, we computed the arrival date at the first station, and estimated the number of individual Ovenbirds at a station in subsequent days. We recorded the date at which the highest density of Ovenbirds was detected (MaxDate). We then repeated this examination to determine the arrival and MaxDate of Ovenbirds at the remaining stations within a site. We examined the population averaged effect of predicted Ovenbird density at a station on the station-level arrival date of Ovenbirds and the stations MaxDate using Generalized Estimating Equations (GEE).

Results

We estimated the arrival date for Tennessee Warbler at 129 stations, Ovenbird at 70 stations, and Yellow-rumped Warbler at 69 stations (Figure 1.1 panels B-D). Focal species arrival distribution varied by species with Yellow-rumped Warblers arriving first (mean: May 8th, SD: +/- 4.7 days, range: 26 days; April 23rd - May 20th) followed by Ovenbirds (mean: May 16th, SD: +/- 3.2 days, range: 16 days; May 11th - May 26th) and finally Tennessee Warblers (mean: May 23rd, SD: +/- 4.5 days, range: 25 days; May 11th - June 4th) (Figure 1.2). The arrival timing of Ovenbird ($W=0.979$, $p=0.303$) and Yellow-rumped Warblers ($W=0.975$, $p=0.335$) was normally distributed whereas Tennessee Warbler arrival timing was not ($W=0.918$, $p > 0.001$). Higher predicted density from `cure4insect` was a significant predictor of earlier arrival across all species (Table 1.1, Figure 1.3). The relative predictive strength of density varied marginally by species.

Within the vegetation model set, the best model varied between species. While the global model was selected for Yellow-rumped Warbler, the top Tennessee Warbler model removed longitude while the top Ovenbird model had both age and longitude removed (Table A2.2). Tennessee Warblers and Ovenbirds arrived at stations dominated by deciduous forest earlier than other vegetation types with Tennessee Warblers also arriving earlier than average at mixedwood stations (Figure 1.6). These species also arrived significantly later at black spruce and pine dominated stations. Vegetation type did not appear to influence the arrival date of Yellow-rumped Warblers. Station latitude positively affected Tennessee Warbler arrival date with individuals of this species arriving later at more northerly stations. Both increasing latitude

and longitude delayed Yellow-rumped Warbler arrival with the latest individuals arriving in the northwestern part of Alberta. We observed earlier arrival of Tennessee Warblers and later arrival of Yellow-rumped Warblers in more mature forest stands regardless of vegetation type.

The GEEs for Ovenbirds that evaluated how each station in a site was filled found that earlier arrival date and MaxDate were observed at stations with higher predicted density. This suggests that stations of higher predicted density are not only settled first but are also generally filled to capacity before surrounding stations are settled (Arrival: $\beta \pm SE = -4.298 \pm 0.897$, $z = -4.79$, $p < 0.001$; Figure 1.4; Table 1.2. MaxDate: $\beta \pm SE = -2.966 \pm 1.382$, $z = -2.15$, $p = 0.032$; Figure 1.5; Table 1.3).

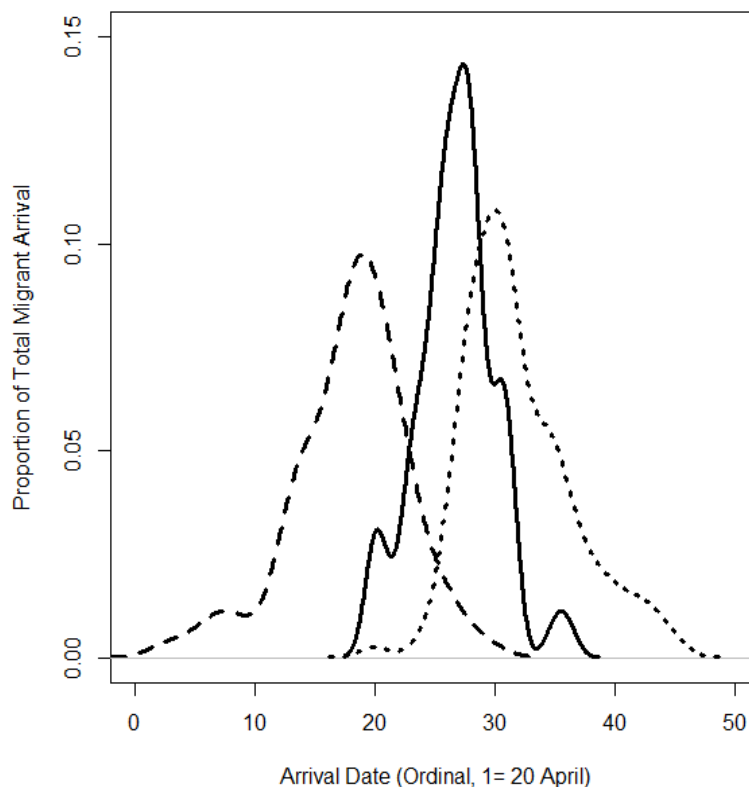


Figure 1.2. Focal species arrival distributions. Yellow-rumped Warblers arrived first in Alberta (dashed line; mean: May 8th, SD: ± 4.7 days, range: 26 days; April 23rd - May 20th) followed by Ovenbird (solid line; mean: May 16th, SD: ± 3.2 days, range: 16 days; May 11th - May 26th). Tennessee Warblers were the last of the three focal species to arrive (dotted line; mean: May 23rd, SD: ± 4.5 days, range: 25 days; May 11th - June 4th). Ovenbird ($W=0.979$, $p=0.303$) and Yellow-rumped Warblers ($W=0.975$, $p=0.335$) arrival is normally distributed, Tennessee Warbler arrival timing is non-normal ($W=0.918$, $p > 0.001$).

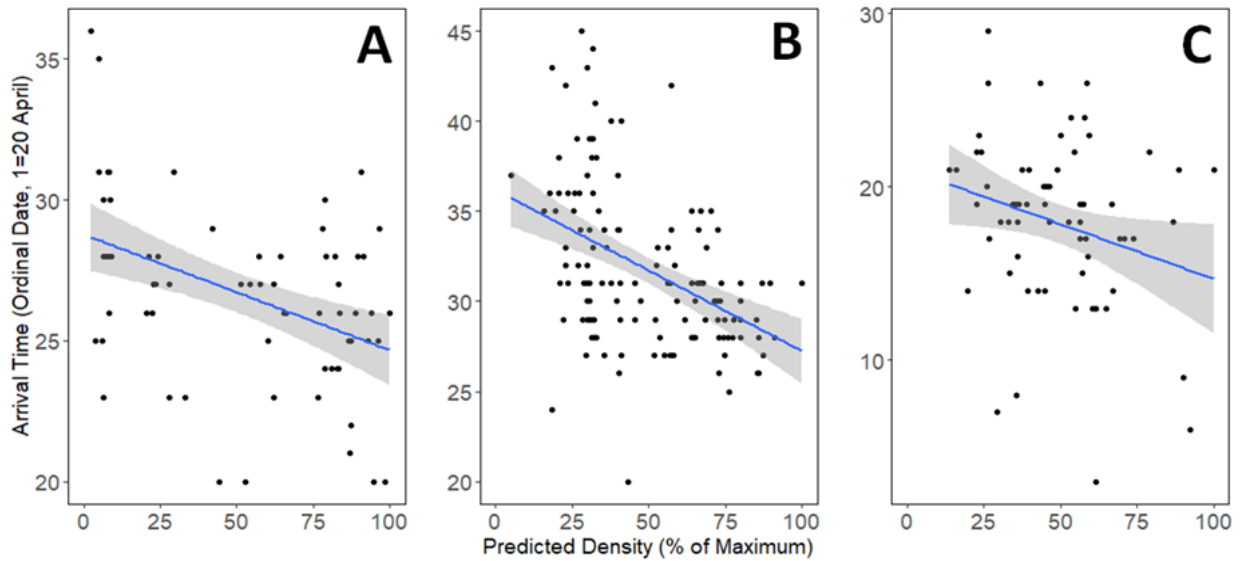


Figure 1.3. Modelled density effect on the arrival. Ovenbird (A, n=70), Tennessee Warbler (B, n=129) and Yellow-rumped Warbler (C, n=69) arrival was earlier across all focal species when the predicted density of the station increased ($p < 0.05$).

Table 1.1. Modelled effects of density on migrant arrival time of three focal species. Standardized effect sizes (β) are presented +/- standard error of the estimate. Top models selected through AIC are shown. Density is a significant predictor of migrant arrival time across all focal species (Significance levels, $p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: ***).

Species (Arrival ~)	n	Predictor	β	t	P
Ovenbird	70	Intercept	137.729+/-0.309	168.919	<0.001***
		Density	-1.044+/-0.327	-3.197	0.002**
		2016	0.073+/-0.414	0.177	0.86
		2017	-1.300+/-0.406	-3.203	0.002**
		2018	-1.090+/-0.368	-2.962	0.004**
Tennessee Warbler	129	Intercept	142.828+/-0.35	169.148	<0.001***
		Density	-1.961+/-0.357	-5.496	<0.001***
Yellow-rumped Warbler	69	Intercept	128.928+/-0.527	72.019	<0.001***
		Density	-1.226+/-0.538	-2.281	0.026*
		2016	-1.243+/-0.768	-1.617	0.111
		2017	0.537+/-0.799	0.672	0.504
		2018	0.744+/-0.733	1.015	0.314

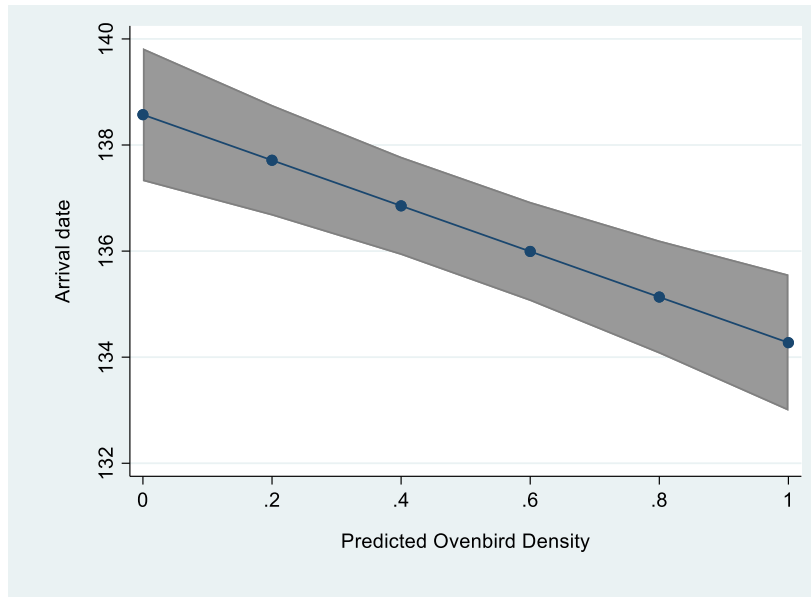


Figure 1.4. Population averaged effect of predicted Ovenbird density on local arrival date. Shaded area represents the 95% confidence interval of the estimate. Generally, Ovenbirds settle higher predicted density territories first before settling into stations with lower predicted density.

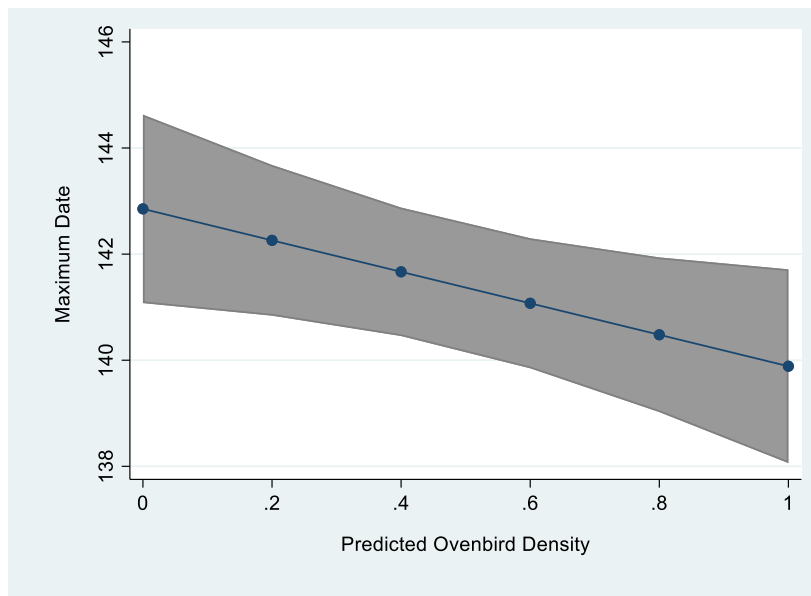


Figure 1.5. Population averaged effect of predicted Ovenbird density on territory saturation date (Maximum Date). Shaded area represents the 95% confidence interval of the estimate. Generally, Ovenbirds fill higher predicted density territories first before filling stations with lower predicted density.

Table 1.2. Generalized Estimating Equation output of predicted density on local arrival date of Ovenbirds. Lower (LCI) and upper (UCI) 95% confidence intervals of the estimate are provided. The effect of predicted density on Ovenbird local arrival date is significant, Ovenbirds generally settle territories of higher predicted density first. Effect sizes (β) are presented +/- standard error of the estimate.

Arrival~	β	z	p	LCI	UCI
Density	-4.298 +/- 0.897	-4.79	<0.001	-6.057	-2.539
Constant	138.6 +/- 0.639	-216.9	<0.001	137.3	139.8

Table 1.3. Generalized Estimating Equation output of predicted density on the date of territory situation (MaxDate) by Ovenbirds. Lower (LCI) and upper (UCI) 95% confidence intervals of the estimate are provided. The effect of predicted density on Ovenbird MaxDate is significant, Ovenbirds generally fill territories of higher predicted density first. Effect sizes (β) are presented +/- standard error of the estimate.

MaxDate~	β	z	p	LCI	UCI
Density	-2.966 +/- 1.382	-2.15	0.032	-5.675	-0.258
Constant	142.853 +/- 0.906	157.64	>0.001	141.077	144.630

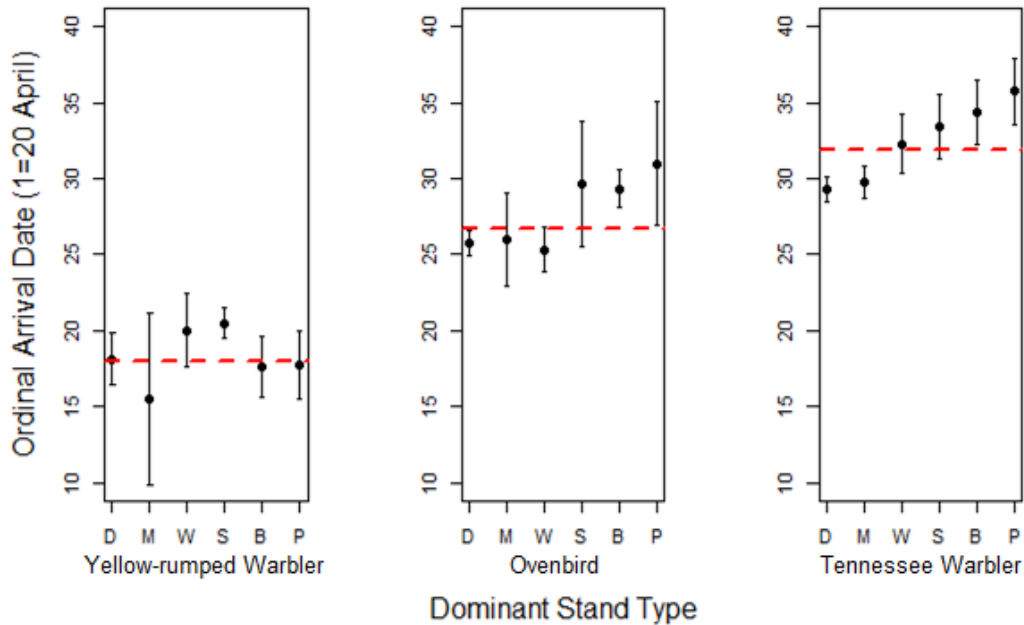


Figure 1.6. Mean migrant arrival by dominant stand type. Yellow-rumped warblers (left panel, n=69) have no difference in arrival date by vegetation type. Ovenbird (centre panel, n=70) arrival appears to be different in two major vegetation groups which correspond to differences expected from predicted density. Tennessee warblers (right panel, n=129) exhibit a slow and consistent filling of territories across vegetation types. (D=Deciduous, M=Mixedwood, W=White Spruce, S=Shrub, B=Black Spruce, P=Pine). Arrival dates are transformed from raw ordinal date to number of days after April 20th. Red dashed line is the average arrival across all vegetation types. Error bars are 95% confidence intervals of the mean arrival date.

Discussion

Although previous cross-species comparisons are absent from the literature, the effect of local migrant density and territory quality on arrival timing is well documented. Early arriving bar-tailed godwits (*Limosa lapponica*) are shown to settle territories of higher density first (Gunnarsson *et al.* 2006). These high-density territories also provided increased prey abundance and adult survivorship indicating higher quality. Similarly, predicted density of our focal species is inversely related to migrant arrival. The species considered in our study also selected territories with higher predicted densities where habitat preferences exist. Ovenbirds settled territories dominated by deciduous forest that provide reportedly high-quality Ovenbird habitat (Gibbs and Faaborg 1990, Mazerolle and Hobson 2004, Mattsson and Niemi 2008). Tennessee Warblers arrived at both deciduous and mixedwood dominated territories

disproportionally early corresponding to habitat containing higher densities of Tennessee Warbler year over year (Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project 2019b), but this behaviour may not reflect true habitat quality within a year. Tennessee Warblers occur at highest abundance in coniferous dominated areas of the western boreal forest (Machtans and Latour 2003). The incongruity between field observation and the measured arrival of Tennessee Warblers may be linked to the annual population fluctuations of spruce budworm (Blancher 2003). Despite our inability to predict budworm induced density fluctuations through cure₄insect, budworm activity in Alberta was relatively stable throughout our study period and thus we are likely detecting stable habitat associations through arrival (Government of Alberta 2017). As habitat generalists, Yellow-rumped Warblers showed no by-habitat arrival patterns as perceived habitat quality is believed to be functionally equivalent for this species across vegetation types (Mahon *et al.* 2016). Therefore, the arrival timing of our focal species can distinguish areas of high density where they are predicted to exist and may indicate perceived habitat quality across the landscape.

Locally, the arrival of Ovenbirds follows a similar pattern as territories of higher predicted density are settled first. This finding may reflect local relative qualities of Ovenbird territories. Order of local arrival timing is associated with the lay date of Bell's Vireo (*Vireo bellii*) occurring first in earlier settled territories which provide improved seasonal reproductive success (Joos *et al.* 2014). Haché *et al.* (2013) observed increased densities and earlier local settlement of an eastern population of Ovenbirds in undisturbed deciduous forest characteristic of high-quality Ovenbird habitat. Additionally, measuring the daily local density fluctuations of Ovenbird within sites reveals that the date of territory saturation (MaxDate) may be similarly influenced by the predicted density of the territory. Combined, our analysis of local arrival timing suggests that Ovenbirds not only settle into territories of higher predicted density first, but that these potentially high-quality territories are generally filled first. These local Ovenbird arrival patterns reflect both the pattern of territory selection observed at the provincial scale and potentially, the influence of intraspecific competition on arrival timing. Local territory filling across the Ovenbird population takes place over approximately three days. High competition for limited productive space may produce narrow arrival windows (Kokko 1999). However, such narrow arrival windows appear to be characteristic of warblers in the western boreal regardless of recorded habitat specificity. Five warbler species breeding in the western boreal all have a documented arrival window of less than five days (Flockhart 2010). This narrow local arrival window may partly be a response to a relatively short breeding season in the boreal forest rather than the specificity of habitat requirements outright. Within a critical period around settlement,

a short delay of local arrival may greatly impact individual seasonal reproductive success across species (Smith and Moore 2005, Joos *et al.* 2014). The arrival distributions we document here suggest that perhaps provincially, arrival windows can be significantly narrowed in response to habitat specificity. The Ovenbird settlement across the province was on average 9.5 days shorter than our other focal species. This indicates that for habitat specialists, the timing of arrival both provincially and locally appears tightly linked to the predicted density of individuals at a site which reflects territory quality for our focal species.

However, our measured density values may not accurately represent territory density as we did not vocally identify individual Ovenbirds or consider structural habitat features that may have influenced detection. Local arrival patterns also might have been a product of spatial proximity of stations, a narrow arrival window, or by sampling a limited number of local territories. Additionally, without directly measuring territory features we cannot isolate the fine scale drivers of early arrival within stand types. Our greatest obstacle is the uncertainty of individual reproductive success, without this measure we cannot rule out ecological traps (Van Horne 1983; Remès 2003). However, we believe that provincially derived density models can reasonably approximate territory quality given the consistency of local and provincial arrival patterns with reported habitat associations from literature. Future studies should expand the number and structural diversity of territories examined locally and explore microhabitat quality, individual condition, and consider in the field identification of Ovenbirds combined with bioacoustic surveillance and subsequent automated individual recognition.

Apart from density dependent measures of habitat quality, other factors contribute to provincial migrant arrival timing. We detected weak linear forest age responses for Yellow-rumped and Tennessee Warblers, both reportedly found at higher densities in older forests (Machtans and Latour 2003; Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project 2019b; Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project 2019c). Tennessee Warblers responded as expected with models predicting arriving earlier in stations dominated by older stands; yet Yellow-rumped Warblers settled younger stations first regardless of vegetation type despite a preference for mature forest (Leston *et al.* 2018). However, this weak effect likely reflects the relative predictive strength of dominant stand vegetation type on migrant arrival and territory quality (Marshall and Cooper 2004). Both Tennessee and Yellow-rumped Warblers are considered habitat generalists but weak preferences for different stand ages do exist (Machtans and Latour 2003; Mahon *et al.* 2016). Pine forests and shrub are the preferred vegetation cover for Yellow-rumped Warbler territories, both of which tend to be

younger naturally in our study area thus producing a correlated age effect. The relative predictive strength of latitude appears to increase with habitat generalization possibly caused by competition for limited productive territory space expected for specialists. However, this effect may be a product of habitat preference and migration distance. Short distance migrants such as Yellow-rumped Warblers typically have longer stopover which ultimately prolongs migration (Paxton and Moore 2017). Tennessee Warbler migration speed is therefore faster than Yellow-rumped Warblers as they have further to travel, but slower than Ovenbird due to relaxed competition for breeding territory upon arrival. Thus, arrival may reflect both local trends in habitat preference while accounting for large scale phenomenon that ultimately reflect seasonal reproductive success.

Measuring arrival reveals trends in habitat selection that reflect density while incorporating other features of migrant life history, which are often correlated with seasonal reproductive success. We have shown that arrival provides detailed information that rivals that collected from density derived from point counts but with the additional benefits inherent in acoustic sampling (Buxton *et al.* 2016; Oliver *et al.* 2018). Bioacoustic monitoring of arrival provides the spatial resolution we need to assess local settlement and habitat quality on a landscape scale (Chalfoun and Martin 2007). Applying this technique at the species level across this spatial scale is novel and can be easily adapted to the entire migrant community. To date, differential migrant arrival timing is understudied in the literature but provides a wealth of information on habitat use and selection (Johnson 2007). We recommend future field studies to confirm the accuracy of first detection on station occupancy and test the relationship between arrival and reproductive success. Ultimately, bioacoustic arrival estimation should be incorporated into field monitoring and automatic acoustic processing. Over time, arrival datasets may provide additional information relating to the abundance of prey across landscape and species level responses to climate change. The boreal forest is changing quickly and understanding the implications of species level habitat choice using migrant arrival time provides fast and reliable information that can guide land management and species conservation in the future (Ball *et al.* 2016; Rosenberg *et al.* 2019).

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Appendix 1. Comparison of arrival date predictive ability under three different arrival definitions

Introduction

Arrival on breeding territory is an important event in the annual cycle of migratory organisms. The timing of arrival represents the sum of environmental controls of migration (*e.g.*, carry-over effects, stopover duration, and weather) and individual condition (*e.g.*, natal latitude, genetics, and available fat reserves) (Møller 1994; Gunnarsson *et al.* 2006; Jonzén *et al.* 2006; Both 2010; Tøttrup *et al.* 2010; Oliver *et al.* 2018). Consequently, arrival timing presents a potentially important determinant of individual seasonal success (Jonzén *et al.* 2006; Joos *et al.* 2014). Arrival timing may also explain trends at the population level as migrants do or do not shift timing in response to climate change (Jonzén *et al.* 2007). Although migration monitoring documents the en route movement of migrants, behaviour upon arrival at the actual breeding territory is poorly understood (Tryjanowski and Sparks 2001; Johnson 2007). Collecting arrival data requires trained observers who are restricted to localized field stations within migrant breeding ranges (Gunnarsson *et al.* 2006; Buxton *et al.* 2016; Oliver *et al.* 2018). Thus, conducting long-term arrival monitoring at breeding sites at large spatial extents is both financially taxing and logistically difficult (Buxton *et al.* 2016) limiting our ability to address some important questions about arrival timing at a landscape scale.

Passive acoustic monitoring is increasingly used to measure the activity of vocal organisms in remote locations (Laiolo 2010; Furnas and Callas 2015; Shonfield and Bayne 2017). A single acoustic recorder (ARU) can collect hundreds of hours of recordings on a customizable schedule permitting a suite of behavioural response measures such as site occupancy or breeding status to be derived (Furnas and Callas 2015; Upham-Mills *et al.* 2020). Simultaneous recordings from ARU arrays allow for high spatial and temporal resolution when estimating arrival time. With standardized deployment protocols and data management, audio recordings generated by ARUs also provide a permanent record which can be used to assess changes in arrival timing between years. Birds are well suited for using passive acoustic monitoring to assess arrival as they communicate chiefly through sound, respond quickly to environmental change (Laiolo 2010), and sing most frequently while establishing their territory (Wilson and Bart 1985).

Despite the suitability of passive acoustic monitoring, few studies have used bioacoustics to estimate migrant arrival (Johnson 2007; Buxton *et al.* 2016; Oliver *et al.* 2018). Two studies we know of used acoustic indices to estimate arrival of migrant communities. Buxton *et al.* used the

Acoustic Complexity Index (ACI) to detect abrupt changes in the soundscape to identify a 'spring transition' (2016) from only resident species being present to residents and migrants being present. Oliver *et al.* developed methods for estimating arrival through both a supervised and unsupervised approach built around a Vocal Activity Index (2018). These studies although ground-breaking in the field, have some issues for estimating certain elements of arrival timing. First, acoustic indices can be complicated by surrounding noise and are considered coarse metrics of activity at a site (Buxton *et al.* 2016). Second, indices are restricted to community arrival estimates, masking the more important species-specific arrival times. While these studies suggest ARUs can collect dependable arrival data, the methods they present have been limited geographically to simple northern communities with relatively few species. While more labor intensive, listening to recordings to find the first detection of a species each year may provide higher resolution data that address more specific questions than indices can provide. Regardless of whether human listening or computer-based indices are used to estimate arrival, there are several key uncertainties in how one defines arrival that need to be addressed.

We compare the predictive ability of three common definitions of species-level arrival timing. Two traditional methods used at migration monitoring stations are translated into a bioacoustic equivalent, allowing a simultaneous comparison of arrival as defined by different methods across a large geographic area. The first detection of the species (Lozano *et al.* 1996; Arvidsson and Neergaard 1991; Tranjanowski and Sparks 2001; Gordo *et al.* 2008; Hollander *et al.* 2012; Joos *et al.* 2014) and the first instance of three consecutive days of detection (MacMynowski and Root 2007; Choi *et al.* 2010) have been used previously to define migrant arrival time. However, estimating arrival is complex when using bioacoustics and sources of non-detection (*e.g.*, migrant stopover, possible eviction, death) may introduce unexpected errors. To explore the predictive effects of detection error, we develop an arrival definition that combines measures of focal species detection probability to identify unexpected detection gaps. These three definitions and subsequently estimated arrival dates are modelled to predict the movement of three boreal migrant warblers. By completing this comparison, we aim to identify a single definition that best reflects the arrival of boreal migrants that can be applied to future analyses.

Methods

Study area and station selection

We compiled acoustic recordings taken across four field seasons (2015-2018) in the eastern boreal forest region of Alberta (54°N-60°N, 114° W - 110°W). We selected survey sites from a

pool of 263 available sites previously deployed by the Alberta Biodiversity Monitoring Institute (ABMI) as part of their acoustic monitoring program (Figure 1.1). Sites consist of four stations spaced 600m apart with autonomous recording units (ARUs) located at each station. In 2018, we deployed eight additional sites in the Slave River Lowland ecoregion to supplement ABMI acoustic surveillance at the northern limit of our study area. All sites within the pool were grouped into one-degree latitude bands and two sites per survey year were chosen randomly from each band. Stations included in analysis were selected randomly from within the selected site. Station recordings were first examined visually using Audacity® 2.1.3 (Audacity Team 2017) software to confirm the presence of focal species. Where the species was not detected, a new station was selected randomly from the site selected. If the species was not detected at any station within a site, a new site was selected randomly from the pool such that the latitude band was included in analysis. If the species is not detected within any site within a latitude band during one survey year, sites deployed in different years within the same band are selected randomly and included if the focal species is detected to supplement spatial data gaps.

Recorders and Recording Schedule

Wildlife Acoustics® Songmeter SM2, SM2+, SM3, and SM4 models were used to collect acoustic recordings (Wildlife Acoustics, Inc., Maynard, Massachusetts, USA). The ARU model deployed often varied between stations and sites. ARUs deployed by the ABMI during the previous autumn begin recording in March of the survey year and stop recording upon collection in July. Acoustic recordings were processed as .wav files using Kaleidoscope audio processing software (Wildlife Acoustics, Inc., Maynard, Massachusetts, USA). Recordings were processed visually using spectrograms generated using Audacity® 2.1.3 (Audacity Team 2017) software. Spectrograms were visualized using a 2048 FFT Hanning window and a 44,100Hz sampling rate. Multiple daily recordings were taken on a set schedule designed by the ABMI to measure songbird community diversity. To estimate the arrival of songbirds we chose to process only recordings that correspond to dawn chorus. Territorial birds are most vocal at dawn, therefore using dawn recordings permits more efficient assessment of species presence (Wilson and Bart 1985). We examined two recordings per day: the first was ten minutes long beginning at dawn+00:30, and the other was three minutes long beginning at dawn+01:30. Detection of the focal species on either recording was considered as a detection for the entire day. Recordings were examined from April 20th – June 15th representing the range of arrival for most boreal migrants. Recordings disrupted by acute noise (*e.g.*, wind, rain) were removed as they prevented accurate and standardized detection of focal species across recording stations.



Figure A1.1. Location of potential sampling sites. We selected sites from a pool of 263 sites across the eastern boreal forest region of Alberta. For each species, we employed a stratified sampling design selecting 48 stations controlling for latitude and year including 2 stations from each latitude band year combination.

Study Species

We estimated the arrival date of three boreal migrants, Ovenbird (OVEN; *Seiurus aurocapilla*), Tennessee Warbler (TEWA; *Leiothlypis peregrina*) and Yellow-rumped Warbler (YRWA; *Setophaga coronata*). These warbler species were chosen to complement the activity of typical boreal migrants while controlling for differences in life histories and vocal detectability (Flockhart 2010). All focal species included in this analysis are known to sing during migration.

Arrival Definitions

Our three definitions of migrant arrival on breeding territory were:

1- First Detection: “Arrival date is the first date on which the focal species is detected at a station”.

This definition is the most widely used arrival estimator, (Lozano *et al.* 1996; Arvidsson and Neergaard 1991; Tryjanowski and Sparks 2001; Gordo *et al.* 2008; Hollander *et al.* 2012; Joos *et al.* 2014). Species arrival using first detection typically requires only a single observation of an individual on territory to confirm arrival. First detection however may describe the movement of aberrantly early migrants or reflect annual changes in population size resulting in a disconnect between arrival date and the behaviour of the population (Tryjanowski and Sparks 2001; Lehikoinen *et al.* 2004; Sparks *et al.* 2005). However, arrival defined by first detection generates estimates that correlate well with expected trends in reproductive success and territory quality (Smith and Moore 2005; Gunnarsson *et al.* 2006). In our comparison, arrival by first detection is the date on which the focal species is first detected at the station, given the species is not detected in the previous seven days.

2- Three-consecutive: “Arrival date is the first date on which the focal species is detected at a station given subsequent detection of the species on the following two days”.

The three-day consecutive arrival definition is used infrequently in the literature (Choi *et al.* 2010, Thériault *et al.* 2012). This method allows for settlement to stabilize and possibly reduces error. This method requires additional monitoring effort and may result in later arrival estimates if species are not easily detected. In this comparison, three-consecutive arrival date is defined as the first detection date of the species given the species is detected on at least two subsequent consecutive days and the species is not detected in the seven days before estimated first detection. When these criteria are not met, the arrival date is moved to the first date that satisfies the requirements. The initial first detection requires a non-detection period of seven previous days; however, if the date must be moved this requirement is nullified.

3 - Detection-gap: “Arrival date is the first date on which the focal species is detected at a station given the absence of species-specific detection gaps in the following six subsequent days”.

This novel definition attempts to reduce unnecessary sampling effort while also controlling the false negative rate. This definition identifies erroneous arrival dates using unexpected species-specific detection gaps. Detection gaps are calculated using the detection history in a six-day settlement period following the first detection of a species at a station. First, an average daily detection probability for each species is calculated from the six-day detection history following first detection at all stations. This global value is calculated as total days the species is detected divided by the number of total sampling days. This value is then inverted, producing a species-

specific probability of non-detection. Consecutive days of non-detection, or gaps, were then assigned a probability which is the non-detection probability raised to the power of the number of days in the gap. This value decreases as the gap size grows representing the probability of the focal species remaining at the station through consecutive sampling days and remaining undetected. The length of the gap in days that is required to lower the probability of detection below 5% establishes the maximum length of the gap allowed. Therefore, stations where these gaps are not observed in the detection history are still expected to be occupied by the focal species. Under this definition, the first arrival date is the first day where the species is detected given there are no species-specific detection gaps within the subsequent six days and the species is not detected in the seven days before the estimated first detection. When these criteria are not met, the arrival date is moved to the first date that satisfies the requirements. The initial first detection requires a non-detection period of seven previous days; however, if the date must be moved this requirement is nullified.

Arrival Definition Comparison

Latitude is expected to be strongly related to migrant arrival (Sparks *et al.* 2005). Therefore, any reasonable definition of arrival should produce values that can be predicted by latitude. We used linear regression to model how latitude influenced arrival time and the significance of the predictor ($\alpha = 0.05$). Raw arrival dates were converted to ordinal date (1 January = 1) in Rstudio before inclusion in analysis (R package ‘lubridate’ version 1.7.4; Spinu *et al.* 2018, RStudio Team 2020).

Modelling migrant arrival time from such a large spatial range makes validation of true arrival time logistically unfeasible. Instead, we assessed model fit using a combination of modelled adjusted r^2 and estimate standard error. Three-consecutive and detection-gap arrival definitions permit the moving of the arrival date; however, there are instances where the required criteria will produce unrealistically delayed arrival estimates. Stations where arrival could not be estimated between May 1st and June 15th following any one of the arrival definitions were removed from the analysis so sample sizes remained consistent between all three definitions. All analyses were conducted using R Statistical Environment (RStudio Team 2020).

Results

Of 144 species-station-arrivals, we could estimate the arrival using all three methods for 142 stations with one Tennessee Warbler station removed and one Ovenbird station removed.

Removed stations were the result of applying the three-consecutive and detection gap definitions respectively. Our detection-gap method calculated maximum allowed gaps of 2 days for Ovenbird and Yellow-rumped Warbler, and 3 days for Tennessee Warbler. Arrival defined by first detection produces estimates with the lowest standard error across all species (Table 1.1). This definition also explained the most variation for Tennessee Warblers and Yellow-rumped Warblers but explained 3% less than the detections derived from the detection-gap definition for Ovenbird arrivals. The three-consecutive definition performed the worst of all three definitions producing estimates with high error and relatively small explanatory power. Detection-gap performed well for Ovenbird and Yellow-rumped Warblers but had the lowest adjusted r^2 for Tennessee Warbler across the three definitions. Modelled latitude effects were similar between definitions for all focal species (Figure 1.2). Latitude was a significant predictor of migrant arrival in 8 of 9 species-method combinations and was only non-significant when applying the three-consecutive method to Tennessee Warbler.

Conclusion

A successful bioacoustic arrival estimator should be efficient to collect, be accurate, and be able to reveal commonly understood patterns of migration and arrival (Oliver *et al.* 2018). Our comparison suggests that the choice in arrival definition is relatively trivial as effect size and predictive value for latitude effects was similar across definitions. Thus, the choice in definition should be focused more so on the efficiency of data collection rather than the method. First detection is commonly used in other research programs and provides accurate data with limited effort. Therefore, we recommend that bioacoustically derived arrival time is best described using the first detection of a migrant at a station. However, this comparison should be repeated in the field on a smaller scale before these conclusions are used in monitoring programs outside of our survey area.

Table A1.1. Summary statistics of fitted models. All arrival definitions produce similar latitude predictions across all focal species (Arr.def: FD - first detection; DG - detection-gap method; 3Con - three-consecutive method). First detection produced the smallest errors of the estimate (+/- SE) and RSE across all species and explained the most latitude variance for Tennessee and Yellow-rumped Warblers. Latitude was a significant predictor of migrant arrival in 8 of 9 species-method combinations.

Species	Arr. def	Intercept (+/- SE)	Latitude (+/- SE)	F	df	RSE	Adj.R ²	p-value (Lat)
Ovenbird								
	FD	84.96+/-16.96	0.92+/-0.30	9.64	45	3.441	0.158	0.003
	DG	76.27+/-18.08	1.09+/-0.32	11.71	45	3.669	0.189	0.001
	3Con	76.17+/-23.44	1.11+/-0.41	7.256	45	4.755	0.120	0.009
Tennessee Warbler								
	FD	97.54+/-18.28	0.81+/-0.32	6.311	45	3.602	0.104	0.016
	DG	83.12+/-24.74	1.07+/-0.43	6.103	45	4.874	0.010	0.017
	3Con	104.7+/-31.84	0.73+/-0.56	1.693	45	6.271	0.015	0.200
Yellow-rumped Warbler								
	FD	72.69+/-17.23	0.98+/-0.30	10.58	46	3.567	0.169	0.002
	DG	71.22+/-18.07	1.01+/-0.32	10.16	46	3.741	0.163	0.002
	3Con	74.39+/-20.35	0.97+/-0.36	7.451	46	4.212	0.121	0.008

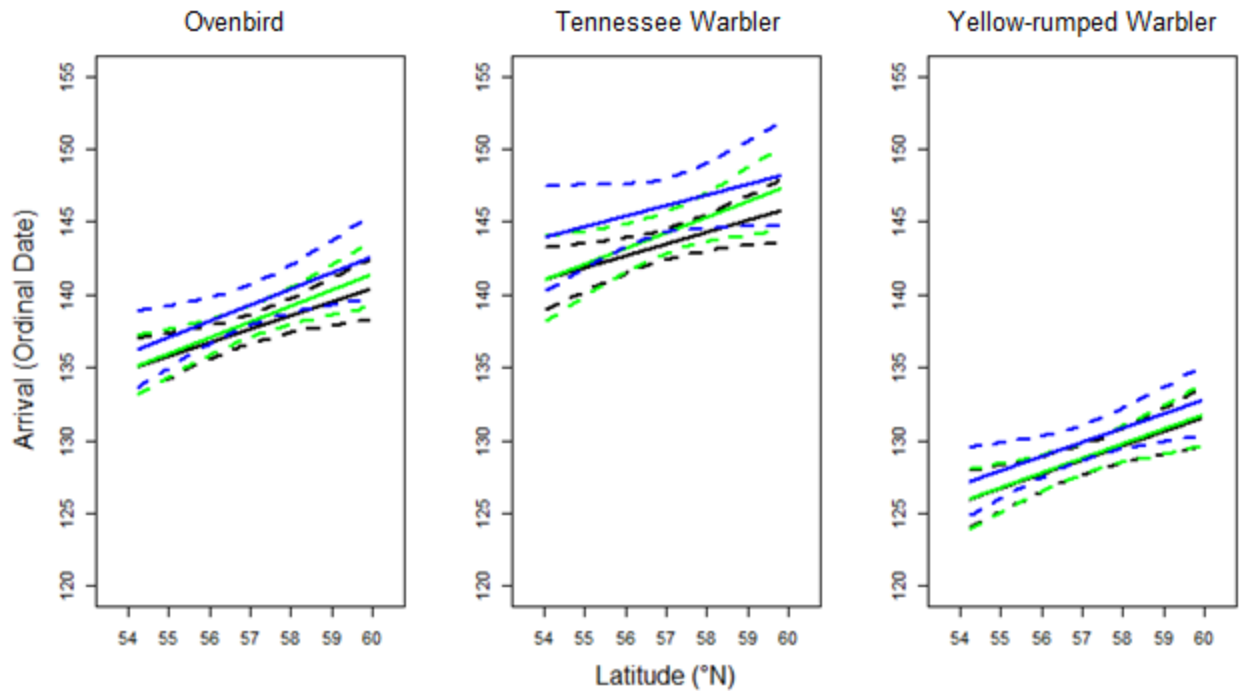


Figure A1.2. Latitude effect under different arrival definitions. Similar latitude responses are predicted using each of the three arrival definitions (black line: first detection, green line: detection-gap method, blue line: three-consecutive method). No difference in method effectiveness is observed for any of the focal species. Dashed lines represent 95% confidence intervals of the estimate.

Appendix 2. Additional Tables

Table A2.1. AIC and Δ AIC values of candidate arrival models. Migrant arrival time modelled in two different datasets: the Dominant Stand Models consider the physical and temporal features of the settled territory (VEG = generalized vegetation type, LA = Latitude, LO = Longitude, Y= Survey Year, A = Estimated age of dominant generalized vegetation type) whereas the Predicted Density Models model consider only the estimated density of the species on the territory (PD = Predicted Density, Y= Survey Year). Overall, vegetation-based models performed better for all species. Latitude was also an important predictor and included in the top model for all considered species. Age was an important predictor for the arrival of Tennessee and Yellow-rumped warbler arrival. All predictors are included in the top Yellow-rumped warbler model. Predicted Density models explained less of the data but performed similarly to the vegetation when predicting Yellow-rumped warbler arrival.

Model (Arrival ~ ...)	OVEN		TEWA		YRWA	
	AIC	Δ AIC	AIC	Δ AIC	AIC	Δ AIC
Dominant Stand Models Modelset						
VEG	352.62	21.37	727.13	21.24	421.45	16.59
VEG + LA	351.91	20.66	723.59	17.70	413.67	8.81
VEG + LO	349.06	17.81	729.12	23.23	422.61	17.75
VEG + Y	331.85	0.60	727.58	21.69	417.38	12.52
VEG + A	353.99	22.74	711.01	5.12	422.18	17.31
VEG + LA + LO	348.44	17.19	725.46	19.57	414.36	9.51
VEG + LA + Y	331.25	-	718.92	13.03	412.29	7.43
VEG + LA + A	352.34	21.09	709.45	3.56	411.57	6.71
VEG + LO + Y	332.07	0.82	712.32	6.43	415.63	10.77
VEG + LO + A	350.49	19.24	729.31	23.42	422.99	18.13
VEG + A + Y	333.13	1.88	711.19	5.30	417.46	12.60
VEG + LA + LO + Y	331.51	0.26	720.90	15.01	410.56	5.70
VEG + LA + LO + A	348.97	17.72	711.28	5.39	411.31	6.45

VEG + LO + A + Y	333.24	1.99	711.40	5.51	414.66	9.80
VEG + LA + A + Y	331.41	0.16	705.89	-	408.53	3.68
VEG + LA + LO + A + Y	331.5	0.25	707.08	1.19	404.86	-
Predicted Density Models Modelset						
PD	353.32	22.07	723.49	17.6	411.75	6.89
PD + Y	338.62	7.37	724.99	19.1	406.31	1.45

Table A2.2. Dominant stand model set effects on migrant arrival time. Standardized effect sizes (β) are presented +/- SE. Top model for each focal species is presented. The reference vegetation cover is Black Spruce as it was typically provided the lowest predicted density of all cover types. 2015 is the reference year and was selected to identify changes in arrival in successive years. Arrival is influenced by station level vegetation cover for Ovenbirds and Tennessee Warblers and correlates with differences in predicted density from cure4insect. Stand age effects varied between Yellow-rumped Warbler and Tennessee Warblers but are relatively small. Spatial effects on arrival varied across all species but were most influential on Yellow-rumped Warbler arrival (Significance levels, $p < 0.05$: *, $p < 0.01$: **, $p < 0.001$: ***).

Species (Arrival ~)	n	Predictor	Estimate	T	p
Ovenbird	70	Intercept	137.729 +/-0.285	484.189	<0.001*
		Deciduous	-0.974 +/-0.456	-2.135	0.037*
		Mixedwood	-0.391 +/-0.359	-1.089	0.281
		Pine	0.5467 +/-0.328	1.669	0.100
		Shrub	0.483 +/-0.372	1.297	0.200
		White Spruce	-0.721 +/-0.367	-1.967	0.054
		Latitude	0.453 +/-0.300	1.508	0.137
		2016	0.207 +/-0.385	0.539	0.592
		2017	-1.235 +/-0.386	-3.204	0.002**
		2018	-1.183 +/-0.358	-3.306	0.002**
Tennessee	129	Intercept	142.930 +/-0.321	445.302	<0.001*

Warbler		Deciduous	-2.390+/-0.485	-4.925	<0.001*	
		Mixedwood	-0.831+/-0.390	-2.134	0.035*	
		Pine	-0.007+/-0.411	-0.018	0.985	
		Shrub	-0.795+/-0.439	-1.811	0.073	
		White Spruce	-0.831+/-0.452	-1.839	0.068	
		Latitude	0.987+/-0.377	2.622	0.01**	
		Stand Age	-1.115+/-0.375	-2.975	0.004**	
		2016	0.078+/-0.430	0.181	0.857	
		2017	0.553+/-0.444	1.246	0.215	
		2018	-0.664+/-0.448	-1.482	0.141	
	Yellow-rumped Warbler	69	Intercept	128.928+/-0.499	258.362	0.004**
			Deciduous	-0.085+/-0.687	-0.123	0.902
		Mixedwood	-0.999+/-0.603	-1.655	0.103	
		Pine	-0.556+/-0.640	-0.885	0.38	
		Shrub	-0.071+/-0.551	-0.13	0.897	
		White Spruce	-0.022+/-0.578	-0.039	0.969	
		Latitude	1.971+/-0.605	3.26	0.002**	
		Longitude	1.338 +/-0.605	2.211	0.031*	
		Stand Age	1.571+/-0.606	2.594	0.012*	
		2016	-0.288+/-0.773	-0.373	0.71	
		2017	1.613+/-0.836	1.929	0.059	
		2018	1.355+/-0.803	1.687	0.097	