Bioacoustically derived migration arrival times in boreal birds: implications for assessing habitat quality

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ABSTRACT. Long-distance migrant songbirds are declining globally. Reversing declines requires a good understanding of habitat quality. Local studies have shown that territory settlement date (arrival) is generally correlated with density and productivity. Despite widespread acceptance, large-scale multispecies demonstrations of arrival time being correlated with habitat quality are lacking. We investigated whether arrival date estimated from eczonal scale bioacoustic monitoring could be predicted by an independent estimate of estimated density for Ovenbird (Seiurus aurocapilla), Tennessee Warbler (Leiothlypis peregrina), and Yellow-rumped Warbler (Setophaga coronata). We also examined local Ovenbird settlement patterns by comparing relative arrival and observed local density differences between nearby territories. Arrival date was estimated as the first focal species detection date on a breeding territory and the cure4insect R package was used to predict estimated average density. Using predicted average density as a habitat quality proxy, we found earlier arrivals in higher quality territories (Ovenbird 1.04 +/- 0.33 days earlier, Tennessee Warbler 1.96 +/- 0.36 days earlier, Yellow-rumped Warbler 1.23 +/- 0.54 days earlier). We also showed that arrival time was earlier in habitats preferred by each species. Spatial patterns of arrival varied among species although latitude was always an important predictor. Locations where predicted Ovenbird densities were estimated to be higher were filled before sites with lower predicted density but only 600 m away (2.9 +/- 1.4 days earlier). Correlating migrant arrival time and density suggests density is a reasonable measure of habitat quality. Combined, density and arrival data from bioacoustics provide a low-cost habitat-assessment tool that better informs the types of forest that need to be protected for species of concern, which will be particularly important as land-use and climate change impacts increase in the boreal forest.

Les dates d’arrivée des migrations d’oiseaux boréaux obtenues de manière bioacoustique : implications pour la qualité de l’habitat

Les populations de passereaux migrateurs de longues distances sont en déclin dans le monde entier. Pour inverser cette tendance, il est indispensable de bien comprendre la qualité de l’habitat. Des études locales indiquent que la date d’implantation sur le territoire (d’arrivée) est généralement liée à la densité et à la productivité. Bien que cette idée soit largement acceptée, nous manquons de preuves concernant le lien entre la date d’arrivée en masse d’espèces multiples et la qualité de l’habitat. Nous avons cherché à savoir si la date d’arrivée estimée n fonction d’une surveillance bioacoustique à l’échelle des écozones pouvait être prévue par une estimation indépendante de la densité de l’habitat. Des études locales indiquent que la date d’arrivée relative et observée des différences de densité locales entre les territoires voisins. La date d’arrivée a été estimée comme la première date de détection de l’espèce focale sur un territoire de reproduction et nous avons utilisé l’ensemble cure4insect R pour prévoir la densité moyenne estimée. En utilisant la densité moyenne prédite comme un indicateur de la qualité de l’habitat, nous avons constaté des arrivées plus précoces dans les territoires de qualité supérieure (parulines couronnées (Seiurus aurocapilla), la paruline obscure (Leiothlypis peregrina) et la paruline à croupion jaune (Setophaga coronata)). Nous avons également examiné les modèles d’implantation des parulines couronnées en comparant la date d’arrivée relative et observée des différences de densité locales entre les territoires voisins. La date d’arrivée a été estimée comme la première date de détection de l’espèce focale sur un territoire de reproduction et nous avons utilisé l’ensemble cure4insect R pour prévoir la densité moyenne estimée. En utilisant la densité moyenne prédite comme un indicateur de la qualité de l’habitat, nous avons constaté des arrivées plus précoces dans les territoires de qualité supérieure (parulines couronnées 1.04 +/- 0.33 jours plus tôt, parulines obscures 1.96 +/- 0.36 jours plus tôt, paruline à croupion jaune 1.23 +/- 0.54 jours plus tôt). Nous avons également noté que la date d’arrivée était plus précoce dans les habitats préférés de chaque espèce. Les modèles spatiaux d’arrivée variaient entre les espèces, même si la latitude demeure un élément prédictif important. Les emplacements où les densités de parulines couronnées étaient estimées comme supérieures étaient peuplés avant les sites où la densité prédite était inférieure, bien qu’elles ne soient distantes que de 600 mètres (2.9 +/- 1.4 jours plus tôt). La corrélation de la date d’arrivée des oiseaux migrateurs et de la densité suggère que la densité est une mesure raisonnable de la qualité de l’habitat. Combinées, les données de densité et de date d’arrivée obtenues par mesures bioacoustiques fournissent un outil économique d’évaluation de l’habitat qui informe mieux les types de forêt qui doivent être protégés pour les espèces considérées, ce qui deviendra de plus en plus important à mesure que l’utilisation des terres et le changement climatique affecteront l’augmentation des populations dans la forêt boréale.

Key Words: arrival; bioacoustics; density; habitat quality; migration

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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 (Bets et al. 2006). Thus, understanding the habitat requirements of migrant birds across their entire life cycle is vital in conserving these species.

Our understanding of habitat selection by birds 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 (Machtans and Latour 2003, Toms et al. 2006, Ball et al. 2016). However, the utility of abundance or density as a measure of habitat quality has been questioned (Remés 2003). Density may accurately reflect habitat quality locally but may misrepresent habitat quality across the landscape because of 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 (e.g., observer access restrictions to field sites during territory settlement, accommodation of field staff in remote locations) making it difficult to confirm the relationship between density and demography at large spatial extents (Vaughan and Ormerod 2003, Bets et al. 2006, Furnas and Callas 2015). Therefore, other cost-effective methods of assessing habitat importance over large areas through metrics other than density and demography are needed (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). Additionally, individuals in good physical condition typically arrive earlier and may be more likely to have a second brood or successfully replace a failed clutch (Kokko 1999, Gunnarsson et al. 2006). Competition for high quality breeding territories is high at settlement and birds must arrive early to secure space from competitors. Therefore, it is generally assumed that earlier settlement typically identifies high quality territories and subsequent settlement patterns should provide insights into perceived habitat quality (Kokko 1999, Joos et al. 2014, Samponius and Both 2017). Thus, population level patterns in habitat importance may be assessed by relative arrival timing, because it helps us understand 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 cost-effectively (Buxton et al. 2016, Paxton and Moore 2017, Oliver et al. 2018). Estimating arrival is a relatively novel application of bioacoustics and is tested primarily through acoustic indices in remote northern songbird community soundscapes. We argue that species-level arrival can also be measured from acoustic surveillance, and provides arrival dates that may even be more accurate than traditional methods of migration monitoring, such as mist netting and human-based point count surveys, which are restricted to smaller spatial extents and dependent on the availability of human observers (Oliver et al. 2018).

We explored spatial and temporal factors influencing the arrival timing of three boreal migrant bird 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 predicted 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 developed models to predict arrival time as a function of vegetation cover, forest age, latitude, and longitude as predictors under the premise that it may inform which elements of a high density site are most important to these species. We predicted 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.

Although understanding regional patterns of arrival is important, there may be additional insights that can be gained from looking at arrival patterns locally. Local breeding density is often used as a proxy for territory quality if ecological traps do not occur (Robertson and Hutto 2006, Hollander et al. 2012) However, behavioral processes such as conspecific attraction and competition can also be 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 nearby, or whether high and low density sites in the same general area are settled simultaneously, we estimated the arrival of Ovenbird (Seiurus aurocapilla) at four locations 600 m apart within each site. Specifically, we determined the day at which the maximum local count occurred at each station. We hypothesized that because of the habitat specificity of the Ovenbird, regional patterns in arrival timing would be generally reflected in local arrival timing and fine-tuned in response to subsequent territory saturation following arrival.
METHODS

Study area
The study area included much of the Alberta boreal forest region (54°N, 60°N; -114°W, -120°W; Panel A, Fig. 1.1). However, our study area is largely focused within the Lower Athabasca Planning Region (LAPR) of northeastern Alberta. The area is marked by industrial development, primarily in the energy, forestry, and agricultural sectors. This area also is characterized by a mosaic of upland deciduous forests dominated by trembling aspen (Populus tremuloides), coniferous upland forests largely comprising white spruce (Picea glauca) or jack pine (Pinus banksiana), and wetlands including black spruce (Picea mariana), bogs, and fens. Although there are differences in the distribution of forest types at a landscape scale, all the forest types considered in our study were available across the area evaluated.

Fig. 1. Survey area and sampling stations. Panel A represents the survey area in grey within the province of Alberta covering most of the boreal forest region (54 to 60 degrees North). Survey area consists of five LUFs representing Albertan watersheds. Panels B to D represent stations included in the analyses: panel B, Ovenbird (Seiurus aurocapilla), 70 stations; panel C, Tennessee Warbler (Leiothlypis peregrina), 129 stations; panel D, Yellow-rumped Warbler (Setophaga coronata), 69 stations. Icons represent the approximate station location and sampling year (triangles, 2015; squares, 2016; diamonds, 2017; stars, 2018).

Site selection
We conducted four years (2015–2018) of acoustic surveillance across the boreal forest region of Alberta. 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. A site typically consisted of four acoustic recording units (ARUs) spaced 600 m 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 10-minute recording at dawn + 00:30 and a three-minute recording at dawn + 01:30. We listened to recordings from 20 April until 14 June. The first stage of data processing included listening to each location every fifth day to determine if the species was ever observed. If the focal species was detected on any recording from stage one, the station was flagged and added to a pool of available listening data for further processing. In the second stage, recordings from flagged stations were examined each day to refine the estimated arrival date to the first date the focal species was detected at a station. The first day was determined by continually searching backwards (i.e., getting closer to 20 April) until we found a period of time where the species was not observed within the seven days prior to the first day of detection. We examined seven days prior to the first detection of the species to limit false-negative error. Stations without focal species detection were removed from analysis and randomly replaced with a new station from within the site until a focal species was detected. Sites without focal species detection were excluded.

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). The Ovenbird is a short-to-long range Neotropical migrant with individuals breeding in Alberta and 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, ABMI and BAM 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 but are more likely to be 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, ABMI and BAM 2019b). The Yellow-rumped Warbler is a short-range migrant with individuals breeding in Alberta and 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, ABMI and BAM 2019c). All focal species are found throughout the study area and sing during migration.

Recorders and recording 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 we deployed often varied between and within sites. All ARUs were deployed before migrants returned 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 formats 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). Spectrograms were visualized using a 2048 FFT Hanning window and a sampling rate of 44,100 Hz. To estimate the arrival date of songbirds, we examined recordings taken during the dawn chorus because 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 14 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 because they prevented accurate and standardized detection of focal species.

Ecozonal 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 and took far more effort to calculate (Appendix 1). Additionally, arrival windows of migratory warblers in northern Alberta are locally narrow with settlement often completed within two to five days, potentially limiting the importance of any slight 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 the day of the year (1 January = 1) in RStudio before inclusion in analysis using R package lubridate 1.7.4 (Spinu et al. 2018, RStudio 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 ARU location and extracted all vegetation data within a 150 m radius. Station locations were measured using a GPS and are accurate to within ~10 m. 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 vegetation 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, age estimates were unavailable for a small portion of stations. Only when the dominant stand age was unknown for all stands within the buffer classified as the dominant vegetation type did we use average age of all vegetation types within the buffer to estimate the age of the dominant vegetation type. 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 5 km of the station) because 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 estimates of expected average density using the cure4insect package in RStudio (RStudio Team 2019, Solymos 2020). This package used over 60,000 point counts to create a model that predicts average density for the focal species during the breeding season across Alberta. The model used to create cure4insect includes variables such as anthropogenic disturbance, climatic conditions, spatial location, landcover characteristics, forest type, forest age, and whether the stand originated from fire or harvest. In addition, it takes into account larger scale availability of habitat (i.e., patch size). 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 predict an estimated density for each station we visited. Predicted average density values were then ranked from lowest to highest by dividing all density estimates by the maximum predicted average density. This standardized effect sizes across species.

Local arrival estimation

We assessed the local arrival of Ovenbirds across 116 recording stations within 29 sites. In this situation, a maximum of four ARUs spaced 600 m apart in locations where territories could be settled were monitored within a site. Ovenbirds have territory sizes between 0.5 and 1.5 ha in size (Bayne et al. 2005) so it is very unlikely the same individuals were being counted at each station. Only after an Ovenbird arrival was determined at the first station did we determine the arrival time of Ovenbirds at the other three stations. To assess how the space around an ARU station was filled, we counted 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 distinguished individual Ovenbirds by visual spectrogram inspection, estimating the number of individuals as the number of overlapping and structurally distinct Ovenbird songs. 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 at each station over this period and defined the first date this value was reached as the Maximum Date (MaxDate).

Exploration of arrival covariates

In a series of models, we assessed how density, spatial coordinates and vegetation conditions influenced arrival data by fitting
species arriving at more northerly stations. Both increasing and decreasing 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.

Results

We estimated the arrival date for Tennessee Warbler at 129 stations, Ovenbird at 70 stations, and Yellow-rumped Warbler at 69 stations (Panels B, C, D, Fig. 1). Focal species arrival distribution (Fig. 2) varied by species with Yellow-rumped Warblers arriving first (mean: 8 May; SD: +/- 4.7 days; range: 26 days; 23 April to 20 May) followed by Ovenbirds (mean: 16 May; SD: +/- 3.2 days; range: 16 days; 11 May to 26 May), and finally Tennessee Warblers (mean: 23 May; SD: +/- 4.5 days; range: 25 days; 11 May to 4 June). The arrival timing of Ovenbird (W = 0.979, p = 0.303) and Yellow-rumped Warblers (W = 0.975, p = 0.335) are normally distributed. Tennessee Warbler arrival timing is non-normal (W = 0.918, p > 0.001).

Higher predicted density from cure4insect was a significant predictor of earlier arrival across all species (Table 1, Fig. 3). The relative predictive strength of density varied marginally by species. Within the vegetation model set, the best model varied between species. Whereas the global model was selected for Yellow-rumped Warbler, the top Tennessee Warbler model removed longitude, and the top Ovenbird model had both age and longitude removed (Table A2.2, Appendix 2). Tennessee Warblers and Ovenbirds arrived at stations dominated by deciduous forest earlier than other vegetation types, while Tennessee Warblers also arriving earlier at average at mixedwood stations (Fig. 4). 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.

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
Table 1. Modeled 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 (Seiurus aurocapilla) | 70  | Intercept         | 137.729+/-0.309 | 168.919 | < 0.001*** |
|                     |     | Density 2016      | -1.044+/-0.327 | -3.197  | 0.002**  |
|                     |     | Density 2017      | -1.300+/-0.406 | -3.203  | 0.002**  |
|                     |     | Density 2018      | -1.090+/-0.368 | -2.962  | 0.004**  |
| Tennessee Warbler (Leiothlypis peregrina) | 129 | Intercept         | 142.828+/-0.35 | 169.148 | < 0.001*** |
|                     |     | Density 2016      | -1.961+/-0.357 | -5.496  | < 0.001*** |
| Yellow-rumped Warbler (Setophaga coronata) | 69  | Intercept         | 128.928+/-0.527 | 72.019  | < 0.001*** |
|                     |     | Density 2016      | -1.226+/-0.538 | -2.281  | 0.026*   |
|                     |     | Density 2017      | -1.243+/-0.768 | -1.617  | 0.111    |
|                     |     | Density 2018      | 0.537+/-0.799  | 0.672   | 0.504    |

Fig. 3. Modeled density effect on the arrival. Arrival date provided as day of the survey year (1 = 1 January). Ovenbird, Seiurus aurocapilla (A, n = 70), Tennessee Warbler, Leiothlypis peregrina (B, n = 129), and Yellow-rumped Warbler, Setophaga coronata (C, n = 69) arrival was earlier when the predicted density of the station increased (p < 0.05).

Fig. 4. Mean migrant arrival by dominant stand type. Arrival date provided as day of the survey year (1 = 1 January). Yellow-rumped Warblers, Setophaga coronata (left panel, n = 69) have no difference in arrival date by vegetation type. Ovenbird, Seiurus aurocapilla (center panel, n = 70) arrival appears to be different in two major vegetation groups that correspond to differences expected from predicted density. Tennessee Warblers, Leiothlypis peregrina (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). Red dashed line is the average arrival across all vegetation types. Error bars are 95% confidence intervals of the mean arrival date.

Table 2. Generalized Estimating Equation (GEE) output of predicted density on local arrival date of Ovenbirds (Seiurus aurocapilla). 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  |

preferences for the most part. Our predicted density estimate is strongly influenced by forest type and age, so this is not surprising but suggests that the cues are used by individual birds when they make settlement decisions, to some degree influencing the number of individuals that settle there. As more arrival data becomes available, it would be useful to assess if additional covariates (climate, patch size) predict arrival time or if other behavioral processes (i.e., conspecific attraction) could be detected.
Fig. 5. Population averaged effect of predicted Ovenbird (Seiurus aurocapilla) density on local arrival date. Arrival date provided as day of the survey year (1 = 1 January). 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.

Fig. 6. Population averaged effect of predicted Ovenbird (Seiurus aurocapilla) density on territory saturation date (Maximum Date). Arrival date provided as day of the survey year (1 = 1 January). 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 3. Generalized Estimating Equation (GEE) output of predicted density on the date of territory situation (MaxDate) by Ovenbirds (Seiurus aurocapilla). 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 |

Ovenbirds settled territories dominated by deciduous forest that provide reportedly high quality Ovenbird habitat (Gibbs and Faaborg 1990, Mazeroise and Hobson 2004, Mattsson and Niemi 2008). Tennessee Warblers arrived at both deciduous and mixedwood dominated territories early, corresponding to habitat containing higher densities of Tennessee Warbler (ABMI and BAM 2019b), but this behavior may not reflect habitat quality within every year. Tennessee Warblers in some years are found in highest abundance in coniferous dominated areas of the western boreal forest (Machtans and Latour 2003). This incongruity may be linked to the annual population fluctuations of spruce budworm (Blancher 2003). Spruce budworm activity in Alberta was relatively stable throughout our study period and thus we are likely detecting low budworm habitat associations during this period (Alberta Agriculture and Forestry 2017). As habitat generalists, Yellow-rumped Warblers showed no by-habitat arrival patterns because 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 may actually be providing greater insight into the locations of perceived habitat quality for this species.

Locally, the arrival of Ovenbirds follows a similar pattern because territories of higher predicted density were settled first. This finding likely reflects local qualities of Ovenbird territories but could also reflect conspecific attraction. 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 revealed that the date of territory saturation (MaxDate) may also be influenced by the predicted density of the territory. Combined, our analysis of local arrival timing suggests that Ovenbirds are not only settling into territories of higher predicted density first, but also that these potentially high quality territories are generally filled first. These local Ovenbird arrival patterns reflect both the pattern of territory selection observed at an ecozonal 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 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 suggest at the ecozonal scale, arrival windows are narrower for species with narrower habitat breadth. The Ovenbird settlement across the province was 9.5 days shorter on average than the other species.

However, our measured density values may not accurately represent actual territory density because we did not vocally identify individual Ovenbirds or consider structural habitat features that may have influenced detection. Local arrival patterns might have been a product of spatial proximity of the 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 a forest stand. Our greatest obstacle is the uncertainty of individual reproductive success; without this measure we cannot rule out ecological traps (Van Horne 1983, Remés 2003). However, we believe derived density models can reasonably approximate territory quality across the ecozone given the consistency of local and ecozonal arrival patterns with reported habitat associations from the literature. Future studies should expand the number and structural diversity of territories examined locally and explore microhabitat quality, individual condition, and consider in-field identification of birds combined with bioacoustic surveillance and subsequent automated individual recognition.

Apart from density dependent measures of habitat quality, other factors contribute to ecozonal 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, ABMI and BAM 2019b, 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 types for Yellow-rumped Warbler territories, both of which tend to be naturally younger 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 stopovers, which ultimately prolong migration (Paxton and Moore 2017). Tennessee Warbler migration speed is therefore faster than Yellow-rumped Warblers because they have further to travel, but potentially slower than Ovenbird because of relaxed competition for breeding territory upon arrival. Thus, arrival may reflect both local trends in habitat preference while accounting for large-scale phenomena that ultimately reflect seasonal reproductive success. Measuring arrival reveals trends in habitat selection that reflect density and also incorporate other features of migrant life history, which are often correlated with seasonal reproductive success.

We have shown that arrival provides detailed information that is correlated with density derived from point counts (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). With a growing amount of bioacoustic data becoming available, future studies will be better able to quantify spatial patterns of arrival at much larger scales, which may help us better understand phenomena such as the timing and frequency of leap-frog migration (Fraser et al. 2018). To do this, a more integrated system of sharing acoustic data is needed and recording devices need to be deployed prior to arrival. We recommend future field studies to confirm the accuracy of first detection on station occupancy, and to 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 important information that can guide land management and species conservation in the future (Ball et al. 2016, Rosenberg et al. 2019).

Responses to this article can be read online at: https://www.ace-eco.org/issues/responses.php/2224

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LITERATURE CITED

Alberta Agriculture and Forestry. 2017. Forest health and adaptation: annual report. Alberta Agriculture and Forestry, Government of Alberta, Edmonton, Alberta, Canada.

Alberta Biodiversity Monitoring Institute (ABMI). 2015. Manual for species modeling and intactness. Version 2016-04-14, ABMI, University of Alberta, Edmonton, Alberta, Canada.

Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project (ABMI and BAM). 2019a. Ovenbird (Seiurus aurocapillus). Alberta Biodiversity Monitoring Institute, University of Alberta, Edmonton, Alberta, Canada. https://beta.abmi.ca/biobrowser/species-detail.html?tsn=726205

Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project (ABMI and BAM). 2019b. Tennessee Warbler (Oreothlypis ruficapilla). Alberta Biodiversity Monitoring Institute, University of Alberta, Edmonton, Alberta, Canada. https://beta.abmi.ca/biobrowser/species-detail.html?tsn=99001334

Alberta Biodiversity Monitoring Institute and Boreal Avian Modelling Project (ABMI and BAM). 2019c. Yellow-rumped Warbler (Setophaga coronata). Alberta Biodiversity Monitoring Institute, University of Alberta, Edmonton, Alberta, Canada. https://beta.abmi.ca/biobrowser/species-detail.html?tsn=99001401

Arvidsson, B. L., and R. Neergaard. 1991. Mate choice in the Willow Warbler - a field experiment. Behavioral Ecology and Sociobiology 29:225-229. https://doi.org/10.1007/BF00166406

Audacity Team. 2017. Audacity: free audio editor and recorder, Version 2.1.3. http://www.audacityteam.org/download

Ball, J. R., P. Sólóymos, F. K. A. Schmiegelow, S. Haché, J. Schieck, and E. M. Bayne. 2016. Regional habitat needs of a nationally listed species, Canada Warbler (Cardellina canadensis), in Alberta, Canada. Avian Conservation and Ecology 11(2):10. https://doi.org/10.5751/ACE-00916-110210

Bayne, E. M., S. L. Van Wilgenburg, S. Boutin, and K. A. Hobson. 2005. Modeling and field-testing of Ovenbird (Seiurus aurocapillus) responses to boreal forest dissection by energy sector development at multiple spatial scales. Landscape Ecology 20:203-216. https://doi.org/10.1007/s10980-004-2265-9

Betts, M. G., A. W. Diamond, G. J. Forbes, M.-A. Villard, and J. S. Gunn. 2006. The importance of spatial autocorrelation, extent, and resolution in predicting forest bird occurrence. Ecological Modelling 191:197-224. https://doi.org/10.1016/j.ecolmodel.2005.04.027

Blancher, P. 2003. The importance of Canada’s boreal forest to landbirds. The Canadian Boreal Initiative and the Boreal Songbird Initiative, Seattle, Washington, USA. https://www.borealbirds.org/publications/importance-canadas-boreal-forest-landbirds

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment 2(8):403-410. https://doi.org/10.1890/1540-9295(2004)002[0403:AHESCB]2.0.CO;2

Both, C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. Current Biology 20(3):243-248. https://doi.org/10.1016/j.cub.2009.11.074

Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296-298. https://doi.org/10.1038/35077063

Brawn, J. D., S. K. Robinson, and F. R. Thompson. 2001. The role of disturbance in the ecology and conservation of birds. Annual Review of Ecology and Systematics 32(1):251-276. https://doi.org/10.1146/annurev.ecolsys.32.081501.114031

Buxton, R. T., E. Brown, L. Sharman, C. M. Gabriele, and M. F. McKenna. 2016. Using bioacoustics to examine shifts in songbird phenology. Ecology and Evolution 6(14):4697-4710. https://doi.org/10.1002/ece3.2242

Chalfoun, A. D., and T. E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44(5):983-992. https://doi.org/10.1111/j.1365-2664.2007.01352.x

Choi, Y. S., Y. K. Lee, and J. C. Yoo. 2010. Relationships of settlement date and body size with reproductive success in male Oriental Great Reed Warbler Acrocephalus orientalis. Zoological Studies 49(3):398-404.

Cornell, K. L., and T. M. Donovan. 2010. Scale-dependent mechanisms of habitat selection for a migratory passerine: an experimental approach. Auk 127(4):899-908. https://doi.org/10.1525/auk.2010.09171

Currie, D., D. B. A. Thompson, and T. Burke. 2000. Patterns of territory settlement and consequences for breeding success in the Northern Wheatear Oenanthe oenanthe. Ibis 142(3):389-398. https://doi.org/10.1111/j.1474-919X.2000.tb04435.x

Environmental Systems Research Institute (ESRI). 2019. ArcGIS ArcMap, Version 10.7.1. Environmental Systems Research Institute, Redlands, California, USA. https://desktop.arcgis.com/en/arcmap/

Flockhart, D. T. T. 2010. Timing of events on the breeding grounds for five species of sympatric warblers. Journal of Field Ornithology 81(4):373-382. https://doi.org/10.1111/j.1557-9263.2010.00293.x

Fraser, K. C., A. Roberto-Charron, B. Cousens, M. Simmons, A. Nightingale, A. C. Shoe, R. L. Cormier, and D. L. Humph. 2018. Classic pattern of leapfrog migration in Sooty Fox Sparrow Passerella iliaca unalischeschini is not supported by direct migration tracking of individual birds. Auk 135(3):572-582. https://doi.org/10.1642/AUK-17-224.1

Furnas, B. J., and R. L. Callas. 2015. Using automated recorders and occupancy models to monitor common forest birds across a large geographic region. Journal of Wildlife Management 79(2):325-337. https://doi.org/10.1002/jwmg.821

Gibbs, J. P., and J. Faubourg. 1990. Estimating the viability of Ovenbird and Kentucky Warbler populations in forest fragments. Conservation Biology 4(2):193-196. https://doi.org/10.1111/j.1523-1739.1990.tb00108.x

Gordo, O., J. J. Sanz, and J. M. Lobo. 2008. Geographic variation in onset of singing among populations of two migratory birds. Acta Oecologica 34(1):30-64. https://doi.org/10.1016/j.actao.2008.03.006
Gunnarsson, T. G., J. A. Gill, P. W. Atkinson, G. Gélinaud, P. M. Potts, R. E. Croger, G. F. A. Gudmundsson, and W. J. Sutherland. 2006. Population-scale drivers of individual arrival times in migratory birds. Journal of Animal Ecology 75(5):1119-1127. https://doi.org/10.1111/j.1365-2656.2006.01311.x

Haché, S., E. M. Bayne, M.-A. Villard, H. Proctor, C. S. Davis, D. Stralberg, J. K. Janes, M. T. Hallworth, K. R. Foster, E. Chidambara-vasi, A. A. Grossi, C. G. Jamieson, and H. Krikun. 2017. Phylogeography of a migratory songbird across its Canadian breeding range: implications for conservation units. Ecology and Evolution 7(16):6078-6088. https://doi.org/10.1002/ece3.3170

Haché, S., M.-A. Villard, and E. M. Bayne. 2013. Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. Ecology 94(4):861-869. https://doi.org/10.1890/12-1025.1

Hollander, F. A., N. Titeux, and H. Van Dyck. 2012. Territorial resource valuation deviates from habitat quality in an ecologically trapped, long-distance migratory bird. Behavioral Ecology and Sociobiology 66:777-783. https://doi.org/10.1007/s00265-012-1325-4

Hunt, P. D., and D. J. Flaspohler. 1998. Yellow-rumped Warbler (Setophaga coronata), version 2.0. In A. F. Poole and F. B. Gill, editors. Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.376

Janiszewski, T., P. Minias, and Z. Wojciechowski. 2013. Occupancy reliably reflects territory quality in a long-lived migratory bird, the White Stork. Journal of Zoology 291(3):178-184. https://doi.org/10.1016/j.jzo.2012.09

Johnson, M. D. 2007. Measuring habitat quality: a review. Condor 109(3):489-504. https://doi.org/10.1093/condor/109.3.489

Jonzén, N., A. Hedenström, and P. Lundberg. 2007. Climate change and the optimal arrival of migratory birds. Proceedings of the Royal Society 274(1607):269-274. https://doi.org/10.1098/rspb.2006.3719

Jonzén, N., A. Lindén, T. Ergon, E. Knudsen, J. O. Vik, D. Rubolini, D. Piacentini, C. Brinch, F. Spina, L. Karlsson, et al. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. Science 312(5782):1959-1961. https://doi.org/10.1126/science.1126119

Joos, C. J., F. R. Thompson, and J. Faaborg. 2014. The role of territory settlement, individual quality, and nesting initiation on productivity of Bell’s Vireos Vireo bellii bellii. Journal of Avian Biology 45(6):584-590. https://doi.org/10.1111/jav.00400

Kokko, H. 1999. Competition for early arrival in migratory birds. Journal of Animal Ecology 68(5):940-950. https://doi.org/10.1046/j.1365-2656.1999.00343.x

Laioolo, P. 2010. The emerging significance of bioacoustics in animal species conservation. Biological Conservation 143(7):1635-1645. https://doi.org/10.1016/j.biocon.2010.03.025

Lehikoinen, E. S. A., T. H. Sparks, and M. Zalakovicius. 2004. Arrival and departure dates. Advances in Ecological Research 35:1-31. https://doi.org/10.1016/S0065-2504(04)35001-4

Leston, L., E. M. Bayne, and F. K. A. Schmiegelow. 2018. Long-term changes in boreal forest occupancy within regenerating harvest units. Forest Ecology and Management 421:40-53. https://doi.org/10.1016/j.foreco.2018.02.029

Lozano, G. A., S. Perreault, and R. E. Lemon. 1996. Age, arrival date, and reproductive success of male American Redstarts Setophaga ruticilla. Journal of Avian Biology 27(2):164-170. https://doi.org/10.2307/3677146

Machtans, C. S., and P. B. Latour. 2003. Boreal forest songbird communities of the Liard Valley, Northwest Territories, Canada. Condor 105(1):27-44. https://doi.org/10.1093/condor/105.1.27

MacMynowski, D. P., and T. L. Root. 2007. Climate and the complexity of migratory phenology: sexes, migratory distance, and arrival distributions. International Journal of Biometeorology 51:361-373. https://doi.org/10.1007/s00484-006-0084-1

Mahon, C. L., G. Holloway, P. Sólymos, S. G. Cumming, E. M. Bayne, F. K. A. Schmiegelow, and S. I. Song. 2016. Community structure and niche characteristics of upland and lowland western boreal birds at multiple spatial scales. Forest Ecology and Management 361:99-116. https://doi.org/10.1016/j.foreco.2015.11.007

Marshall, M. R., and R. J. Cooper. 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. Ecology 85(2):432-445. https://doi.org/10.1890/02-0548

Mattsson, B. J., and G. J. Niemi. 2008. Causes and consequences of distribution patterns in a migratory songbird across its geographic range. Canadian Journal of Zoology 86(4):314-328. https://doi.org/10.1139/Z07-142

Mazerolle, D. F., and K. A. Hobson. 2004. Territory size and overlap in male Ovenbirds: contrasting a fragmented and contiguous boreal forest. Canadian Journal of Zoology 82(11):1774-1781. https://doi.org/10.1139/z04-175

Møller, A. P. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. Behavioral Ecology and Sociobiology 35:115-122. https://doi.org/10.1007/BF00171501

Moore, F. R., and P. Kerlinger. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74:47-54. https://doi.org/10.1007/BF00377344

Nixon, A. E., R. J. Fisher, D. Stralberg, E. M. Bayne, and D. Farr. 2016. Projected responses of North American grassland songbirds to climate change and habitat availability at their northern range limits in Alberta, Canada. Avian Conservation and Ecology 11(2):2. http://doi.org/10.5751/ACE-00866-110202

Oliver, R. Y., D. P. W. Ellis, H. E. Chmura, J. S. Krause, J. H. Pérez, S. K. Sweet, L. Gough, J. C. Wingfield, and N. T. Boelman. 2018. Eavesdropping on the Arctic: automated bioacoustics reveal dynamics in songbird breeding phenology. Scientific Advances 4(6):1-9. https://doi.org/10.1126/sciadv.aaq1084

Paxton, K. L., and F. R. Moore. 2017. Connecting the dots: stopover strategies of an intercontinental migratory songbird in the context of the annual cycle. Ecology and Evolution 7(17):6716-6728. https://doi.org/10.1002/ece3.3227
Porneluzi, P., M. A. Van Horn, and T. M. Donovan. 2011. Ovenbird (Seiurus aurocapilla), version 2.0. In A. F. Poole and F. B. Gill, editors. Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.88

Remêš, V. 2003. Effects of exotic habitat on nesting success, territory density, and settlement patterns in the Blackcap (Sylvia atricapilla). Conservation Biology 17(4):1127-1133. https://doi.org/10.1046/j.1523-1739.2003.01611.x

Rimmer, C. C., and K. P. McFarland. 2012. Tennessee Warbler (Oreothlypis peregrina) version 2.0. In A. F. Poole and F. B. Gill, editors. Birds of North America. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bna.350

Robertson, B. A., and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87(5):1075-1085. https://doi.org/10.1890/0012-9658(2006)87[1075:AFFUET]2.0.CO;2

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, et al. 2019. Decline of the North American avifauna. Science 366 (6461):120-124. https://doi.org/10.1126/science.aaw1313

RStudio Team. 2019. RStudio: integrated development for R. RStudio, Boston, Massachusetts, USA. http://www.rstudio.com

Samplonius, J. M., and C. Both. 2017. Competitor phenology as a social cue in breeding site selection. Journal of Animal Ecology 86(3):615-623. https://doi.org/10.1111/1365-2656.12640

Shonfield, J., and E. M. Bayne. 2017. Autonomous recording units in avian ecological research: current use and future applications. Avian Conservation and Ecology 12(1):14. https://doi.org/10.5751/ACE-00974-120114

Smith, R. J., and F. R. Moore. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. Behavioral Ecology and Sociobiology 57:231-239. https://doi.org/10.1007/s00265-004-0855-9

Solymos, P. 2020. Package cure4insect: custom reporting for intactness and sector effects. https://abbiobiodiversity.github.io/cure4insect/

Sparks, T. H., F. Bairlein, J. G. Bojarinov, O. Häppop, E. S. A. Lehikoinen, K. Rainio, L. V. Sokolov, and D. Walker. 2005. Examining the total arrival distribution of migratory birds. Global Change Biology 11(1):22-30. https://doi.org/10.1111/j.1365-2486.2004.00887.x

Spiniu, V., G. Grolemund, and H. Wickham. 2018. Package lubridate: make dealing with dates a little easier. Version 1.7.4. https://CRAN.R-project.org/package=lubridate

Thériault, S., M.-A. Villard, and S. Haché. 2012. Habitat selection in site-faithful Ovenbirds and recruits in the absence of experimental attraction. Behavioral Ecology 23(6):1289-1295. https://doi.org/10.1093/beheco/ars119

Toms, J. D., F. K. A. Schmiegelow, S. J. Hannon, and M.-A. Villard. 2006. Are point counts of boreal songbirds reliable proxies for more intensive abundance estimators? Auk 123 (2):438-454. https://doi.org/10.1093/auk/123.2.438

Tottrup, A. P., K. Rainio, T. Coppack, E. S. A. Lehikoinen, C. Rahbek, and K. Thorup. 2010. Local temperature fine-tunes the timing of spring migration in birds. Integrative and Comparative Biology 50(3):293-304. https://doi.org/10.1093/icb/icq028

Tryjanowski, P., and T. H. Sparks. 2001. Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the Red-backed Shrike Lanius collurio. International Journal of Biometeorology 45:217-219. https://doi.org/10.1007/s00484-001-0112-0

Upham-Mills, E. J., J. R. Reimer, S. Haché, S. R. Lele, and E. M. Bayne. 2020. Can singing rate be used to predict male breeding status of forest songbirds? A comparison of three calibration models. Ecosphere 11(1):e03005. https://doi.org/10.1002/ecs2.3005

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47(4):893-901. https://doi.org/10.2307/3808148

Van Wilgenburg, S. L., K. A. Hobson, K. J. Kardynal, and E. M. Beck. 2018. Temporal changes in avian abundance in aspen-dominated boreal mixedwood forests of central Saskatchewan, Canada. Avian Conservation and Ecology 13(1):3. https://doi.org/10.5751/ACE-01145-130103

Vaughan, I. P., and S. J. Ormerod. 2003. Improving the quality of distribution models for conservation by addressing shortcomings in the field collection of training data. Conservation Biology 17 (6):1601-1611. https://doi.org/10.1111/j.1523-1739.2003.00359.x

Wilson, D. M., and J. Bart. 1985. Reliability of singing bird surveys: effects of song phenology during the breeding season. Condor 87:69-73. https://doi.org/10.2307/1367132

Yip, D. A., L. Leston, E. M. Bayne, P. Solymos, and A. Grover. 2017. Experimentally derived detection distances from audio recordings and human observers enable integrated analysis of point count data. Avian Conservation and Ecology 12(1):11. https://doi.org/10.5751/ACE-00997-120111
Appendix 1. Predictive ability of models using three different arrival definitions

We ultimately used the first day we observed each species as the time of arrival in our analyses. However, before selecting this metric we compared the predictive ability of three definitions of arrival timing.

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.

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 less frequently in the literature (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.

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 were 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 was calculated from the six-day detection history following first detection at all stations. This global value was calculated as total days the species is detected divided by the number of total sampling days. This value was 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.

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 (α = 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 r² 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).

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 A1.1).
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 A1.1). 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.

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. Date of first detection is commonly used and our results suggests provides accurate data with the least effort. However, this comparison should be repeated on a smaller scale in other areas before these conclusions are broadly accepted.

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    |               |
Figure A1.1. 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 ΔAIC 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 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 AIC | ΔAIC | TEWA AIC | ΔAIC | YRWA AIC | ΔAIC |
|---------------------|---------|------|---------|------|---------|------|
| 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 |
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     |

Predicted Density Models

| Predictor | Estimate  | T    | p    |
|-----------|-----------|------|------|
| 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 - |
| 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 |
| Year   | Intercept | 2016    | 2017    | 2018    |
|--------|-----------|---------|---------|---------|
| 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 Warbler 129**

| Species          | Intercept | 2016    | 2017    | 2018    |
|------------------|-----------|---------|---------|---------|
| Tennessee Warbler| 142.930+/-0.321 | 445.302 | <0.001*** |         |
| 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**

| Species          | Intercept | 2016    | 2017    | 2018    |
|------------------|-----------|---------|---------|---------|
| Yellow-rumped    | 128.928+/-0.499 | 258.362 | 0.004** |         |
| Warbler          | -0.085+/-0.687 | -0.123  | 0.902   |         |
| Species                | Mixedwood  | Pine        | Shrub       | White Spruce | Latitude   | Longitude  | Stand Age | Year       | 2016        | 2017     | 2018    |
|------------------------|------------|-------------|-------------|--------------|------------|------------|-----------|------------|-------------|----------|---------|
|                        | -0.999+/-.603 | -0.556+/-.640 | -0.071+/-.551 | -0.022+/-.578 | 1.971+/-.605 | 1.338+/-.605 | 1.571+/-.606 | 2016       | -0.288+/-.773 | 1.613+/-.836 | 1.355+/-.803 |
|                        | -1.655     | -0.885      | -0.13       | -0.039       | 3.26       | 2.211      | 2.594     | 2016       | -0.373      | 1.929    | 1.687   |
|                        | 0.103      | 0.38        | 0.897       | 0.969        | 0.002**    | 0.031*     | 0.012*    | 2016       | 0.71        | 0.059    | 0.097   |