

Research



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Habitat loss on the breeding grounds is a major contributor to population declines in a long-distance migratory songbird

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Many migratory species are declining and for most, the proximate causes of their declines remain unknown. For many long-distance Neotropical migratory songbirds, it is assumed that habitat loss on breeding or non-breeding grounds is a primary driver of population declines. We integrated data collected from tracking technology, community science and remote sensing data to quantify migratory connectivity (MC), population trends and habitat loss. We quantified the correlation between forest change throughout the annual cycle and population declines of a long-distance migratory songbird, the Connecticut warbler (*Oporornis agilis*, observed decline: $-8.99\% \text{ yr}^{-1}$). MC, the geographic link between populations during two or more phases of the annual cycle, was stronger between breeding and autumn migration routes ($MC = 0.24 \pm 0.23$) than between breeding and non-breeding locations ($MC = -0.2 \pm 0.14$). Different Connecticut warbler populations tended to have population-specific fall migration routes but overlapped almost completely within the northern Gran Chaco ecoregion in South America. Cumulative forest loss within 50 km of breeding locations and the resulting decline in the largest forested patch index was correlated more strongly with population declines than forest loss on migratory stopover regions or on wintering locations in South America, suggesting that habitat loss during the breeding season is a driver of observed population declines for the Connecticut warbler. Land-use practices that retain large, forested patches within landscapes will likely benefit breeding populations of this declining songbird, but further research is needed to help inform land-use practices across the full annual cycle to minimize the impacts to migratory songbirds and abate ongoing population declines.

1. Introduction

More than half of migratory bird species in North America are experiencing population declines [1]. For most species, the drivers of these declines remain unknown. Migratory populations cross multiple geopolitical boundaries and use various habitat types throughout their journeys making it difficult to identify when and where population limitation occurs and to determine the proximate causes of decline. A primary obstacle for the conservation of most

migratory populations is that migratory connectivity (MC), i.e. where specific populations migrate throughout the annual cycle, is not well understood and therefore limits our ability to identify the threats they face [2,3] and their impacts on fitness and survival [4].

Habitat modification and loss is likely a major contributing factor to ongoing avian population declines [5]. By removing, converting or modifying essential habitat, migratory populations may be directly and indirectly impacted in a variety of ways [6,7] depending on where within a species range the habitat alteration occurs. Habitat loss on breeding areas may increase breeding densities within the remaining habitat in the short term, which in turn results in decreased fecundity via density-dependent mechanisms, ultimately decreasing population size [8]. In non-breeding areas, habitat loss may contribute to population declines either directly [9] or indirectly through carry over effects [10]. Habitat loss at key locations (i.e. stopovers) during migration may limit populations by reducing migratory preparedness and increasing competition for limited food resources [11–13]. Finally, a combination of these factors is likely operating simultaneously. Identifying where and when mortality occurs during the annual cycle remains a major priority but is an elusive goal because of challenges in tracking migratory birds as they move across landscapes.

The advent of tracking technology has provided enormous insights into the annual movements of migratory organisms [14]. For large-bodied species like waterbirds and shorebirds, tracking technology has identified areas to focus conservation efforts [12]. However, for small-bodied birds, tracking technology capable of revealing migratory movements throughout the annual cycle became available only relatively recently [15,16]. Miniaturized tracking technology has been used to better understand species distributions [17], identify where individuals and populations go throughout the year [18], determine critical stopover locations during migration [19] and measure the strength of MC [20,21]. Few studies, however, have used tracking information to better understand how habitat degradation in key areas is correlated with ongoing population declines [6,7,12,22]. For many long-distance Neotropical migrants, a primary cause of decline is assumed to be habitat loss and it is often assumed to occur outside of the breeding season, either along migratory routes [23] or during the non-breeding season [9].

The Connecticut warbler (*Oporornis agilis*) is a medium-sized (approx. 15 g), insectivorous ground foraging warbler that breeds in the boreal forest [24]. Most of the population breeds in the boreal forests of Canada but they also breed in northern regions (Michigan, Minnesota and Wisconsin) of the United States. Based on an annual, standardized breeding bird survey, the Connecticut warbler has been experiencing ongoing population declines (1.4% year⁻¹; [25]) with a total population decline of 62% since the breeding bird survey began in 1966 [25]. Little information is available about their annual phenology (i.e. migration timing), life history, migratory routes or the non-breeding distribution [26]. Here, we tracked Connecticut warblers throughout their range, to (i) identify the strength of MC for distinct breeding populations with varying population trends and (ii) correlate remotely sensed habitat loss in the identified areas with population trend data. After identifying where Connecticut warblers were throughout the year, we extracted habitat loss estimates from breeding, migratory stopover and non-breeding locations

to determine how habitat loss and fragmentation within those regions correlated with observed trends during the breeding season. By including habitat loss and fragmentation metrics at regions throughout their annual cycle in a single analysis, we were able to draw inference about the relative contribution of habitat loss occurring throughout their range to population declines. If habitat loss throughout the annual cycle contributes to ongoing declines, we predicted that populations experiencing the highest amount of habitat loss would also be experiencing the most severe population declines.

2. Methods

(a) Defining ‘natural’ populations

The North American breeding bird survey is a large-scale, annual survey used to monitor the status and trends of North American bird populations [25]. We used breeding bird survey data [26] to delimit ‘natural’ populations following Rushing *et al.* [27]. Breeding bird survey routes that occurred within 250 km of the Connecticut warbler’s breeding range were included resulting in 90 survey routes. We estimated route-level relative abundance and trend estimates between 2000 and 2017. ‘Natural’ populations were identified using clustering based on the Euclidean distance between route locations, estimated route-level abundance and trend estimates [27].

(i) Light-level geolocation

Archival light-level geolocators (geocator hereafter) were deployed on Connecticut warblers within four distinct populations across their breeding range (figure 1). Individuals were captured using mist nets and a simulated territorial intrusion where a conspecific song was played from a speaker to elicit a territorial response. Once captured, individuals were fit with a geocator and released. Geolocators were recovered the following breeding season. We recovered nine geolocators from returning Connecticut warblers from across their breeding range (Québec: $n = 2$ of 12, Minnesota: $n = 1$ of 10, Manitoba: $n = 4$ of 29, Saskatchewan: $n = 0$ of 6, Alberta: $n = 2$ of 29). We were unable to assess whether geolocators impacted the return rates in this study but a recent meta-analysis [28] and previous findings [20] suggest geolocators have no appreciable effect on the survival of similarly sized species. All tags collected data long enough to characterize the location of the stationary non-breeding season to identify where breeding populations wintered. Some tags failed during the middle of the non-breeding season ($n = 4$, mean failure date: 4 April, s.d.: 16.85 days) limiting our analyses to autumn migration and the non-breeding season. Once recovered, ambient light levels recorded by the geolocators were transformed into estimated geographic coordinates using the solar/satellite geolocation for animal tracking package [29] in R [30] (see electronic supplementary material for more detail).

(b) Migratory connectivity

We estimated the strength of MC during three phases of the annual cycle to better understand Connecticut warbler biology and assess how critical phases of the annual cycle are geographically linked [21]. First, we used the geocator information to determine the strength of MC between breeding locations and their first major stopover location prior to making long-distance movements over-water migrating south in the fall. We then estimated MC between the breeding season and locations where individuals made landfall following their over-water flights. Finally, we estimated the strength of MC between breeding and non-breeding seasons. We used 500×500 km target regions that included the eastern coastal regions of the United States and Canada, the

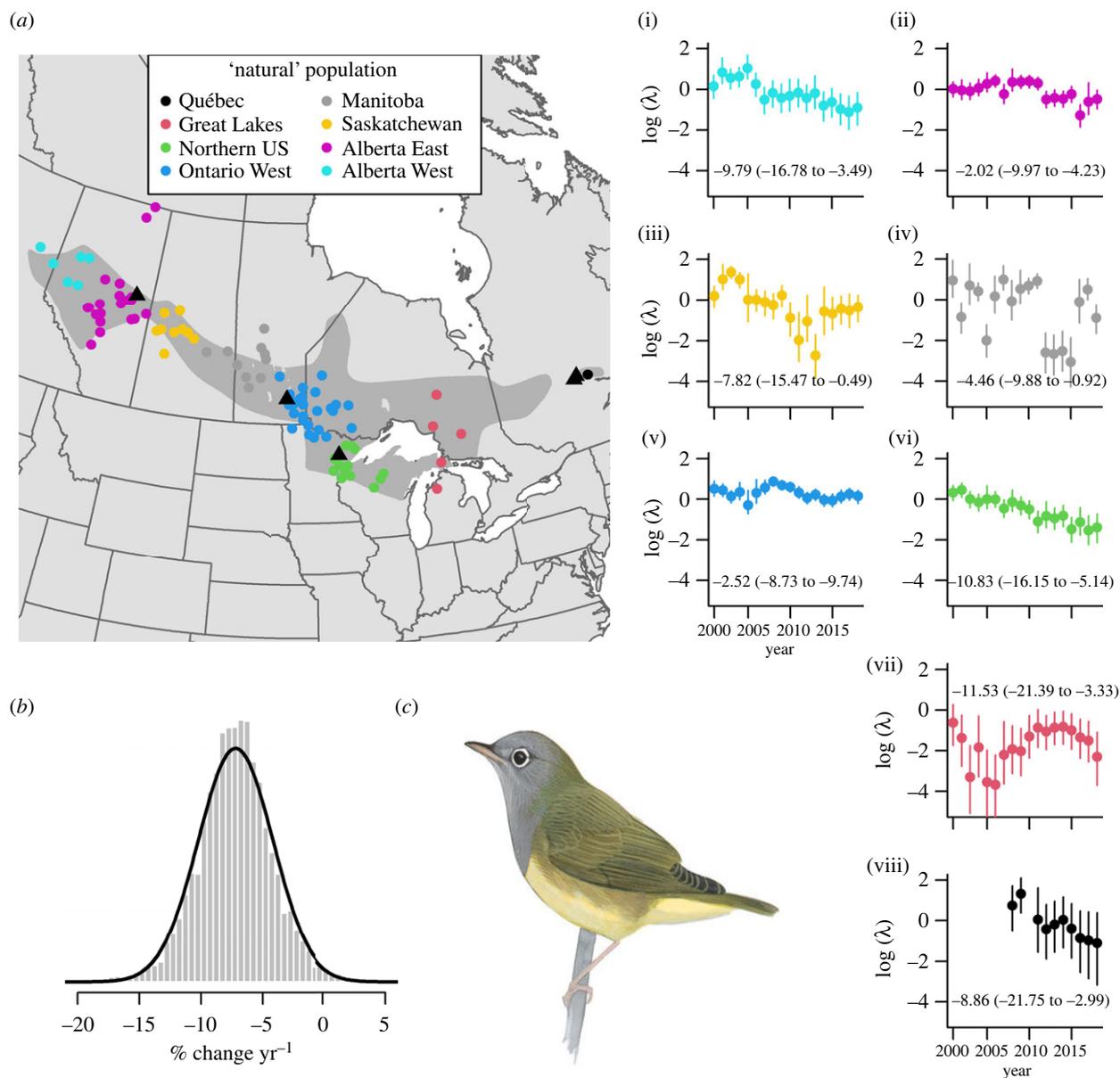


Figure 1. (a) The breeding distribution of the Connecticut warbler (grey polygon) is comprised of eight 'natural' populations. The breeding bird survey locations within each 'natural' population are represented by different colours. The population trend and 95% credible interval are provided alongside the abundance estimates for each 'natural' population. (b) The population-wide trend estimate is also shown. The locations of light-level geolocator deployment are illustrated with a black triangle. (c) Image of Connecticut warbler drawn by David Sibley. (Online version in colour.)

Caribbean basin and northern South America and the entirety of South America for pre-flight, post-flight and non-breeding seasons respectively (electronic supplementary material, figure S1). We estimated MC using the `estMC` function available in the MigConnectivity package [21] in R (v. 3.4.1 [30]). We used the target regions identified for each population to estimate the influence of habitat loss during critical stopover regions and the non-breeding season on observed breeding season declines.

(i) Habitat loss and fragmentation

We summarized the amount of habitat loss per year (2000–2017) within 50 km of breeding bird survey routes to determine whether ongoing declines can be attributed to habitat loss on the breeding grounds. We chose a 50 km radius around each breeding bird survey route to ensure the entire route (approx. 40 km) was included. In addition, for populations where we tracked individuals ($n = 4$ populations), we used locations determined from geolocators to identify specific geographic areas to quantify habitat loss during each phase of the annual cycle. We quantified cumulative habitat loss through time for distinct

regions we were able to identify using geolocators. Because of the uncertainty associated with light-level geolocation [31], those regions included stopover locations prior to and following large water crossings and the stationary non-breeding season in South America. We used a weighted average to summarize habitat loss within the 500×500 km regions identified for each population from 2000 to 2017 to determine whether habitat loss correlates with population declines observed during the breeding season. We used the estimated probability that a population used a particular 500×500 km region derived from the MC metric to calculate a weighted average (electronic supplementary material, figure S1). We assumed that individuals from our sampling locations were representative of the larger population and that the general location of stopover and stationary non-breeding location remained the same among years for the different populations. Finally, we included the total amount of habitat loss throughout the annual cycle by summing breeding, stopover and non-breeding forest loss. Habitat loss was summarized from the Global Forest Change dataset (v. 1.6; [32]) using Google Earth Engine [33].

Habitat fragmentation often accompanies habitat loss and total habitat loss may not capture the influence that habitat fragmentation has on population declines. Therefore, in addition to habitat loss, we quantified metrics that best describe habitat fragmentation within each landscape described above by calculating the percentage of forest cover (PLAND), edge density, patch density, number of habitat patches (NP), largest patch index (LPI), total core area (TCA) and core area index metrics [34] using the LandscapeMetrics R package [35]. We removed highly correlated fragmentation metrics ($r > 0.75$) to reduce redundancy (see, electronic supplementary material, figure S5) resulting in three biologically relevant metrics used to describe fragmentation within the landscapes. Those included LPI which is an area to edge metric, NP which describes the number of patches within the landscape and TCA which describes the amount of core area (non-edge habitat) within a landscape [35]. We defined edge as habitat within 90 m of a patch boundary.

We coupled relative abundance and trend estimates derived from breeding bird survey data with habitat loss and fragmentation within geographic regions used during different phases of the annual cycle identified with tracking technology to assess where within the annual cycle habitat loss has the greatest impact on Connecticut warbler populations. Using a Bayesian framework, we first identified where within the annual cycle habitat loss had the greatest impact on breeding populations. Specifically, we modelled observed counts (y) at each breeding bird survey location i , within the ‘natural’ population pop , in each year t following

$$y_{i,t} \sim \text{Poisson}(\lambda_{i,t})$$

and

$$\log(\lambda_{i,t}) = \alpha_{pop} + \beta_{pop} * t + \beta'_{pop} * X_{i,t} + \beta_{obs} * naive_{i,t} + \omega_{i,t} + \varepsilon_{pop,i,t}$$

where β' indicates a vector of beta estimates. X represents a vector of covariates composed of cumulative habitat loss within 50 km of the breeding bird survey routes, habitat loss at stopover locations pre- and post-Atlantic flights, habitat loss during the non-breeding season and the summation of habitat loss experienced throughout the annual cycle (breeding, stopover and non-breeding). β_{obs} is a parameter to account for naive observers during their first survey year [27]. ω and ε are observer and route-level random effects, respectively. We then fit a separate but similar model that included the habitat fragmentation parameters to better understand how fragmentation resulting from habitat loss and/or conversion impacts breeding populations. We used the same model structure, but the covariate vector included the fragmentation metrics LPI, NP and TCA for each landscape.

We used Gibbs variable selection (see [36]) to determine the relative importance of habitat loss or habitat fragmentation during different stages of the annual cycle. We modelled the β estimates as a joint distribution with an indicator variable γ [36]. As the MCMC updates, γ takes a value of 1 if the associated variable is included in the model and 0 if not [44]. Therefore, summarizing the posterior distribution of γ provides an unbiased estimate of variable importance. We used the posterior mean of γ to evaluate the relative importance of habitat loss and landscape fragmentation occurring throughout the annual cycle on breeding season abundance. Models were run in Just Another Gibbs Sampler (JAGS; [37]) accessed through R via the jagsUI package [38]. We ran three chains of 100 000 iterations with an initial burn-in period of 50 000 iterations following an adaptation phase of 10 000 iterations. We thinned every 15th iteration leaving 9999 draws from the posterior distribution from which we drew our inference. We assessed model fit using a posterior predictive chi-square goodness of fit test statistic [39]. Both habitat loss and

habitat fragmentation models adequately fit the data as indicated by a Bayesian p -value of 0.451 and 0.383, respectively (electronic supplementary material, figure S4).

3. Results

(a) Population trends

Across their range, the Connecticut warbler population declined by -8.99% (95% CI = -15.53 : -2.7) per year between 2000 and 2017 and is composed of eight ‘natural’ populations (figure 1). Trend estimates indicate that all ‘natural’ populations are declining with mean trend estimates ranging from -12.48 to -5.02% per year. The 95% credible interval for nearly half of the ‘natural’ populations ($n = 3$ of 8) did not include zero indicating a statistically significant decline (figure 1). Although the 95% credible interval overlapped zero for five of the eight ‘natural’ populations, between 88.42 and 99.97 per cent of all samples drawn from the posterior distribution ($n = 9999$) were negative trend estimates.

(i) Migratory connectivity

Connecticut warblers from the four tracked populations initiated fall migration in August (Aug. 19 ± 5.28 days) and arrived on the east coast of North America in early September (Sept. 10 ± 6.63 days). All but one Connecticut warbler made long-distance over-water flights from the east coast of North America on their way to South America. Individuals spent 10.5 ± 2.31 days on stopover prior to departing over the Atlantic in early October (Oct. 10 ± 5.82 days). Mean flight time over the Atlantic Ocean was approximately 3 ± 0.65 days. Upon arrival to the stopover in the Caribbean or South America, Connecticut warblers stayed on average 10.71 ± 2.43 days. They arrived on their stationary non-breeding grounds in early November (Nov. 9 ± 3.52 days), 81.5 ± 5.23 days after departing their breeding locations.

Connecticut warblers tended to have population-specific stopover areas prior to and immediately following their long-distance flights over the Atlantic. The strength of MC was stronger between breeding and fall stopover sites (stopover pre-Atlantic: MC = 0.24 ± 0.23 , stopover post-Atlantic: MC = 0.31 ± 0.23) than it was between breeding and non-breeding grounds (MC = -0.2 ± 0.14). Most individuals spent the stationary non-breeding season in an overlapping region of South America which includes southwestern Brazil, eastern Bolivia and northern Paraguay (figure 2).

(ii) Habitat loss and fragmentation

Connecticut warbler breeding abundance in three of eight ‘natural’ populations was negatively correlated with cumulative habitat loss within 50 km of breeding locations (figure 3a) and was the most important variable in the habitat loss model for seven of the eight populations. The effect of habitat loss at stopover locations prior to and following crossing the Atlantic were not identified as important contributors to Connecticut warbler abundance for any of the ‘natural’ populations within our modelling framework ($\gamma < 0.25$). Cumulative habitat loss during the stationary non-breeding season in South America was identified as a highly important variable affecting abundance in the Alberta East breeding population ($\gamma = 0.97$) and slightly important ($0.5 > \gamma > 0.25$) for the remaining tracked populations (Ontario West: $\gamma =$

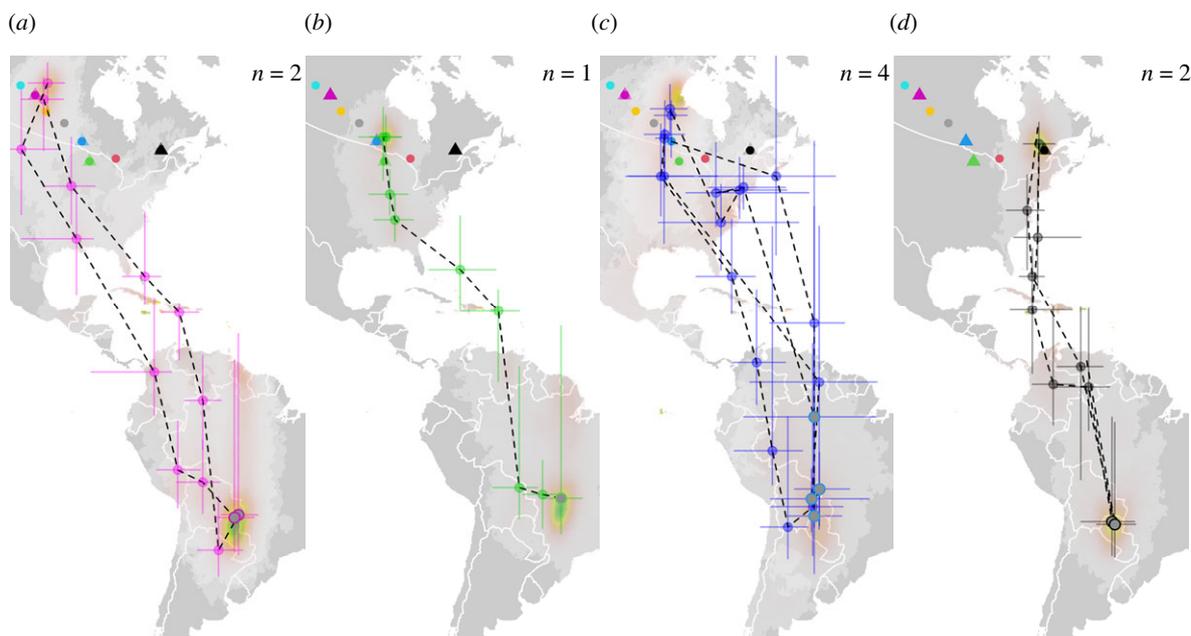


Figure 2. (a–d) Breeding, autumn migratory stopover regions and non-breeding locations of Connecticut warblers captured throughout their breeding distribution. The four ‘natural’ populations, the median (coloured circles) and 95% credible intervals for each location during autumn migration are shown. The stationary non-breeding location of individuals is indicated with a grey filled point. Sample sizes are shown in each panel. Each individual track is connected with a dotted line to distinguish between individuals but does not represent the actual path travelled between stopover locations. The underlying colour ramp represents the uncertainty for the tracking duration. (Online version in colour.)

0.37; Northern US: $\gamma = 0.39$ and Québec: $\gamma = 0.4$). Habitat loss during the stationary non-breeding season was more important than breeding habitat loss for the Northern US population but was not statistically significant ($\beta = 0.15$; 95% CI = $-0.45:1.42$, figure 3; table 1).

Habitat loss increased habitat fragmentation within the landscapes used by Connecticut warblers throughout their annual cycle. LPI on the breeding grounds was identified as an important variable in our fragmentation modelling framework, was positively correlated with Connecticut warbler abundance and was statistically significant in nearly all populations (figure 3). LPI was generally higher on the breeding grounds than within either the stopover region or on the stationary non-breeding grounds (electronic supplementary material, figure S5). Despite the declines in TCA throughout the annual cycle, TCA was not identified as an important feature of the landscape contributing to abundance on the breeding grounds (figure 3c). The NP within 50 km of the breeding bird survey routes was identified as being slightly ($\gamma > 0.25$, $n = 4$ of 8 ‘natural’ populations) to highly important ($\gamma > 0.75$, $n = 2$ of 8 ‘natural’ populations) for many of the sub-populations. Our modelling framework suggests that the NP during the stationary non-breeding period was more important for abundance on the breeding grounds than the NP within landscapes that Connecticut warblers used during a migratory stopover (figure 3d). The effect that NP had on breeding abundance differed between the phases of the annual cycle. For example, the NP on the breeding grounds was positively correlated with breeding abundance in the Saskatchewan ($\beta = 0.83$; 95% CI = $0:1.54$) and Ontario West ($\beta = 0.85$; 95% CI = $0.46:1.22$) populations while the number of patches on the stationary non-breeding grounds was negatively correlated with observed breeding abundance for the Québec ($\beta = -0.49$; 95% CI = $-4.72:0.4$) and Ontario West ($\beta = -0.75$; 95% CI = $-3.52:0$) populations. The NP during the stationary non-breeding period was positively correlated

with breeding ground abundance within the Alberta East population ($\beta = 0.54$; 95% CI = $0:3.79$); table 2.

4. Discussion

Identifying the causes of population declines for migratory animals is an urgent yet challenging objective for multiple reasons, not the least of which is we still lack essential information on MC for most species [2]. Here, we provide a framework that integrates multiple data sources to identify where within the annual cycle environmental perturbations impact migratory populations. Through the combined use of long-term community science data (breeding bird surveys), tracking technology and remote sensing, we found that the habitat loss and the resulting habitat fragmentation on the breeding grounds were most strongly correlated with population declines for a steeply declining long-distance migratory songbird, the Connecticut warbler.

The strength of MC between breeding locations and key migratory stopover regions was stronger than it was between breeding and non-breeding locations. Our results suggest that during autumn, breeding populations use migratory routes unique to each ‘natural’ population but winter in the same general region of South America. However, our MC inferences are based on tracking information from relatively few individuals. The factors contributing to stronger MC during fall migration are unknown but profitable wind patterns may be responsible [40]. The synchronous timing of departure (Oct. 10 ± 5.82 days) from eastern North America despite individuals breeding across their range suggests that favourable wind patterns during long-distance over-water flights may govern migration timing [41]. Prior to departing the east coast of North America individuals spent on average 10.5 days on the stopover. Although the need to maximize re-fuelling rates is important, the long duration

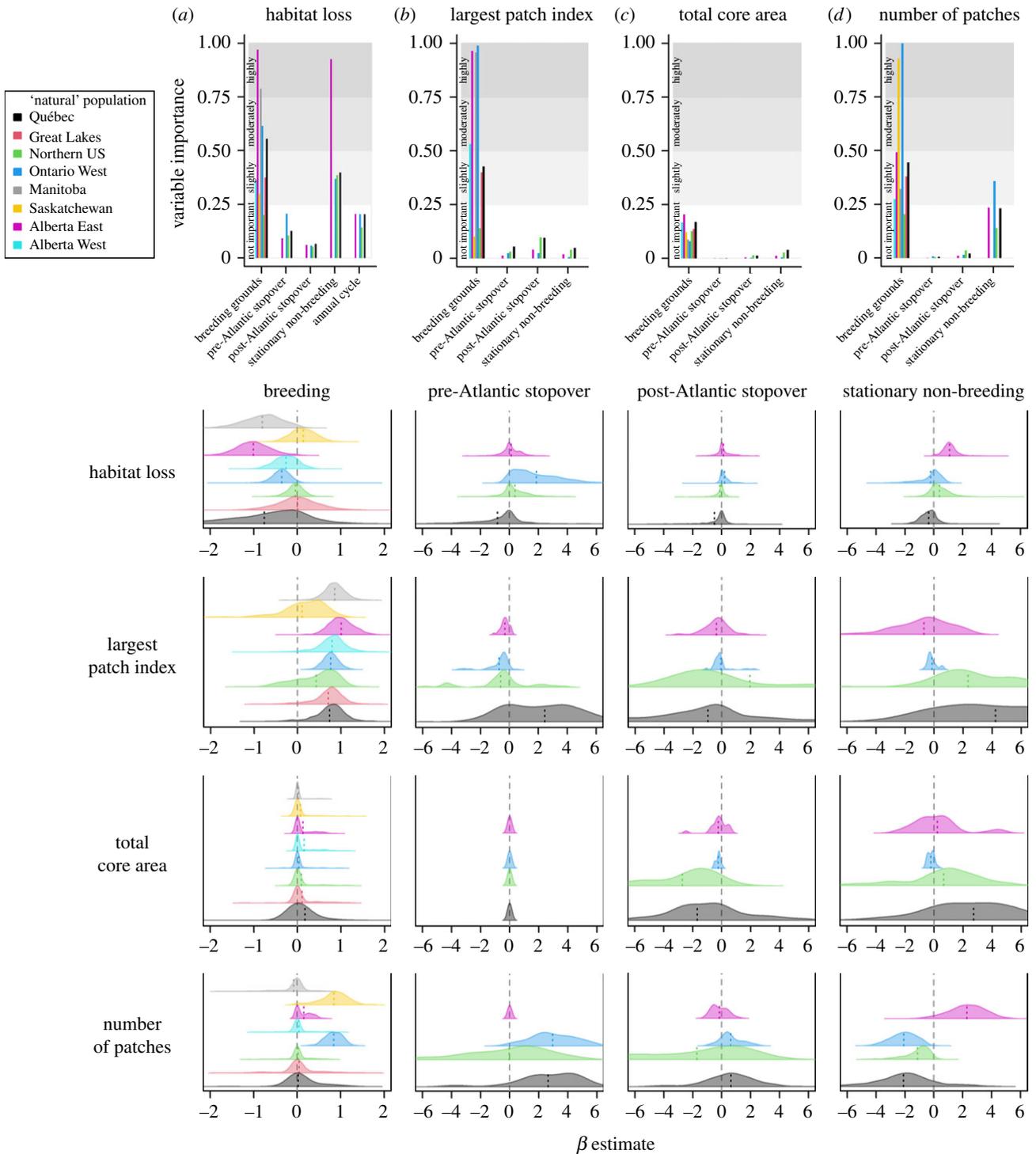


Figure 3. The relative importance of forest loss and forest fragmentation metrics on population declines of Connecticut warblers (a) and the posterior distribution of the β coefficients (b). Indicator values approximating 1 indicate the variable is highly important while values approximating 0 indicate the variable is not important. The colours of the posterior distributions correspond to the 'natural' populations illustrated in figure 1. Indicator variable and β estimates for the effect of forest loss outside of the breeding grounds are shown for only the populations tracked via light-level geolocators. (Online version in colour.)

on stopover may also indicate selection for favourable wind patterns prior to making long-distance over-water flights [41].

Interestingly, several other steeply declining songbird species that breed in North America, the prothonotary warbler (*Protonotaria citrea*; [42]) and purple martin (*Progne subis*; [43]) exhibit similar patterns of MC where populations migrate along different routes but winter in the same general location. Such a pattern could arise if survival varies geographically within the non-breeding distribution [4,44]. If survival varies markedly across the distribution, more individuals wintering in high survival locations will return to the breeding grounds

resulting in weak MC, i.e. the appearance that individuals from across the breeding distribution winter in a similar geographic region. Further research is needed to determine how spatial variation in survival across the annual cycle could influence observed MC patterns [4]. However, the analytical framework employed here could be used to help identify where within the annual cycle migratory populations are limited and could be used for any migratory species where adequate tracking and survey data exist.

Combining tracking technology and remote sensing allowed us to identify how habitat loss and fragmentation at

Table 1. β coefficients between forest loss during different phases of the annual cycle and Connecticut warbler abundance on the breeding grounds. Connecticut warbler 'natural' populations were identified following [30]. Mean β correlations are shown along with the 95% credible interval in parenthesis. Zero values are reported outside of the breeding season for 'natural' populations with no tracking data. The number of Breeding Bird Survey routes comprise the 'natural' population are reported in parentheses.

'natural' population	breeding	pre-Atlantic	post-Atlantic	stationary non-breeding	cumulative
Québec ($n = 1$)	-0.76 (-3.49:0.86)	-0.83 (-6.44:2.67)	-0.5 (-4.12:0.83)	-0.36 (-1.49:0.73)	-0.16 (-0.86:0.24)
Great Lakes ($n = 5$)	0.01 (-1.00:1.04)				
Ontario West ($n = 26$)	-0.04 (-0.43:0.30)	0.37 (-1.18:2.32)	-0.13 (-1.21:0.42)	0.39 (-0.73:1.87)	-0.01 (-0.31:0.25)
Northern US ($n = 13$)	-0.36 (-0.80:0.04)	1.86 (-0.07:5.61)	0.19 (-0.27:1.20)	-0.22 (-2.43:0.88)	-0.05 (-0.76:0.48)
Alberta W. ($n = 6$)	-0.26 (-0.81:0.27)				
Alberta E. ($n = 20$)	-1.01 (-1.74:-0.20)	0.11 (-1.09:1.32)	0.12 (-0.73:1.20)	1.09 (0.15:2.11)	-0.01 (-0.72:0.51)
Saskatchewan ($n = 9$)	0.14 (-0.40:0.70)				
Manitoba ($n = 10$)	-0.80 (-1.79:0.01)				

different times and places in the annual cycle correlate with population declines observed during the breeding season. Our findings, although based on relatively few tracked individuals suggest that habitat loss and fragmentation on the breeding grounds are strongly correlated with population declines. Connecticut warblers exhibit weak MC between breeding and stationary non-breeding seasons, as such our ability to detect a habitat loss or fragmentation signal from the non-breeding grounds is likely diminished. Furthermore, more data were available from the breeding grounds and at a finer spatial resolution (Breeding Bird Survey) than from the non-breeding phases of the annual cycle. The combination of archival tracking technology with inherent location uncertainty and relatively few tracked individuals may have decreased our ability to detect the full extent of how non-breeding season habitat loss and fragmentation impact Connecticut warbler abundance. However, this study illustrates that tracking data combined with other data sources can improve our understanding of the biology and threats to little-known species.

Tracking data were only available during autumn migration and the stationary non-breeding season, as such our findings do not consider the role of habitat loss in regions used during spring migration on population dynamics. Connecticut warblers undertake large over-water flights during southward migration in autumn [26], and it is possible they use alternate routes during their journey north in spring and are impacted by habitat loss in regions not included in our analyses. However, community science (also referred to as citizen science) observations submitted to eBird suggest that Connecticut warblers migrate primarily through the Caribbean Basin and into eastern North America as they migrate north in the spring—the same general regions used during fall we identified with light-level geolocators (electronic supplementary material, figure S6). That said, the evidence that habitat loss and resulting fragmentation on the breeding grounds are most strongly correlated with ongoing declines suggests it is likely an important contributing factor in population declines.

Little is known about the basic biology of Connecticut warblers despite ongoing population declines (approx. 70% decline since 1966). For example, information as fundamental as the non-breeding distribution and patterns of habitat use are essentially undescribed in the scientific literature [24,26].

The primary wintering locations identified here encompassed the northern Gran Chaco ecoregion, a region including southern Brazil, eastern Bolivia and northern Paraguay, further south than previously thought although few observations and captures from that region exist [24]. The Gran Chaco ecoregion is a global deforestation hotspot [32,45] and lost greater than 20% of its forest between 1985 and 2013 (142 000 km²; [45]). The deforestation rate in the region has increased substantially since 2000 [45]. Remotely sensed land cover data indicate the region is dominated by savanna (37.28%) and grassland (23.65%) ecosystems. However, the forested areas within the region where Connecticut warblers winter are comprised deciduous broadleaf (12.79%) and evergreen broadleaf (7.77%) forest types. Agriculture is common in the region with croplands encompassing about 5% (4.39%) of the landscape. Commodity driven deforestation and shifting agricultural practices are the dominant causes of permanent forest loss in the region [46]. Continued expansion and further encroachment of agriculture could pose a threat to these forested areas in future [45,47]. Inherent location uncertainty associated with the light-level geolocation [31] precluded us from inferring habitat associations during the winter period. However, the forested areas in southern Brazil, eastern Bolivia and northern Paraguay appear to support Connecticut warblers from across their breeding range. Therefore, continued forest loss in the region will likely impact Connecticut warbler populations across their breeding distribution.

The breeding range of Connecticut warblers falls primarily within warm continental and subarctic ecoregions, but specific habitat requirements differ across their breeding range [48]. In the northwestern portion of their breeding distribution, they breed in upland aspen (*Poplar* sp.) stands [49,50] while across most of their distribution they breed in wet, tamarack (*Larix laricina*)/black spruce (*Picea mariana*) [51] and jack pine (*Pinus banksiana*) stands [52]. Cumulative habitat loss within 50 km of breeding bird survey routes had stronger effects on population declines in areas where they breed in wet, tamarack/black spruce and jack pine stands. While the underlying mechanism contributing to the observed differences between forest types are not well understood, the potential regeneration time of the forest structure to a state needed for successful reproduction may differ depending on whether they breed in

Table 2. β coefficients for three habitat fragmentation parameters, TCA, number of patches (NP) and LPI throughout the annual cycle on Connecticut warbler abundance on the breeding grounds. The mean effect size along with the 95% credible interval are reported. β coefficients where the 95% credible interval does not include zero are indicated with italic font. The effect sizes outside the breeding season are reported as zero for 'natural' populations without tracking data.

fragmentation metric	Québec	Great Lakes	Ontario West	Northern US	Alberta W.	Alberta E.	Saskatchewan	Manitoba
TCA								
breeding	1.03 (−0.5:7.28)	0.34 (−0.54:1.15)	0.33 (−0.5:1.09)	0.08 (−0.63:0.63)	0.40 (−0.08:0.93)	0.41 (0.06:0.78)	0.37 (−0.25:1.34)	0.19 (−0.43:0.69)
pre-Atlantic	0	0	0	0	0	0	0	0
post-Atlantic	−1.68 (−10.48:4.62)	−2.72 (−9.44:0.36)	−0.24 (−0.49:−0.01)	−0.24 (−0.49:−0.01)	−0.24 (−1.74:0.54)	−0.24 (−1.74:0.54)	−0.24 (−1.74:0.54)	−0.24 (−1.74:0.54)
stationary non-breeding	2.72 (−3.8:9.99)	0.65 (−5.76:5.3)	−0.22 (−0.5:0.14)	−0.22 (−0.5:0.14)	0.22 (−2.21:4.48)	0.22 (−2.21:4.48)	0.22 (−2.21:4.48)	0.22 (−2.21:4.48)
NP								
breeding	−0.47 (−4.53:1.31)	0.3 (−2.91:1.19)	0.03 (−0.84:0.8)	0.85 (0.46:1.22)	0.08 (−1.15:1.06)	0.29 (0.05:0.55)	0.89 (0.29:1.56)	0.39 (−1.74:0.81)
pre-Atlantic	0.01 (0:0)	0 (0:0)	0 (0:0)	0.02 (0:0)	0 (0:0)	0 (0:0)	0 (0:0)	0 (0:0)
post-Atlantic	0.64 (−3.73:3.91)	−1.72 (−9.16:3.37)	−0.63 (−0.73:2.26)	0.63 (−0.73:2.26)	−0.16 (−1.02:0.86)	−0.16 (−1.02:0.86)	−0.16 (−1.02:0.86)	−0.16 (−1.02:0.86)
stationary non-breeding	−2.11 (−7.29:2.69)	−1.13 (−3.41:0.02)	−2.09 (−3.98:−0.51)	−2.09 (−3.98:−0.51)	2.29 (−0.23:4.53)	2.29 (−0.23:4.53)	2.29 (−0.23:4.53)	2.29 (−0.23:4.53)
LPI								
breeding	0.74 (−0.23:1.41)	0.71 (−0.19:1.29)	0.43 (−0.61:1.12)	0.76 (0.42:1.13)	0.79 (−0.02:1.5)	1 (0.46:1.59)	0.11 (−1.68:0.92)	0.85 (0.38:1.33)
pre-Atlantic	0.73 (0:2.54)	−0.02 (0:0)	−0.02 (0:0)	−0.02 (0:0)	0 (0:0)	0 (0:0)	0 (0:0)	0 (0:0)
post-Atlantic	−0.96 (−9.12:8.13)	1.95 (−5.39:21.17)	−0.07 (−1.02:2.05)	−0.07 (−1.02:2.05)	−0.37 (−2.61:1.35)	−0.37 (−2.61:1.35)	−0.37 (−2.61:1.35)	−0.37 (−2.61:1.35)
stationary non-breeding	4.22 (−2.52:13.24)	2.33 (−9.57:7.95)	−0.14 (−0.53:0.57)	−0.14 (−0.53:0.57)	−0.71 (−4.99:2.23)	−0.71 (−4.99:2.23)	−0.71 (−4.99:2.23)	−0.71 (−4.99:2.23)

wet, tamarack stands or upland aspen woodlands and may contribute to ongoing population declines.

Habitat loss and the resulting fragmentation on the breeding grounds are strongly correlated with observed population declines for the Connecticut warbler. Our findings suggest that large intact forest patches within the landscape are positively correlated with Connecticut warbler abundance. Therefore, Connecticut warbler populations would likely benefit from land management practices that retain large, intact forest patches within the landscape. Although the specific causes of habitat loss were not identified here, conversion of forest to agriculture [53,54], peat mining [55] and forestry practices are common in the region and have impacts on breeding bird species. Curtis *et al.* [46] found that forestry and wildfire are the primary sources of forest cover loss within the warm continental and subarctic ecoregions in North America, but most of these losses will recover with subsequent tree regrowth. However, these disturbances affect forest age structure and composition that may result in habitat loss for the Connecticut warbler. Forestry within the northern temperate/boreal forest is an important industry. In Canada, where the vast majority of Connecticut warblers breed, the forestry industry employs over 200 000 people and accounts for over 7% of all Canadian exports totalling over \$25 billion for the Canadian economy [56]. As

such, without some immediate policy action for habitat protection, the continued harvesting of forest products and the resultant change in forest age structure and composition will continue and may further influence declines of this poorly known species.

Ethics. Animal handling protocols were approved by the Smithsonian's National Zoological Park International Animal Care and Use Committee (NZIP-IACUC no. 17-05).

Data accessibility. Movement data associated with the manuscript can be found in movebank.org. Movebank ID = 613 824 346. Breeding bird survey data are available at <https://www.pwrc.usgs.gov/BBS/Raw-Data/>.

Authors' contributions. M.T.H. and P.P.M. conceived the idea for the manuscript. M.T.H., E.B., E.M., J.A.T., B.D., J.I. and P.P.M. conducted fieldwork. M.T.H. conducted the analyses and wrote the initial manuscript. All authors edited and approved of the final version of the manuscript.

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References

1. North American Bird Conservation Initiative. 2016 The State of North America's Birds 2016. See <https://www.stateofthebirds.org/2016/>.
2. Marra PP, Hunter D, Perrault AM. 2011 Migratory connectivity and the conservation of migratory animals. *Envtl. L.* **41**, 317.
3. Martin TG, Chadès I, Arcese P, Marra PP, Possingham HP, Norris DR. 2007 Optimal conservation of migratory species. *PLoS ONE* **2**, e751. (doi:10.1371/journal.pone.0000751)
4. Rushing CS, Van Tatenhove AM, Sharp A, Ruiz-Gutierrez V, Freeman MC, Sykes PW, Given AM, Sillett TS. 2020 Integrating tracking and resight data from breeding painted bunting populations enables unbiased inferences about migratory connectivity and winter range survival. *BioRxiv* 2020.07.23.217554. (doi:10.1101/2020.07.23.217554)
5. Sorte FAL, Fink D, Blancher PJ, Rodewald AD, Ruiz-Gutierrez V, Rosenberg KV, Hochachka WM, Verburg PH, Kelling S. 2017 Global change and the distributional dynamics of migratory bird populations wintering in Central America. *Glob. Change Biol.* **23**, 5284–5296. (doi:10.1111/gcb.13794)
6. Rushing CS, Ryder TB, Marra PP. 2016 Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. *Proc. R. Soc. B* **283**, 20152846. (doi:10.1098/rspb.2015.2846)
7. Kramer GR *et al.* 2018 Population trends in *Vermivora* warblers are linked to strong migratory connectivity. *PNAS* **115**, E3192–E3200. (doi:10.1073/pnas.1718985115)
8. Lambert JD, Hannon SJ. 2000 Short-term effects of timber harvest on abundance, territory characteristics, and pairing success of ovenbirds in riparian buffer strips. *Auk* **117**, 687–698. (doi:10.2307/4089593)
9. Taylor CM, Stutchbury BJM. 2016 Effects of breeding versus winter habitat loss and fragmentation on the population dynamics of a migratory songbird. *Ecol. Appl.* **26**, 424–437. (doi:10.1890/14-1410)
10. Norris DR, Marra PP. 2007 Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* **109**, 535–547. (doi:10.1093/condor/109.3.535)
11. Dossman BC, Matthews SN, Rodewald PG. 2017 An experimental examination of the influence of energetic condition on the stopover behavior of a Nearctic–Neotropical migratory songbird, the American redstart (*Setophaga ruticilla*). *Auk* **135**, 91–100. (doi:10.1642/AUK-17-67.1)
12. Studds CE *et al.* 2017 Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nat. Commun.* **8**, 14895. (doi:10.1038/ncomms14895)
13. Rakhimberdiev E *et al.* 2018 Fuelling conditions at staging sites can mitigate Arctic warming effects in a migratory bird. *Nat. Commun.* **9**, 4263. (doi:10.1038/s41467-018-06673-5)
14. Bridge ES *et al.* 2011 Technology on the move: recent and forthcoming innovations for tracking migratory birds. *BioScience* **61**, 689–698. (doi:10.1525/bio.2011.61.9.7)
15. McKinnon EA, Love OP. 2018 Ten years tracking the migrations of small landbirds: lessons learned in the golden age of bio-logging. *Auk* **135**, 834–856. (doi:10.1642/AUK-17-202.1)
16. Bridge ES, Kelly JF, Contina A, Gabrielson RM, MacCurdy RB, Winkler DW. 2013 Advances in tracking small migratory birds: a technical review of light-level geolocation. *J. Field Ornithol.* **84**, 121–137. (doi:10.1111/jof.12011)
17. Heckscher CM, Taylor SM, Fox JW, Afanasyev V. 2011 Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. *Auk* **128**, 531–542. (doi:10.1525/auk.2011.10280)
18. Hallworth MT, Marra PP. 2015 Miniaturized GPS tags identify non-breeding territories of a small breeding migratory songbird. *Sci. Rep.* **5**, 11069. (doi:10.1038/srep11069)
19. Cooper NW, Hallworth MT, Marra PP. 2017 Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird. *J. Avian Biol.* **48**, 209–219. (doi:10.1111/jav.01096)
20. Hallworth MT, Sillett TS, Van Wilgenburg SL, Hobson KA, Marra PP. 2015 Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. *Ecol. Appl.* **25**, 336–347. (doi:10.1890/14-0195.1)
21. Cohen EB, Hostetler JA, Hallworth MT, Rushing CS, Sillett TS, Marra PP. 2018 Quantifying the strength of migratory connectivity. *Methods Ecol. Evol.* **9**, 513–524. (doi:10.1111/2041-210X.12916)
22. Fraser KC *et al.* 2012 Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore.

- Proc. R. Soc. B **279**, 4901–4906. (doi:10.1098/rspb.2012.2207)
23. Sheehy J, Taylor CM, Norris DR. 2011 The importance of stopover habitat for developing effective conservation strategies for migratory animals. *J. Ornithol.* **152**, 161–168. (doi:10.1007/s10336-011-0682-5)
 24. Pitocchelli J, Jones J, Jones D, Bouchie J. 2020 Connecticut warbler (*Oporornis agilis*). Birds of the World. See <https://birdsoftheworld.org/bow/species/conwar/cur/introduction>.
 25. Sauer JR, Link WA, Hines JE. 2020 The North American breeding bird survey. Analysis Results 1966–2019. U.S. Geological Survey data release. See <https://doi.org/10.5066/P96A7675>.
 26. McKinnon EA, Artuso C, Love OP. 2017 The mystery of the missing warbler. *Ecology* **98**, 1970–1972. (doi:10.1002/ecy.1844)
 27. Rushing CS, Ryder TB, Scarpignato AL, Saracco JF, Marra PP. 2016 Using demographic attributes from long-term monitoring data to delineate natural population structure. *J. Appl. Ecol.* **53**, 491–500. (doi:10.1111/1365-2664.12579)
 28. Brlik V *et al.* 2020 Weak effects of geolocators on small birds: a meta-analysis controlled for phylogeny and publication bias. *J. Anim. Ecol.* **89**, 207–220. (doi:10.1111/1365-2656.12962)
 29. Wotherspoon S. 2017 SGAT: Solar/Satellite Geolocation for Animal Tracking. See <https://github.com/SWotherspoon/SGAT>.
 30. R Core Team. 2017 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
 31. Lisovski S *et al.* 2018 Inherent limits of light-level geolocation may lead to over-interpretation. *Curr. Biol.* **28**, R99–R100. (doi:10.1016/j.cub.2017.11.072)
 32. Hansen MC *et al.* 2013 High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853. (doi:10.1126/science.1244693)
 33. Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. 2017 Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* **202**, 18–27. (doi:10.1016/j.rse.2017.06.031)
 34. Wang X, Blanchet FG, Koper N. 2014 Measuring habitat fragmentation: an evaluation of landscape pattern metrics. *Methods Ecol. Evol.* **5**, 634–646. (doi:10.1111/2041-210X.12198)
 35. Hesselbarth MHK, Sciaini M, With KA, Wiegand K, Nowosad J. 2019 Landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* **42**, 1648–1657. (doi:10.1111/ecog.04617)
 36. Hooten MB, Hobbs NT. 2015 A guide to Bayesian model selection for ecologists. *Ecol. Monogr.* **85**, 3–28. (doi:10.1890/14-0661.1)
 37. Plummer M. 2003 JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In *Proc. of the 3rd Int. Workshop on Distributed Statistical Computing, 20–22 March, Vienna, Austria*. See <https://www.r-project.org/conferences/DSC-2003/Proceedings/Plummer.pdf>.
 38. Kellner K. 2016 jagsUI: a wrapper around rjags to streamline JAGS analyses. R package version 1. See <https://cran.r-project.org/package=jagsUI>.
 39. Kéry M, Royle JA. 2016 *Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS*, 1st edn. New York, NY: Academic Press. See <https://www.elsevier.com/books/applied-hierarchical-modeling-in-ecology-analysis-of-distribution-abundance-and-species-richness-in-r-and-bugs/kery/978-0-12-801378-6>.
 40. Kranstauber B, Weinzierl R, Wikelski M, Safi K. 2015 Global aerial flyways allow efficient travelling. *Ecol. Lett.* **18**, 1338–1345. (doi:10.1111/ele.12528)
 41. McLaren JD, Shamoun-Baranes J, Bouten W. 2012 Wind selectivity and partial compensation for wind drift among nocturnally migrating passerines. *Behav. Ecol.* **23**, 1089–1101. (doi:10.1093/beheco/ars078)
 42. Tonra CM *et al.* 2019 Concentration of a widespread breeding population in a few critically important nonbreeding areas: migratory connectivity in the prothonotary warbler. *Condor* **121**, duz019. (doi:10.1093/condor/duz019)
 43. Fraser KC *et al.* 2013 Consistent range-wide pattern in fall migration strategy of purple martin (*Progne subis*), despite different migration routes at the Gulf of Mexico. *Auk* **130**, 291–296. (doi:10.1525/auk.2013.12225)
 44. Ruiz-Gutiérrez V, Doherty PF, Eduardo Santana C, Martínez SC, Schondube J, Munguía HV, Iñigo-Elias E. 2012 Survival of resident Neotropical birds: considerations for sampling and analysis based on 20 years of bird-banding efforts in Mexico. *Auk* **129**, 500–509. (doi:10.1525/auk.2012.11171)
 45. Baumann M, Gasparri I, Piquer-Rodríguez M, Pizarro GG, Griffiths P, Hostert P, Kuemmerle T. 2017 Carbon emissions from agricultural expansion and intensification in the Chaco. *Glob. Change Biol.* **23**, 1902–1916. (doi:10.1111/gcb.13521)
 46. Curtis PG, Slay CM, Harris NL, Tyukavina A, Hansen MC. 2018 Classifying drivers of global forest loss. *Science* **361**, 1108–1111. (doi:10.1126/science.aau3445)
 47. Romero-Muñoz A *et al.* 2019 Habitat loss and overhunting synergistically drive the extirpation of jaguars from the Gran Chaco. *Divers. Distrib.* **25**, 176–190. (doi:10.1111/ddi.12843)
 48. Solymos P, Stralberg D. 2020 BAM generalized national models documentation, version 4.0. Zenodo. (doi:10.5281/zenodo.4042821)
 49. Schieck J, Song SJ. 2006 Changes in bird communities throughout succession following fire and harvest in boreal forests of western North America: literature review and meta-analyses. *Can. J. For. Res.* **36**, 1299–1318. (doi:10.1139/x06-017)
 50. Kirk DA, Diamond AW, Hobson KA, Smith AR. 1996 Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. *Can. J. Zool.* **74**, 1749–1770. (doi:10.1139/z96-193)
 51. Lapin CN, Etterson MA, Niemi GJ. 2013 Occurrence of the Connecticut warbler increases with size of patches of coniferous forest. *Condor* **115**, 168–177. (doi:10.1525/cond.2013.110202)
 52. Blais V. 2014 Caractérisation et utilisation de l'habitat par la Paruline à gorge grise (*Oporornis agilis*) dans les pinèdes grises du Lac-Saint-Jean, Québec. MSc thesis, Université du Québec à Chicoutimi, Québec, Canada.
 53. Hobson KA, Bayne EM, Van Wilgenburg SL. 2002 Large-scale conversion of forest to agriculture in the boreal plains of Saskatchewan. *Conserv. Biol.* **16**, 1530–1541. (doi:10.1046/j.1523-1739.2002.01199.x)
 54. Young JE, Sánchez-Azofeifa GA, Hannon SJ, Chapman R. 2006 Trends in land cover change and isolation of protected areas at the interface of the southern boreal mixedwood and aspen parkland in Alberta, Canada. *Forest Ecol. Manage.* **230**, 151–161. (doi:10.1016/j.foreco.2006.04.031)
 55. Desrochers A, Rochefort L, Savard J-PL. 1998 Avian recolonization of eastern Canadian bogs after peat mining. *Can. J. Zool.* **76**, 989–997. (doi:10.1139/z98-028)
 56. Government of Canada. 2014 How does the forest industry contribute to Canada's economy? See <https://www.nrcan.gc.ca/forests/report/economy/16517> (accessed 15 November 2018).