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## Population and Migratory Ecology of Canada Warblers (*Cardellina canadensis*) in the Central Appalachian Mountains, West Virginia, USA

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**Population and Migratory Ecology of Canada Warblers (*Cardellina canadensis*) in the  
Central Appalachian Mountains, West Virginia, USA**

**Stephanie H. Augustine**

**Thesis submitted to the Davis College of Agriculture, Natural Resources, and Design**

**at**

**West Virginia University**

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## *Abstract*

### Population and Migratory Ecology of Canada Warblers (*Cardellina canadensis*) in the Central Appalachian Mountains, West Virginia, USA

Stephanie H. Augustine

Nearctic-Neotropical migrant birds experience a wide range of environmental conditions throughout their annual cycle; thus, it is particularly challenging to evaluate the spatial factors that may influence population growth. The Canada Warbler (*Cardellina canadensis*) faces substantial range-wide population declines, but little study has been conducted regarding elements occurring across the entire year that drive demographic rates. The aims of this research are (1) determine the relationship between Canada Warbler population demographic rates and environmental conditions along an elevation gradient in the central Appalachian Mountains and (2) ascertain the nonbreeding season location and migratory routes used by the central Appalachian population, which is near the southern extent of the entire breeding range. Research occurred from 2019 – 2021 at six study sites ranging in elevation from 526 – 1282m spanning an approximate 130km north-south gradient within the Monongahela National Forest, West Virginia, USA. To determine the relationship between demographic rates and environment, I assessed adult annual survival and daily nest survival. I uniquely color-banded 203 adult male Canada Warblers in 2019 and 2020, and resighted marked birds in 2020 and 2021. I modeled survival in response to predictor variables including elevation, rhododendron coverage, available stream length, topographic position, and aspect. I implemented a spatial Cormack-Jolly-Seber model with Bayesian methods and compared models using DIC criteria. To determine nest survival, I located nests and monitored their outcomes using motion-sensitive game cameras. I modeled daily nest survival as a function of elevation, rhododendron coverage, other shrub coverage, topographic position, and aspect using Bayesian methods and compared models using DIC. I found that elevation was the best predictor of adult survival, which increased from 0.573 (95% credible intervals (CI) = 0.333 – 0.820) at 555 m to 0.702 (95% CI = 0.493 – 0.871) at 1255 m, although the slope coefficient of the elevation effect overlapped 0. I located 12 nests in 2021, of which 9 fledged successfully. The intercept-only model was the best predictor of daily survival, which, exponentiated over the 19-day nesting period, resulted in a posterior mean nest survival of 0.604 (95% CI = 0.527 – 0.696). To elucidate the migration ecology of the population, I deployed 32 light-level geolocator tags on adult males in 2020 and retrieved tags in 2021. I recovered 13 (40.1%) geolocators, of which 10 provided data on post-breeding (fall) migration routes and nonbreeding season sites, and nine provided data on pre-breeding (spring) migration routes. The nonbreeding sites were clustered nonrandomly in Colombia, indicative of potential population connectivity. Post-breeding migration was largely overland through Mexico and Central America, with potential trans-Gulf flights by some birds. Pre-breeding migration routes by each individual were significantly ( $t = -4.75$ ,  $df = 8$ ,  $p = 0.001$ ) further east than the post-breeding route, based on the minimum (westernmost) longitude recorded during migration (mean difference = 232km), consistent with a pattern of anticlockwise loop migration. Overall, my research documented critically lacking information on region-specific relationships between demographic rates and environmental conditions and provides the first insight into the migratory ecology of a population of Canada Warblers near the southern extent of their breeding range. My results fill crucial ecological knowledge gaps for an imperiled species and serve as a foundation for full annual cycle demographic modeling.

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## ***Introduction***

Spatial and temporal variability of the resources which comprise a species' habitat influence the demographic rates of the species, and therefore long-term persistence of a population (Block and Brennan 1999). Many Nearctic-Neotropical migratory songbird species have shown evidence of substantial population declines in recent years (Rosenberg et al. 2019) creating an urgent need to understand the environmental drivers of population growth. Fundamentally, habitat quality is defined by population demographic rates. The combination of environmental features which permit survival and reproduction characterize the habitat of a given species, and variation in the environment produces a spectrum of habitat quality (Hall et al. 1997, Johnson 2007). While indices of the relative value of different habitats may be obtained from data such as species presence/absence, population density, or individual physical condition, defining habitat quality requires understanding how environmental features correlate with population growth (Johnson 2007, Boves et al. 2015).

Despite the importance of understanding the intrinsic habitat-demography relationship, information about the environmental drivers of demographic rates is limited for many declining species. Canada Warblers (*Cardellina canadensis*) are a neotropical migrant songbird species that has exhibited range-wide average annual declines of -1.3% between 1966 – 2019 with higher rates of declines in the United States than Canada (Sauer et al. 2020). West Virginia, with an average upward trend of 2.4%, is the only state with an increase in apparent abundance over the survey period (Sauer et al. 2020). This species breeds in forested areas across southern boreal Canada and the northeastern United States, with a narrow elevation-restricted distribution along the Appalachian corridor south through Tennessee and into northern Georgia (Reitsma et al. 2009). Environmental characteristics of the forests they occupy varies throughout their breeding

range, generally consisting of low canopies with complex understories developed under canopy gaps, leading to pockets of locally high abundance but regionally low densities (Hallworth et al. 2008a, Chace et al. 2009, Reitsma et al. 2009, Grinde and Niemi 2016). An obligate single-brood species, nests are built on or very near the ground by the female, who typically lays 3 – 5 eggs and is the sole incubator for 11 – 12 days, followed by an approximately eight-day nestling period provisioned by both sexes (Reitsma et al. 2009, 2018). Evidence of differential habitat selection across their spatial distribution (Crosby et al. 2019) highlights the need for assessment of factors which limit Canada Warbler populations, but most research has been conducted on populations at high latitudes (e.g., Sodhi et al. 1995, Hallworth et al. 2008a, b, Reitsma et al. 2008, Chace et al. 2009, Goodnow and Reitsma 2011, Ball et al. 2016, Demko et al. 2016, Flockhart et al. 2016, Grinde and Niemi 2016, Hunt et al. 2017, Westwood et al. 2019). Moreover, most do not report adult annual survival rates (but see Wilson et al. 2018), which is considered the most influential driver of population growth rates for many avian species (Sæther and Bakke 2000). Few studies have considered the southern extent of the breeding range, such as West Virginia, where abundance is increasing (but see Weakland et al. 2002, Becker et al. 2012, Dimmig et al. 2022), illustrating a considerable ecological knowledge gap which may be critical to inform conservation management of this declining species.

Demographic variation measured in the breeding season may be driven by events occurring across the full annual cycle of a migratory species (Faaborg et al. 2010, Marra et al. 2015a), and thus knowledge of regional nonbreeding season ecology is crucial to fully understand population dynamics. Full annual cycle modeling of migratory species requires knowledge of the movement of populations between breeding and nonbreeding distributions, and subsequent population responses to environmental predictors (Faaborg et al. 2010, Hostetler et

al. 2015, Marra et al. 2015a, Cooper et al. 2017). Neotropical migrant birds spend less than one third of the year on the breeding grounds, where the majority of demographic and habitat studies have occurred, but populations are quantifiably influenced by resources and stressors present during migration and the nonbreeding period (Faaborg et al. 2010, Hostetler et al. 2015, Schuster et al. 2019). Technology capable of tracking the movement of birds continues to be miniaturized for deployment on smaller species, leading to new revelations about migratory population connectivity, stopover ecology, and year-round influences on demography (Marra et al. 2011, McKinnon et al. 2013, Cooper et al. 2017). Light-level geolocators are currently the best available option for tracking small songbirds over large geographic ranges and have been deployed on several Parulid species (e.g., Hallworth et al. 2015, Wolfe and Johnson 2015, Cooper et al. 2017, Larkin et al. 2017, Raybuck et al. 2017), with only one known published study on Canada Warblers, which occurred on northern portion of their breeding range (Roberto-Charron et al. 2020). The nonbreeding season of Canada Warblers is less studied than the breeding season, but populations are known to overwinter at mid- to high elevations in South America, primarily on the slopes of the Andes Mountains in Colombia, Ecuador, and Peru, with scattered records in Venezuela (Reitsma et al. 2009, González-Prieto et al. 2017). The first study to use geolocators to track Canada Warblers found that several populations from a vast longitudinal distribution across Canada and the northern United States converged on migration through Mexico and Central America and wintered in northern South America (Roberto-Charron et al. 2020). However, hypotheses regarding causes of range-wide population declines due to events in the wintering range remain largely untested, and this study will provide data necessary to begin linking population dynamics during the breeding and nonbreeding seasons.

In this project, I investigated the demographic rates and migration ecology of a population of Canada Warblers breeding in the central Appalachian Mountains of West Virginia, USA. To evaluate demographic rates, in Chapter 1, I quantified adult annual survival and nest success and evaluated how each varied across an elevation gradient and in response to other environmental variables. To elucidate migration ecological traits, in Chapter 2, I tracked adult males using light-level geolocators and mapped overwintering locations and migratory pathways. These complementary studies fill crucial knowledge gaps in the natural history of this declining species and build the foundation to model Canada Warbler population dynamics across the full annual cycle.

***Chapter 1: Annual survival of Canada Warblers (*Cardellina canadensis*) increases with elevation in central Appalachia, USA***

**INTRODUCTION**

The abiotic and biotic attributes that constitute the resources available to a species are not uniformly distributed across the environment. The suite of environmental features which allow the species to survive and reproduce comprise the habitat of the species, therefore the available resources in the habitat intrinsically influence the rates of survival and reproduction (Hall et al. 1997, Block and Brennan 1999, Johnson 2007). The spatial and temporal heterogeneity of environmental features engenders inequality of resource availability that is reflected in the variable demographic rates of the population (Block and Brennan 1999, Johnson 2007). High-quality habitat can therefore be defined as the combination of environmental attributes which support positive population growth. To quantify habitat quality for a species, we must first understand the relationship between the environment and demographic rates. In this chapter, I examine how survival and reproduction of a population of Canada Warblers in West Virginia vary along a gradient of physical and biological features, to better understand the complex relationship between species and habitat.

There are myriad documented approaches for assessing avian habitat, including individual-level metrics of resource use, physical condition, and reproductive success, as well as population-level metrics of distribution, density, and survival, as a function of environmental features (Block and Brennan 1999, Johnson 2007, Boves et al. 2015). Depending on the objective of the research, each approach has benefits and limitations. When assessing habitat quality from the perspective of an individual bird, researchers have used criteria such as body mass, fat reserves, feather growth rate, and other physical or physiological parameters (Johnson



2007). Two major assumptions limit the usability of the individual condition approach: that different body conditions are an effect of differential habitat use, rather than a cause, and that the measured individual conditions result in disparate rates of survival or reproductive output (Johnson 2007). Furthermore, dissonance between results of studies that consider data of the individual or the population may lead to conflicting inferences about habitat quality. In a study of Cerulean Warblers, the lower individual reproductive output observed in areas of heavy timber harvest was offset by the higher densities of breeding pairs in this habitat (Boves et al. 2015). Thus, heavy timber harvest supported an overall higher reproductive rate for the population, which was critical information for the regional Cerulean Warbler habitat management strategy (Boves et al. 2015). This discrepancy highlights how individual-focused studies may not accurately reflect population outcomes and demonstrates the utility of population-level assessment.

Despite the advantage of population-level metrics, not all are equally informative of habitat quality. Population distribution may vary across the landscape, but greater abundance, occupancy probability, or density, may not solely be a result of higher quality habitat (Van Horne 1983, Hall et al. 1997, Johnson 2007). Correlating abundance alone with environmental features to establish a habitat quality gradient assumes that the individuals disperse equally into habitat which maximizes fitness, known as an ideal free distribution (Fretwell and Lucas 1970, Johnson 2007). However, individuals may occupy lower quality habitat because of numerous external influences, including temporal lag in response to changing habitat, incomplete information about available resources, or costs of dispersal to higher quality habitat (Johnson 2007). In many small songbirds like Canada Warblers, territorial behavior leads to the highest quality habitat preemptively occupied by the most competitive individuals, known as an ideal

despotic distribution (Block and Brennan 1999, Johnson 2007, Reitsma et al. 2008). Assuming individuals have complete knowledge of available habitat quality, this may cause less competitive individuals, such as young birds, to cluster in lower quality habitat at higher densities but not survive or reproduce at comparable rates, which may lead to a habitat sink (VanHorne 1983, Johnson 2007). In addition to spatial variability of occupancy and abundance, habitat quality may be quantified using temporal trends. Conceptually, higher quality habitat would be occupied more frequently and for longer durations (Sergio and Newton 2003), but the efficacy of this approach is limited by the necessary time investment to study. Additionally, when considering environmental attributes either spatially or temporally, it is insufficient to solely quantify the presence of species-specific resources, such as potential nest sites and food availability, since usage of these resources may be limited by abiotic physical barriers or biotic influences of predation or competition (Cody 1981, Hall et al. 1997, Block and Brennan 1999, Johnson 2007). Despite these limitations, population-level measures of distribution and abundance across varying environmental conditions explore the relationship between environment and population, and direct further research effort. Building on such a foundation, the most robust approach to determine the biotic and abiotic attributes which contribute to population growth for a species is the empirical evaluation of demographic rates of reproduction and survival in the context of environmental features (Block and Brennan 1999, Johnson 2007, Boves et al. 2015, Slevin et al. 2018).

Nest success is an important demographic process commonly studied in birds to evaluate the response of reproductive output to environmental predictors of habitat quality. In a striking example of long-term avian habitat conservation management, researchers found that more Seychelles Warbler young fledged and reached independence in territories with greater coverage

by seeded *Morinda* trees, which host a greater abundance of insects and are preferentially used by Seychelles Warblers for foraging over other available tree species (Komdeur and Pels 2005). Interactive effects between environment and demography may also account for differential reproductive output. Black-throated Blue Warbler reproductive success compared between high and low shrub density habitats revealed higher overall productivity in high shrub density areas (Holmes et al. 1996). The effect was compounded by older birds preferentially occupying the high shrub density areas, and frequently double-brooding successfully (Holmes et al. 1996). Studies of Canada Warbler reproductive success in different environmental conditions are limited. Using proxy estimates such as observing conspicuous male provisioning behavior or detecting at least one fledgling in the focal male's territory, researchers determined that territory size was either positively associated with (Flockhart et al. 2016) or was not associated with (Hallworth et al. 2008a) apparent reproductive success. Similar to the Black-throated Blue Warbler, the observed correlation between high reproductive success and older male Canada Warblers appeared to be caused by higher pairing rates of older males; no difference was detected in reproductive success between age classes when only paired males were considered (Reitsma et al. 2008). Evaluating finer scale nesting habitat for Canada Warblers also demonstrated a positive relationship between nest success and higher densities of small stems (Goodnow and Reitsma 2011) and vegetation cover within 3-6 m of the ground (Becker et al. 2012).

The relative contribution to population growth by reproductive and survival rates varies depending on the life history strategy of the species (Sæther and Bakke 2000). While assessing the factors which influence annual survival probability may be more challenging, particularly over broad spatial scales experienced by migratory birds, adult survival is considered the

stronger driver of population growth in many songbirds (Sæther and Bakke 2000). In both dickcissels and bobolinks, assessment of population models based on four years of data indicated adult survival was the most critical parameter influencing population persistence, and estimates were much less sensitive to changes in nest predation, parasitism, and renesting attempts (Fletcher et al. 2006). Canada Warblers are another example of a songbird species in which survival may be the primary driver of population dynamics. Recorded declines in apparent abundance across the breadth of their range underscore the need for insight into drivers of population demographic rates (Wilson et al. 2018). In the eastern portion of their breeding grounds, Wilson et al. (2018) estimated adult male Canada Warbler annual survival probability of 0.44 with no evidence for reduced breeding productivity, concluding low survival is likely driving population declines. Consequently, my study of Canada Warbler annual survival in response to environmental features will aid in filling this critical gap in ecological knowledge of the relationship between demography and environment.

Studies investigating Canada Warbler habitat selection demonstrated similarities and differences in the environmental features occurring across the northern portion of their breeding range. Forest structure appears to be a stronger predictor than forest type, since populations occupy a spectrum of northern hardwood, mixed forest, and conifers. In contrast, strong association with structurally low canopies, emergent trees, light gaps, and a complex understory is noted in multiple studies (Hallworth et al. 2008b, Chace et al. 2009, Goodnow and Reitsma 2011, Becker et al. 2012, Grinde and Niemi 2016). Emergent trees are used by males as song perches, and light gaps lead to dense undergrowth which provides concealment for nests (Chace et al. 2009, Goodnow and Reitsma 2011). Understory complexity also provides the mid-strata deemed important in Canada Warbler foraging behavior (Sodhi et al. 1995, Chace et al. 2009,

Céspedes and Bayly 2019). In West Virginia, Dimmig et al. (2022) observed a strong correlation between occupancy and stem density of rhododendron (*Rhododendron maximum*, a dense, thicket-forming shrub), as well as association with riparian areas; both features contribute to understory complexity. The dearth of research on this species at southern latitudes and the potential for range-wide variation in what defines high-quality habitat provides ample justification for demographic research in this region (Becker et al. 2012, Crosby et al. 2019). Furthermore, the fact that West Virginia is the only state where Canada Warblers have experienced significant population increases in the face of a range-wide downward trend (Sauer et al. 2020, Dimmig et al. 2022) evidences the relevance of understanding region-specific relationships between demographic rates and environment characteristics.

Variables that influence habitat quality may co-occur along gradients of environmental conditions at many spatial scales. Elevation is an ultimate driver of many resources, with changes in weather patterns altering habitat variables such as vegetation growth and food availability (Stevens 1992, Badyaev and Ghalambor 2001, Banko et al. 2002, Gaston 2003). Climatically, elevation gradients of temperate regions resemble latitudinal gradients on a narrower spatial scale, which may drive changes in resource availability and therefore population demography (Able and Noon 1976, Sanders and Rahbek 2012, Halbritter et al. 2013, Boyle et al. 2016). Relative position within complex topography also alters microclimate and habitat variables and therefore distribution; for example, Cerulean Warblers specialize in steep upper slopes and ridgelines (Nareff et al. 2019). With a geographically narrow distribution in the Appalachian corridor through West Virginia, recent work indicated a peak in Canada Warbler occupancy probability at mid-elevations (~930 m) (Dimmig et al. 2022). If variation in habitat quality along the elevation gradient is the underlying cause of occupancy variation, with low

elevations lacking suitable habitat, it should be reflected in the demographic rates of populations at different elevations. Regarding topographic complexity, Canada Warblers were positively associated with riparian areas (Dimmig et al. 2022) which are linked to lower topographic positions.

In this project, I assessed population demography of Canada Warblers breeding in the central Appalachian Mountains at six sites across three elevation strata in the Monongahela National Forest, West Virginia, USA. My novel demographic research seeks to quantify how survival and reproductive rates correlate with environmental features to measure habitat quality. The study objectives were: (1) estimate adult annual survival and nest survival rates of Canada Warblers across an elevation gradient in central Appalachia; and (2) investigate if variation in demographic rates correspond with factors associated with occupancy probability, including elevation, rhododendron, surface water, as well as slope position and slope aspect. My project quantitatively approached the challenge of describing habitat quality for this declining species, in a region with considerable range restrictions likely driven by a narrow spectrum of favorable environmental conditions.

### *Hypotheses and Predictions*

1. If Canada Warbler habitat quality, as measured by demography, varies along the elevation gradient to correspond with previously estimated occupancy probability in the central Appalachians of the Monongahela National Forest, WV, then I predict that apparent survival and reproductive success will exhibit a quadratic relationship with elevation, with highest demographic rates at mid-elevations.

2. If habitat quality is influenced by rhododendron, then I predict that survival and reproductive success will positively correlate with higher coverage by rhododendron
3. If habitat quality is influenced by surface water, then I predict that survival and reproductive success will increase with greater amounts of available surface water.
4. If habitat quality is influenced by topographic position, I predict survival and reproductive success will be higher in areas of lower topographic position, correlating to valleys.

## **METHODS**

### *Study Area*

I conducted fieldwork on public lands in the Monongahela National Forest (MNF), West Virginia, USA. The MNF was established in 1920 and encompasses almost 371,000 hectares of federally protected land across the central Appalachian Mountains, with elevations ranging 300 – 1500m (USDA 2011). My study sites are distributed across the Allegheny Highlands Section of the Appalachian Plateau Physiographic Province in the west of the MNF. The region is characterized by the complex topography resulting from mixed flats, folds, and faults (WV Geological & Economic Survey 2020). More than 70 tree species comprise the diverse forest types that vary across the elevation gradient of the MNF (USDA 2011). Below 900 m, mixed oak and mixed mesophytic forest types are dominant, transitioning to northern hardwood between 900 m and 1,150 m, with remnant boreal red spruce forests predominant above 1,150 m (USDA 2011, Dimmig et al. 2022)

### *Site Selection*

Within the MNF, I evaluated survival and reproduction along an elevation gradient. To stratify my sites, I used the same three elevation bands Dimmig et al. (2022) used to model Canada Warbler occupancy dynamics in the region:  $< 853$  m,  $853 - 1,158$  m, and  $> 1,158$  m. The 853 m cutoff was selected based on literature suggesting this is the lower limit for Canada Warblers in the Appalachians (Harding et al. 2017), and the middle stratum was delineated to form approximately equal elevation bands (Dimmig et al. 2022). I selected two locations within each stratum that had relatively high detections of Canada Warblers in point counts (Dimmig et al. 2022). The six sites spanned an approximately 130 km north-south geographic range (Figure 1.1), had areas of 72 – 209 ha, and encompassed elevations of 527 – 1293 m (Table 1.1). Dimmig et al. (2022) rarely detected Canada Warblers above 1,158 m, the lower cutoff of the highest elevation stratum. As such, mean elevations of each total high-elevation site search area were all  $< 1,158$  m, with portions of the sites above the cutoff. Sites were generally characterized by lack of recent timber harvest (Dimmig et al. 2022), high density of rhododendron, and were typically bisected by non-ephemeral streams (Figure 1.2). Higher latitude and lower elevation sites consisted chiefly of mixed mesophytic forest transitioning to dry oak and oak-pine mesic forest upslope; southern sites contained predominantly northern hardwood and red spruce forests, with mixed mesophytic patches. Four of the sites were bordered or bisected by gravel roads only accessible with a US Forest Service key and thus subject to minimal vehicular travel, and two were accessed with marked hiking trails.

### *Study Design: Mark-Resight*

To estimate Canada Warbler survival rates, I used a mark-resight study conducted 2019 – 2021. Mark-resight is a type of a mark-recapture study design, where each “capture” event does



not need to be a physical capture of the animal but may be an encounter with the individual through visual observation based on some unique identifying information (Pollock et al. 1990). In this case, birds were captured, marked, and released, with a unique combination of colored leg bands (Figure 1.3). Because I studied interannual survival, populations were assumed to be closed within a single breeding season, with mortality or emigration events assumed to occur between breeding seasons (Pollock et al. 1990).

*Field Methods: Establishing a marked population*

In 2019, the marked population was established by focusing initial capture efforts at and around point count locations surveyed by Dimmig et al. (2022). To initially mark individuals, I surveyed each study site for Canada Warblers between May and July by listening for songs of territorial males and using conspecific audio playback to elicit a response when no singing males were detected. When I located an individual, I attempted capture using an audio lure of a speaker broadcasting Canada Warbler song placed near two mist nets (6 m x 2.6 m; 30 mm mesh) deployed in an “L” formation parallel and perpendicular to understory growth as structure permitted. Once captured, I determined the sex (male, female, or unknown) and age (hatch-year, second-year, after-second year, or after-hatch year) of the bird via plumage characteristics (Pyle 1997) (Figure 1.4). I additionally recorded individual morphometric attributes including mass (g), wing chord (mm), tail length (mm), tarsus length (mm), and presence of a cloacal protuberance or brood patch. Birds were marked with an aluminum band issued by the United States Geological Survey and a unique combination of three plastic color bands.

*Field Methods: Surveying for marked birds*

In 2020 and 2021, I systematically searched each site based on the known capture locations of Canada Warblers from the previous year, using a modification of typical territory spot-mapping (Bibby et al. 2000). I generated 210 m radius buffers around recorded bird locations from the previous year(s) and combined them into a single boundary for each site. I defined the 210 m buffer based on literature reporting the largest defended area by a singing male as 1.5 ha, which corresponds to a circle with a radius of ~70 m (Hallworth et al. 2008a, Reitsma et al. 2009), and set the buffer equivalent to three times that radius. This set reasonable borders for re-sighting individuals and enabled me to search the entire site while allowing for territory shifts to occur between years. To ensure systematic searching even through challenging terrain and to maximize the chance of encountering a marked bird, I generated a grid of points that I visited at least once annually. I overlaid grid points (53 – 92 points per site) spaced 150 m apart at each site (Figure 1.5A). I chose 150 m spacing to account for aural detection limits of Canada Warblers which are estimated to range 60-200m (Matsuoka et al. 2012, Hunt et al. 2017). Field personnel walked slowly to each grid point listening for singing males, and broadcast Canada Warbler song at each grid point for up to three minutes to elicit a response if no birds were otherwise detected. Field personnel recorded tracks with handheld GPS units which I used to plan walking routes through gaps in searched areas. Surveys occurred biweekly for a total of 6-10 days per site spaced evenly across the field season; total time spent searching each site varied proportional to the number of marked birds present at the site.

When a singing male was detected, it was visually identified to determine current mark status. If unmarked, I attempted to capture and mark the bird using the above protocol. If marked, I recorded the color band combination, along with date, time, and GPS location, then

continued surveying. If the complete combination was unable to be accurately determined in the encounter, I visited the location repeatedly until identity could be confirmed. If the bird lost a colored band or I was otherwise unable to confirm identity, the bird was recaptured using the capture protocol above to obtain the unique band ID number, replace missing color bands if applicable, then released. I prioritized resighting as many marked birds as possible, rather than collecting multiple locations of the same individual at each encounter. Some birds were only observed once during the entire field season, and others were present and recorded at several different site visits.

#### *Study Design and Field Methods: Nest Survival*

To estimate Canada Warbler apparent nest survival rates and subsequent reproductive output, I located and tracked nesting attempts during the 2021 field season. Nests were located opportunistically in each elevation strata using behavioral cues from adults. These cues included brooding females which frequently visited the same location in the territory, defensive chipping by either sex as a response to intrusion, or food carrying. Once I located the nest, I determined the nest stage as incubating or nestlings.

To determine nest fates, I used game cameras to continuously observe the nest until fledging or failure. Game cameras were optimal for nest observations for three reasons: minimized personnel time necessary for nest checks, increased accuracy of fail/fledge dates, and identified specific causes of nest failure, such as identity of the predator (Richardson et al. 2009, Cox et al. 2012a, 2012b). The impact of cameras at nests on predation patterns is not yet well-studied, as few studies compare predation rates between camera-monitoring and traditional monitoring with mixed results (Richardson et al. 2009). However, cameras have demonstrated increased reliability of identifying predators, and documented similar nest survival rates by nests

with and without cameras (Williams and Wood 2002) and are a promising field technique to study nesting ecology of many avian taxa (Uhe et al. 2020, Surmacki and Podkowa 2022). I mounted Bushnell Trophy Cam HD cameras on sturdy vegetation (e.g., rhododendron stem) < 1 m from the nest, or onto a dead branch planted upright at the same distance if no suitable vegetation was available (Figure 1.6). Cameras were triggered to take a sequence of three photos when motion was detected by the infrared sensor (Figure 1.7). To minimize human disturbance to the site, I only visited each nest a maximum of two times during the active nesting period. I then visited the nest site after failure or fledging to retrieve cameras and collect data on fine-scale environmental variables.

### *Environmental Variables*

#### SURVIVAL

To summarize the environmental variables for each bird as a potential predictor of survival probability, I approximated the space use of the bird as a circular buffer around the median coordinates of an individual's recorded locations for each year (Reidy et al. 2018) (Figure 1.8). I elected to use the median, rather than mean, x- and y-coordinates, because the median is less affected by a single outlier location and thus likely a more accurate representation of where the bird most frequently occurred (Reidy et al. 2018). Because some birds were only observed once in a year, kernel density or minimum convex polygons were not a viable option to estimate space use. The size of the territory a Canada Warbler defends has been reported with high variability and may depend on many factors, including bird age, habitat conditions, and geographical area. Home range size has been reported between 0.2 – 1.5 ha (Table 1.2) (Hallworth et al. 2008a, 2008b, Reitsma et al. 2008, 2009, Flockhart et al. 2016, Hunt et al. 2017). Based on these published estimates of home range and core use area, I summarized

environmental variables within a circle of radius 50 m, approximately 0.8 ha, to approximate the habitat used by the individual bird and resources available to contribute to survival. I selected the 50 m radius to ensure adequate possible habitat and occurrence points were included without excessive overlap of buffers between birds. Within the circular buffer, I calculated the mean elevation, total linear length of streams, mean cosine of aspect, mean topographic position index (TPI), and area of the buffer with coverage categorized as rhododendron

I used a combination of available spatial data, derived data, and manually processed imagery to quantify environmental variables (Table 1.3). To obtain elevation values, I used a 1:4800 3 m digital elevation model (DEM) (USGS 2021) (Figure 1.5C). I derived aspect values from the 3 m DEM, using a cosine transformation to account for the circular nature of the parameter (Smith et al. 2019). To create a map of TPI, I used the same DEM and subtracted from each focal cell ( $Z_{focal}$ ) the mean elevation ( $Z_{mean}$ ) of neighboring cells within a circular moving window, with a radius of 25 cells (~75m) (Weiss and The Nature Conservancy 2001, Alemayehu et al. 2018).

$$TPI = Z_{focal} - Z_{mean}$$

Thus, negative TPI values indicate valleys, positive TPI indicates ridges, and values near 0 represent flat areas or areas with constant slope (Figure 1.5D). I selected the moving window radius based on trial and error to capture the complex topography of the site, as well as the scale expected to affect an individual bird based on the territory sizes previously discussed. To map streams present within the sites, I used the 1:4800 National Hydrography Dataset which includes perennial, intermittent, and ephemeral streams (USGS 2016).

I manually mapped site coverage by rhododendron (*Rhododendron maximum*) by digitizing polygons from leaf-off satellite imagery (WVGISTC 2018). Rhododendron is an evergreen species that can be differentiated by color and texture from conifers and was well suited for this mapping technique. In some sites at higher elevations, mountain laurel (*Kalmia latifolia*) grew concurrently with or replaced rhododendron. While rhododendron is often associated with protected, mesic soil and mountain laurel with exposed upslope areas, both evergreen species grow in dense thickets and are mostly visually indistinguishable in leaf-off imagery (Chastain and Townsend 2007), so mountain laurel was included and hereafter referred to as “rhododendron” in environmental data analyses. I evaluated the accuracy of this map by recording presence / absence of rhododendron at the same grid points used to guide bird survey effort.

#### NEST SUCCESS

The environmental covariates for the nest success model included elevation, aspect and TPI, calculated as described above. In addition, I collected fine-scale vegetation coverage data at the nest site. I visually estimated rhododendron and total shrub (rhododendron + other species < 1.5 m tall) percent cover of the ground within four 1m x 3m belt transects extending from the nest site in each cardinal direction (Figure 1.9) (Goodnow and Reitsma 2011). The resulting rhododendron and total shrub cover values used as the nest success covariate were the mean values of the four transects.

#### *Statistical Analysis*

#### ANNUAL SURVIVAL

I estimated the annual survival probability of Canada Warblers using a spatial generalization of a Cormack-Jolly-Seber (CJS) model. I fit nine different models of

environmental covariates (Table 1.4) and ranked models according to DIC. The following draws heavily from the model description in Schaub and Royle (2014). The spatial CJS model implicitly assumes the population is open between years but reduces potential negative bias of survival rates reported from traditional CJS models in which survival and permanent emigration from the study area are confounded. Model variables include the encounter histories of marked individuals, their respective locations in Euclidean space, associated environmental covariates, and study area boundaries. By including the locations of the bird each year, small-scale dispersal events are captured by the modeled dispersal kernel. This accounts for birds that may have locally dispersed outside of the study area and are not available for detection but are still alive. For example, in the framework of the model, a bird marked in year one and never detected again could have moved outside of the study area and was unavailable for detection in year two and moved back within the study area but remain undetected during year three.

Implementing the model requires several key assumptions. If a bird was detected one time during the field season, I assumed it was alive during the entirety of that respective field season – subtraction from the population could only occur between annual encounters. Hence, each bird needed only a single encounter within the field season. If I detected a bird multiple times, I used the median coordinates to provide a single location representative of space use. I assumed that survival was not a function of whether the individual was inside or outside of the study area, and that an individual's survival was independent from all other individuals. Furthermore, I assumed an encounter was equally possible anywhere within the boundaries of the study area.

The hierarchical model followed a state-space formulation consisting of the state processes of survival and dispersal, and an observation process, in which only birds alive and

within the study area are available for detection. Within the model, the latent state variable  $z_{i,t}$  denotes whether individual  $i$  is alive at time  $t$  (if alive,  $z_{i,t} = 1$ , if dead,  $z_{i,t} = 0$ ). I assume survival is a Bernoulli random variable where  $s_{i,t}$  is the survival probability between year  $t$  and year  $t+1$ :

$$z_{i,t+1}|z_{i,t} \sim \text{Bernoulli}(z_{i,t}s_{i,t}).$$

The second state process describes the coordinates of the individual in space. I modeled movement as a random walk, assuming its x and y coordinate are normal random variables centered on the previous year's x and y coordinate:

$$x_{i,t+1} \sim \text{Normal}(x_{i,t}, \sigma_x^2),$$

$$y_{i,t+1} \sim \text{Normal}(y_{i,t}, \sigma_y^2).$$

Linear dispersal distance is not directly modeled, rather, it is a derived variable calculated from the variance of known dispersal movements. Expected dispersal distance  $D$  is thus:

$$D = \sqrt{2(\sigma_x^2 + \sigma_y^2)/\pi}.$$

Lastly, the observation model is described as a Bernoulli random variable, conditional on the individual both being alive and located in the study area. The observation process incorporates a test  $r_{i,t}$  of whether individual  $i$  is inside the state-space of the study area  $A$  at time  $t$ , where  $r_{i,t} = 1$  if location  $x_{i,t}, y_{i,t}$  falls inside study area  $A$ , and  $r_{i,t} = 0$  if it does not. To determine whether the  $x, y$  coordinate pair was inside the study area  $A$ , the polygon boundary of each site was divided into 50 m x 50 m grid cells (Figure 1.5B) and if the coordinate fell within any cell, it was within the study area. Therefore, assuming  $p_{i,t}$  are constant across all individuals and over time, the observation model  $O$  is:

$$O_{i,t}|z_{i,t}, r_{i,t} \sim \text{Bernoulli}(z_{i,t}r_{i,t}p_{i,t}).$$



I modeled survival probability as a logit-linear function of environmental covariates:

$$\text{logit}(s_{i,t}) = \Phi_s + \beta_X * X_{i,t}.$$

When a bird was observed at time  $t$ , the environmental covariates associated with the location were known. However, in the years a bird was not observed, environmental variables were missing values. I therefore imputed model covariate values  $X_{j,i}$  of bird  $i$  using the mean  $\mu$  and variance  $\tau$  of the values observed at site  $j$ :

$$X_{j,i} \sim \text{Normal}(\mu_{X,j}, \tau_{X,j}).$$

Because I assumed only small-scale dispersal by individuals, variables imputed from the distribution of observed variables in this way reasonably estimated local conditions.

The models were fit using Bayesian methods, implemented using JAGS 4.3.0 (Plummer 2017) with the *jagsUI* package (Kellner 2021) in R 4.1.2 (R Core Team 2021). I specified a uniform (0, 1) prior for  $p$ ; a logistic (0, 1) prior for  $\Phi$ ; a logistic (0, 1) prior for all slope coefficients  $\beta$ ; and a uniform (0, 600) prior for  $\sigma_x$  and  $\sigma_y$ . I ran three Markov chains, discarding the first 500 samples as burn-in and then continuing to draw posterior samples until convergence was achieved, drawing 1,500 to 12,500 samples from the posterior distribution depending on the model. Models were considered converged using the Brooks-Gelman-Rubin diagnostic ( $\hat{R} < 1.1$ ) (Brooks and Gelman 1998).

#### NEST SUCCESS

I estimated daily nest survival as a function of environmental variables using the nest survival model described by Dinsmore et al (2002). I fit six different models (Table 1.5) and ranked models according to DIC. I assumed that nest fates were accurately determined and were independent, daily nest survival remained constant through the nest cycle, and nest discovery and

camera presence did not alter daily survival probabilities. Because cameras enabled constant effort surveillance, fledging or failure events were recorded and dates were known. I assume whether the nest survives a day is a Bernoulli random variable  $y$  with parameter  $p_{i,t}$ , the probability of the nest  $i$  alive on day  $t$ , conditional on being alive the previous day,  $t - 1$ :

$$y_{i,t} \sim \text{Bernoulli}(p_{i,t} * y_{i,t-1}).$$

I modeled daily nest survival probability as a logit-linear function of environmental covariates  $X$ :

$$\text{logit}(y_{i,t}) = \mu_p + \beta_X * X_{i,t}$$

The models were fit using Bayesian methods, implemented using JAGS 4.3.0 (Plummer 2017) with the *jagsUI* package (Kellner 2021) in R 4.1.2 (R Core Team 2021). I specified a uniform (-20, 20) prior for  $\mu_y$ , and logistic (0, 1) priors for all  $\beta_X$ . I ran three Markov chains for 2000 iterations, discarding the first 1000 iterations as burn-in, and keeping every 5th sample thereafter. Models were considered converged using the Brooks-Gelman-Rubin diagnostic ( $\hat{R} < 1.1$ ) (Brooks and Gelman 1998).

## RESULTS

### *Mark-Resight*

During May to July of 2019 and 2020, a total of 211 unique Canada Warblers were captured and marked. Of these 211, six were AHY females and two were HY of unknown sex and were discarded from further analysis, leaving a final sample of 203 adult male birds distributed across the six study sites. At their first capture, 57 birds were aged as SY, 46 as ASY, and the remaining 100 as AHY. Field personnel in 2019 were unable to age birds as SY or ASY,

thus the high number of AHY birds. Birds were separated into SY and ASY in 2020, but one-year return rates in 2021 did not differ between age classes ( $\chi^2 = 2.1257$ ,  $p = 0.1449$ ). For all male birds, the one-year return rate was 0.33 in 2020 and 0.47 in 2021, with 14% of birds observed all three years, and 60% of banded birds not observed after the year of their capture (Table 1.6). The mean number of locations recorded per bird increased each year as I intentionally dedicated more time to resights, and was 1.2 (SD: 0.62, range: 1-5) when focusing on captures to establish marked population in 2019, 1.9 (SD: 1.33, range 1-7) when time was spent both resighting and capturing additional birds in 2020, and 3.0 (SD 1.56, range 1-7) when only resighting in 2021 (Figure 1.10). Despite increasing time dedicated to resights, there were no birds from year 1 detected in year 3 that were not detected in year 2, suggesting detection probability remained consistent.

#### *Interannual Movement*

The shift in median coordinates of all birds observed in more than one year was a mean of 166 m and a median of 69 m. The distances moved varied among birds; 50% of movements were < 70 m, and 80% of movements were < 140 m (Figure 1.11). There were some larger shifts; 8.4% of interannual movements were > 500 m from their previous coordinates. The largest movement recorded was 2.3 km, a distance shifted twice by the same bird from 2019 to 2020, and 2020 to 2021, with the 2019 and 2021 positions less than 200 m apart. The bird was only seen once in 2020, despite extensive searches.

#### *Adult Annual Survival*

Canada Warbler annual survival probability exhibited a positive linear relationship with elevation. The top model, which included only elevation as a predictor of survival, was 98.8 DIC

units ahead of the next candidate model (Table 1.4). Annual survival probability ranged from 0.573 (95% credible intervals (CI) = 0.333 – 0.820) at 555 m to 0.702 (95% CI = 0.493 – 0.871) at 1255 m (Figure 1.12). However, although the elevation model had a lower DIC value than the intercept-only model ( $\Delta\text{DIC} = 127.6$ ), the 95% credible intervals of the slope coefficients for elevation overlapped 0 (mean log-odds ratio = 0.150, 95% CI -0.335 – 0.602, proportion of posterior mean  $> 0 = 0.746$ ). Although the model incorporating elevation had a greater predictive power than a model assuming constant survival, there is substantial uncertainty in the effect of elevation. After accounting for undetected birds that may have established territories outside study area boundaries, the mean interannual location shift was estimated by the dispersal model to be 391 m (SD = 31.5 m) (Figure 1.13). The probability of detecting a live Canada Warbler that was present within the site was estimated as 0.955 (95% CI = 0.841 – 0.999).

### *Nest Survival*

I located 12 nests during 2021 which contained an average of 4.33 (range 4 – 5) eggs or nestlings, and 9 nests successfully fledged. Fledge dates ranged from 14 June – 24 June 2021. One nest failed during incubation to suspected predation by a large animal (camera was knocked over) and the other two nests failed due to predation by a Broad-winged Hawk (*Buteo platypterus*) and squirrel (*Sciurus sp.*) (Figure 1.14). The intercept-only model was the top model indicated by DIC values (Table 1.5). Slope coefficients of environmental predictors for all models overlapped 0 indicating no clear effect of any of the variables measured. In the intercept-only model, daily nest survival was estimated as 0.957 (95% CI = 0.890 – 0.990), for an overall nest success probability over 19 days of 0.604 (95% CI = 0.527 - 0.696).

## DISCUSSION

Knowledge of region-specific environmental correlates of population demographic rates of Canada Warblers is critical for understanding the potential drivers of range-wide population declines (Wilson et al. 2011). The relationship between Canada Warbler adult survival and elevation suggests an underlying variability of habitat quality. Survival positively correlated with elevation, consistent with findings by Dimmig et al. (2022) which indicated a peak in occupancy probability at 930 m and an overall quadratic effect. While I did not find evidence of a quadratic effect of elevation on survival, it is likely due to the low occupancy probability at the highest elevations of the MNF by Canada Warbler populations of sufficient size to study survival. Despite the statistical uncertainty present in my work and in Dimmig et al. (2022), the consistent direction of the correlation substantiates elevation as an indicator of habitat quality in West Virginia. Elevation ultimately drives habitat variables through interconnected physical processes which impact biotic communities through distribution of resources (Able and Noon 1976, Chastain and Townsend 2008, Sanders and Rahbek 2012, Boyle et al. 2016). Canada Warblers have been shown to select moist areas with complex leafy understory within variable forest types (Mitchell 1999, Gross 2010, Harding et al. 2017). Temperature generally decreases with increasing elevation, resulting in vegetation community occupancy of a climatological niche (Breshears et al. 2008, Freeman et al. 2018). Additionally, at higher elevations in central Appalachia, structural understory growth is promoted by disturbance, and Canada Warblers are positively associated with gap creation through harvest (Weakland et al. 2002, Becker et al. 2012). Higher elevations, cooler temperatures, water availability, and disturbance dynamics may combine to produce amenable habitat characteristics for Canada Warblers at mid and high elevations of central Appalachia.

Elevation as an influence on Canada Warbler population growth may have long-term conservation implications. Montane habitats face unique risks under climate change, where available space upslope decreases to a finite limit, presenting a higher risk of extinction for elevation-dependent species under warming climate (Breshears et al. 2008, Dirnböck et al. 2011, Elsen and Tingley 2015, Freeman et al. 2018). In central Appalachia, Canada Warblers are currently less likely to occupy the highest available elevations (Dimmig et al. 2022), but with the positive correlation between survival and elevation, potential upslope emigration may occur into currently unoccupied habitat. Such a shift may result in local extirpation of low-elevation populations under predicted warmer and drier conditions (Breshears et al. 2008, Elsen and Tingley 2015) but these threats to the persistence of central Appalachian populations may be mitigated by the availability of unoccupied space upslope.

Since specific habitat characteristics differ throughout the Canada Warbler's geographic range (Becker et al. 2012, Ball et al. 2016, Grinde and Niemi 2016, Hunt et al. 2017, Crosby et al. 2019), region-specific demographic assessments are crucial to understanding how environmental conditions impact survival. Estimated annual survival probabilities for adult male Canada Warblers in West Virginia were higher than estimates obtained across the species' eastern breeding region (0.44 [90% CI 0.30 – 0.58]) (Wilson et al. 2011) or measured over the nonbreeding seasons in the Colombian Andes in native forest (0.48 [SE = 0.12]) and coffee plantations (0.53 [SE = 0.11]) (González-Prieto et al. 2017). Inference regarding the higher survival in West Virginia should be drawn with caution, due to different statistical methodologies; Wilson et al. (2011) used mark-recapture data from 16 Monitoring Avian Productivity and Survival stations between 1993 and 2016, and González-Prieto et al. (2017) used a multistate mark-recapture model on three consecutive years of passive mist-net captures.

Incorporating spatial information in my mark-resight study reduces negative bias in apparent survival by de-confounding local movements and survival, which produces higher survival rates believed to better approximate “true” survival (Schaub and Royle 2014). My study also focuses on a narrower geographic area of the breeding season – as opposed to the eastern breeding region defined by Wilson et al. (2011) – which included just south of Lake Superior, east to Maine and south through the Appalachian Mountains – a vast area across which abundance trends are not uniform (Sauer et al. 2020). However, the concomitant trend of increased apparent population growth and estimated higher survival probabilities in West Virginia is indicative of an underlying difference in population demography. Further investigation into full annual cycle population dynamics could incorporate environmental drivers of migratory and nonbreeding season survival to better assess threats to populations of this declining species (Hostetler et al. 2015, Marra et al. 2015a).

Models which included rhododendron coverage, stream length, and topographic position index (TPI) chosen *a priori* as predictors of annual survival due to previous work, may have lacked support because my data represented an insufficient gradient of the variable within the Monongahela National Forest. While Dimmig et al. (2022) found Canada Warbler occupancy probability increased with higher rhododendron stem density and shorter distance to riparian areas, the sampling gradient included many point count locations where the species was absent. However, measuring survival requires individuals to be present. All my study sites included rhododendron, streams, and were centered in valleys of low TPI, resulting in a narrow gradient of these conditions; minimum habitat requirements in West Virginia may be fundamentally defined by these features. Other subtle changes correlated with elevation may therefore be driving the spectrum of habitat quality. Alternatively, the circular buffer used to summarize

environmental conditions (Reidy et al. 2018) may not have captured the scale at which Canada Warblers respond to variation in rhododendron, streams, or TPI.

Incorporating the locations of observed individuals not only de-confounded small-scale movement and survival, but also provided insight into local dispersal dynamics. The observed mean interannual shift of 166 m, and the estimated mean shift of 391 m (after correcting for imperfect detection) was much higher than the observed 25-35 m reported in New Hampshire (Hallworth et al. 2008b). This lesser interannual dispersal in New Hampshire could be attributed to multiple factors: use of a different methodology, not accounting for imperfect detection, or smaller average interannual movements due to relatively high-quality habitat. In New Hampshire, 25% of banded male Canada Warblers were recorded in three consecutive years (Hallworth et al. 2008b), in contrast to only 14% in my study; this may be driven by higher dispersal rates outside of my study area boundaries relative to Hallworth et al (2008b). Some large movements may result in the bird resettling elsewhere in the study area, while others lead to permanent or temporary emigration out of the search area, dependent on dispersal direction. In contrast to Reitsma et al.( 2008) which documented a higher proportion of SY males as transient, the 60% of birds not observed in years after capture did not appear drive by age, suggesting other factors may be driving dispersal probabilities. Further study of these larger dispersal movements would be necessary to parse the interaction between dispersal distance and habitat quality.

Canada Warbler nest survival in the MNF did not appear to be influenced by the chosen environmental predictors, but the small sample of 12 nests limits the strength of model inference. My nest success results are consistent with the range of previous raw nest success data (in the absence of published daily survival rates), from 0.55 in eastern West Virginia to 0.77 in New Hampshire (Goodnow and Reitsma 2011, Becker et al. 2012). My hypothesis that Canada

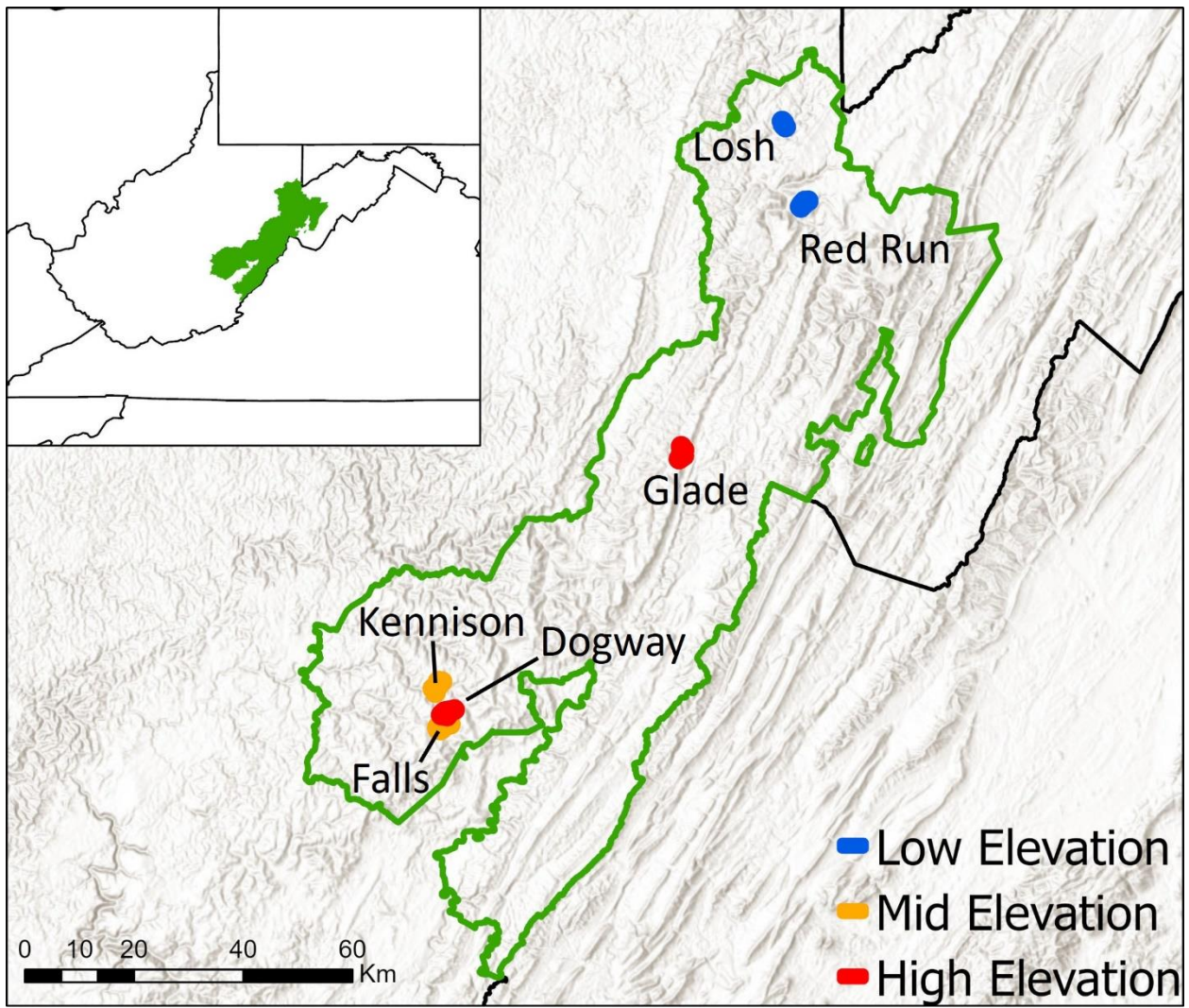


Warbler apparent positive population growth in West Virginia is driven by higher survival rates is supported by the fact that reproductive rates fall within the range of previous studies, but survival rates are higher. The ostensibly greater influence of survival, rather than reproduction, on population growth is consistent with many other songbirds (Sæther and Bakke 2000), and focusing on identifying the drivers of survival will be critical to improve population growth rates across the Canada Warbler range.

If high quality habitat available in West Virginia is driving positive population growth of Canada Warblers, the state may become crucial to Canada Warbler conservation. With a history of timber harvest, forest management may also promote habitat creation in West Virginia; Canada Warblers had increased abundance in light partial post-harvest stands, and comparable nest success post-harvest (Weakland et al. 2002, Becker et al. 2012) relative to my findings in unmanaged habitat. Forest management including partial timber harvest is therefore a possible method to create high quality Canada Warbler habitat in West Virginia, although further study comparing adult survival between managed and unmanaged plots would be necessary to account for the full demographic picture. Demographic study across environmental gradients to identify key habitat components allows conservation managers to prioritize the preservation of existing high-quality habitat for declining species (Buehler et al. 2008, Zitske et al. 2011, Reidy et al. 2018, Westwood et al. 2020, Brambilla et al. 2020). As Canada Warblers decline across most of their breeding range (Sauer et al. 2020), understanding regional variation in environmental influences on population dynamics may be critical for conservation. Moreover, the increasing abundance of the Canada Warbler through the range trailing edge in central Appalachia contrasting with broader population declines emphasizes the need for further study of the

demography-environment relationship to better predict population responses to environmental change.

CHAPTER 1: FIGURES AND TABLES



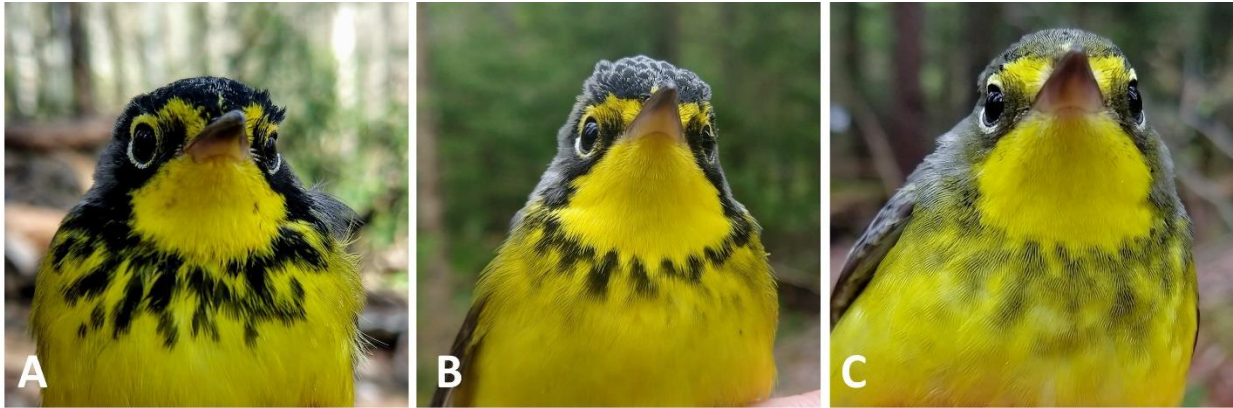
**Figure 1.1** Map of study area with six study sites in eastern West Virginia, with the boundary of the Monongahela National Forest in green (inset). Low, mid, and high elevation sites were defined as < 853 m, 853 – 1,158 m, and > 1,158 m, respectively.



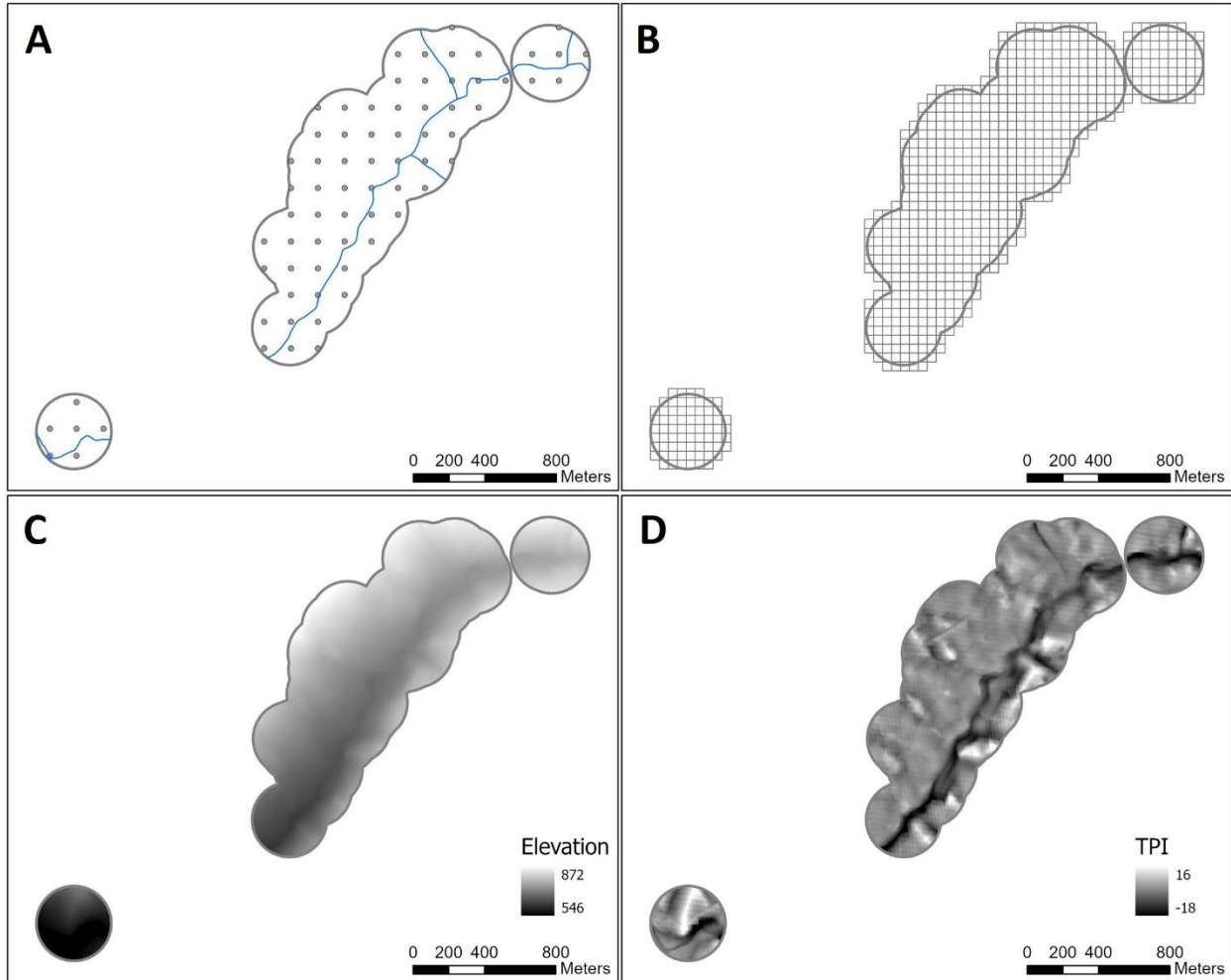
**Figure 1.2** Photographs of Canada Warbler habitat from three of six study sites in the Monongahela National Forest, WV, USA. (A) Unnamed stream tributary of the Cheat River running through low-elevation site Losh, (B) Mature *Rhododendron maximum* growing at high-elevation site Glade, and (C) ~1m tall *Rhododendron* covering the forest floor of mid-elevation site Falls.



**Figure 1.3** Adult male Canada Warbler (*Cardellina canadensis*) marked in 2019 in the Monongahela National Forest, WV, USA and resighted in 2020 with a unique combination of three plastic color bands and one numbered aluminum USGS band.



**Figure 1.4** Plumage variation in Canada Warblers (*Cardellina canadensis*) captured in the Monongahela National Forest, WV, USA in 2020. Differences in ‘necklace’ plumage evident across ages and sexes, where (A) is an after-second-year male, (B) is a second-year male, and (C) is an after-second-year female. Molt limits in primary coverts (not pictured) also distinguish between age classes in either sex.

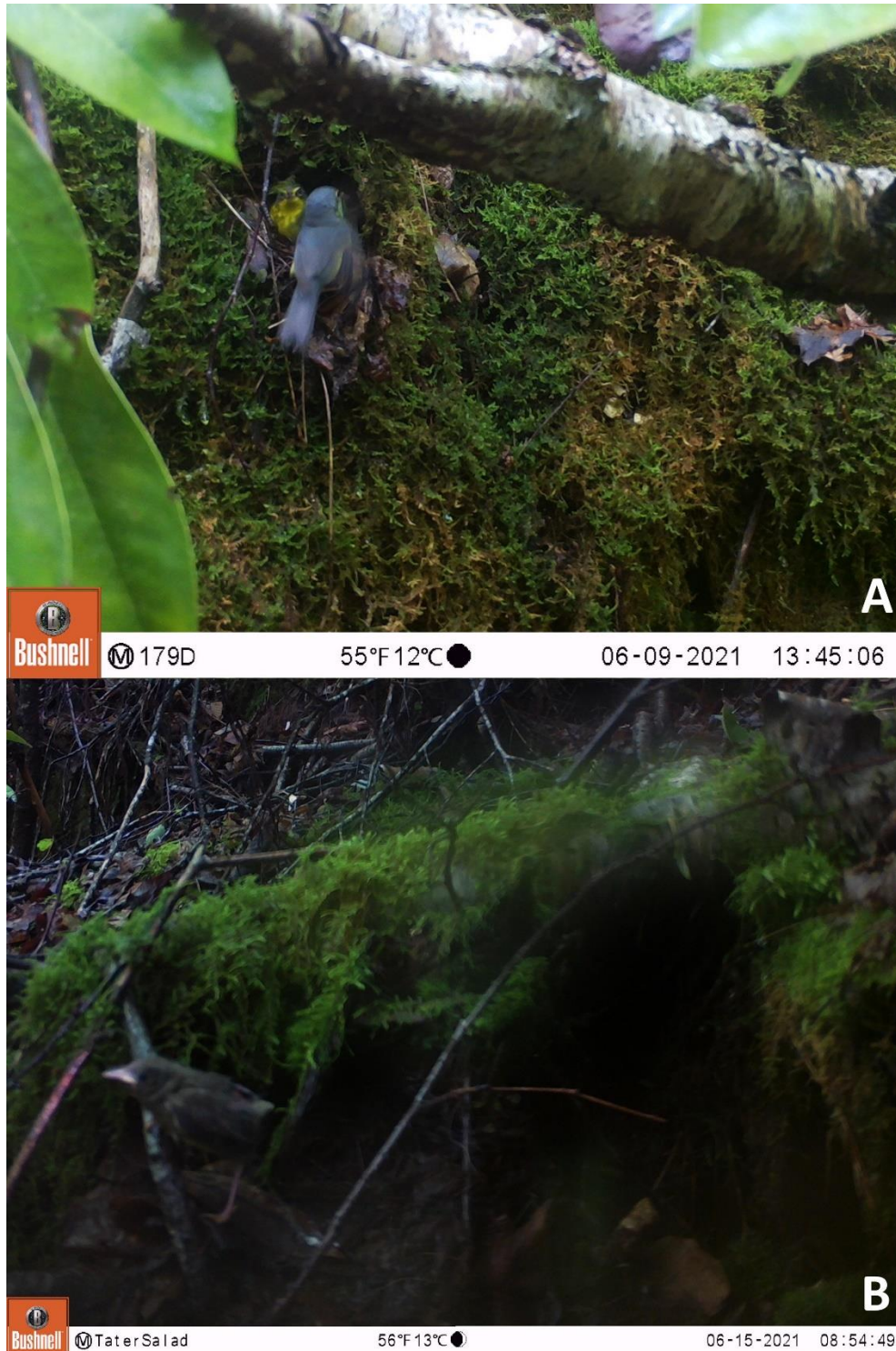


**Figure 1.5** Low elevation site boundary of Red Run in the Monongahela National Forest, WV, USA in 2021 exemplifying (A) search grid points spaced 150 m apart within site boundary, (B) 50 m grid cells for testing if random walk coordinates were inside or outside the site boundary, (C) 3 m Digital Elevation Model overlay of site, and (D) Topographic Position Index overlay generated with a moving window radius of 25 cells or ~75 m.

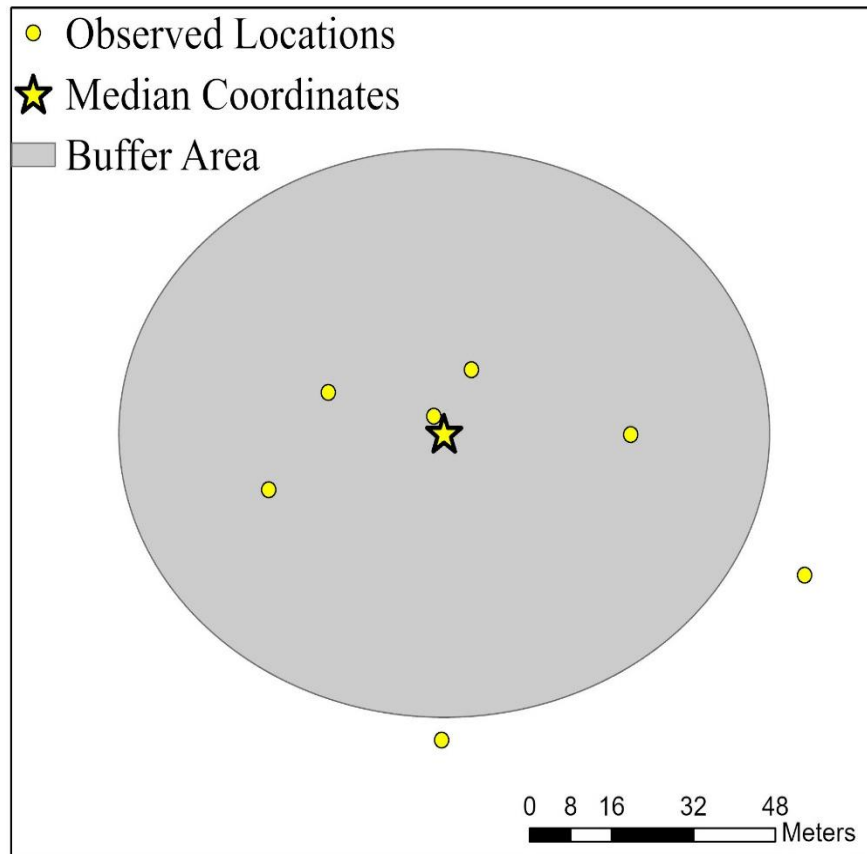


**Figure 1.6** Bushnell Trophy Cam HD mounted on branch implanted into soil set < 1 m from Canada Warbler (*Cardellina canadensis*) nest (circled) at high-elevation site Glade in the Monongahela National Forest, WV, USA in 2021. Cameras recorded 3 pictures each time the motion sensor was triggered (Figure 1.6).

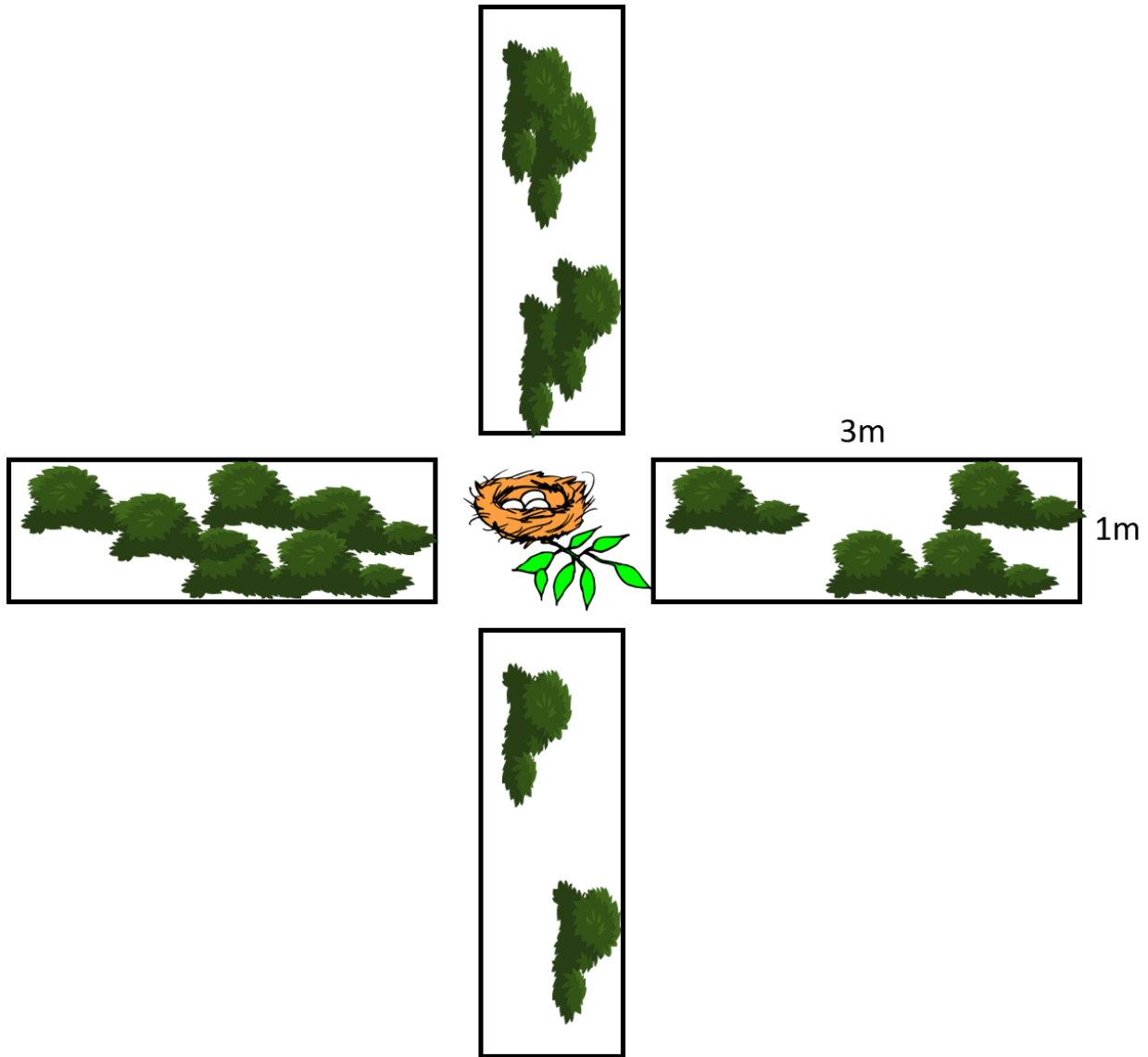




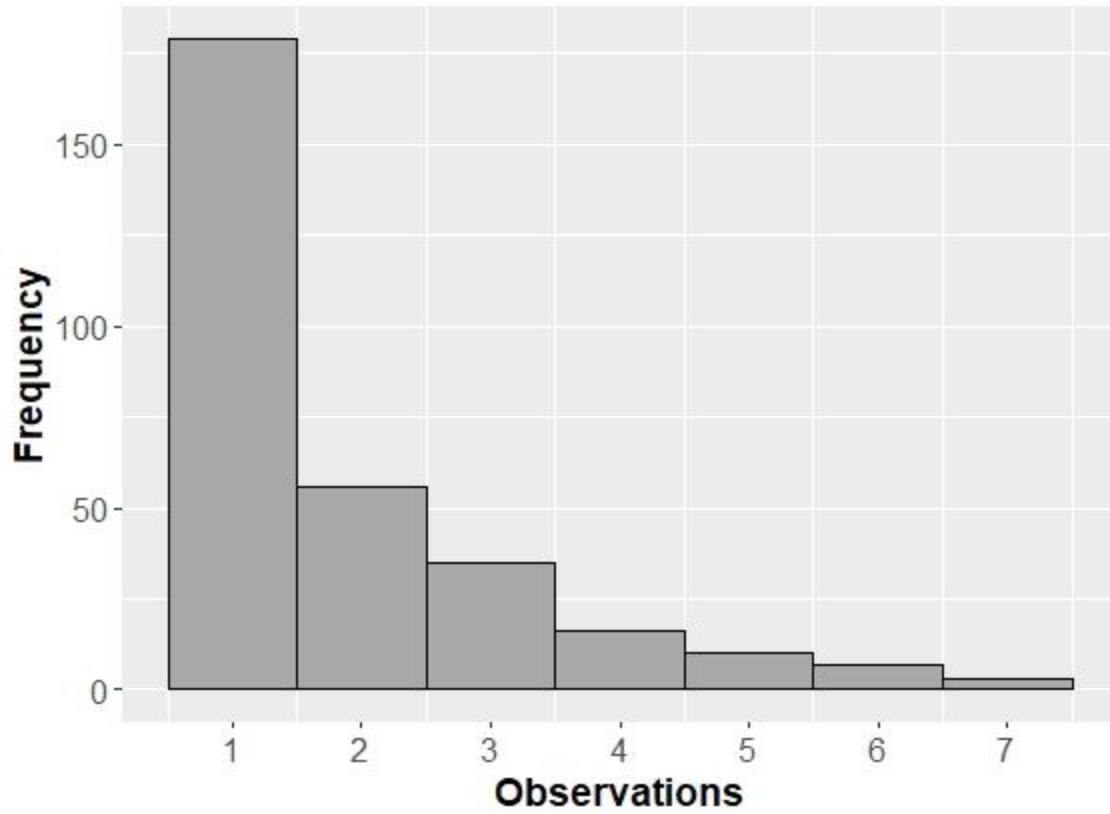
**Figure 1.7** Two different Canada Warbler (*Cardellina canadensis*) nests at low elevation site Red Run in the Monongahela National Forest, WV, USA, in June 2021. Photos of (A) both parents at the nest and (B) fledgling departing the nest captured by Bushnell Trophy Cam HD triggered by infrared motion sensor.



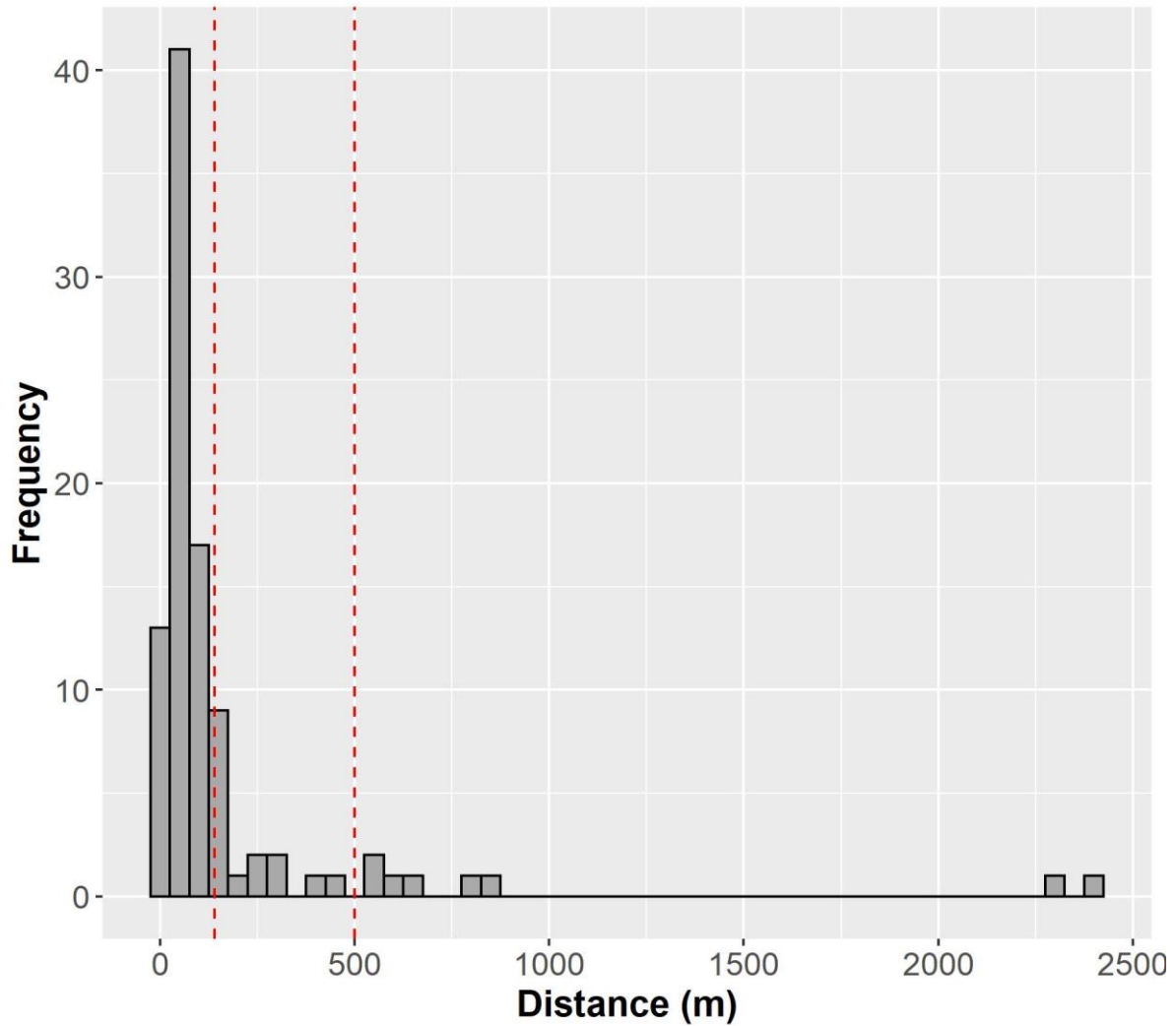
**Figure 1.8** Distribution of coordinates from 2020 observations of one adult male Canada Warbler (*Cardellina canadensis*; Band ID 2870-67124) in the Monongahela National Forest, WV, USA. All observation locations are marked with yellow circles, median location represented with the yellow star, and 50 m circular buffer to summarize environmental variables in grey.



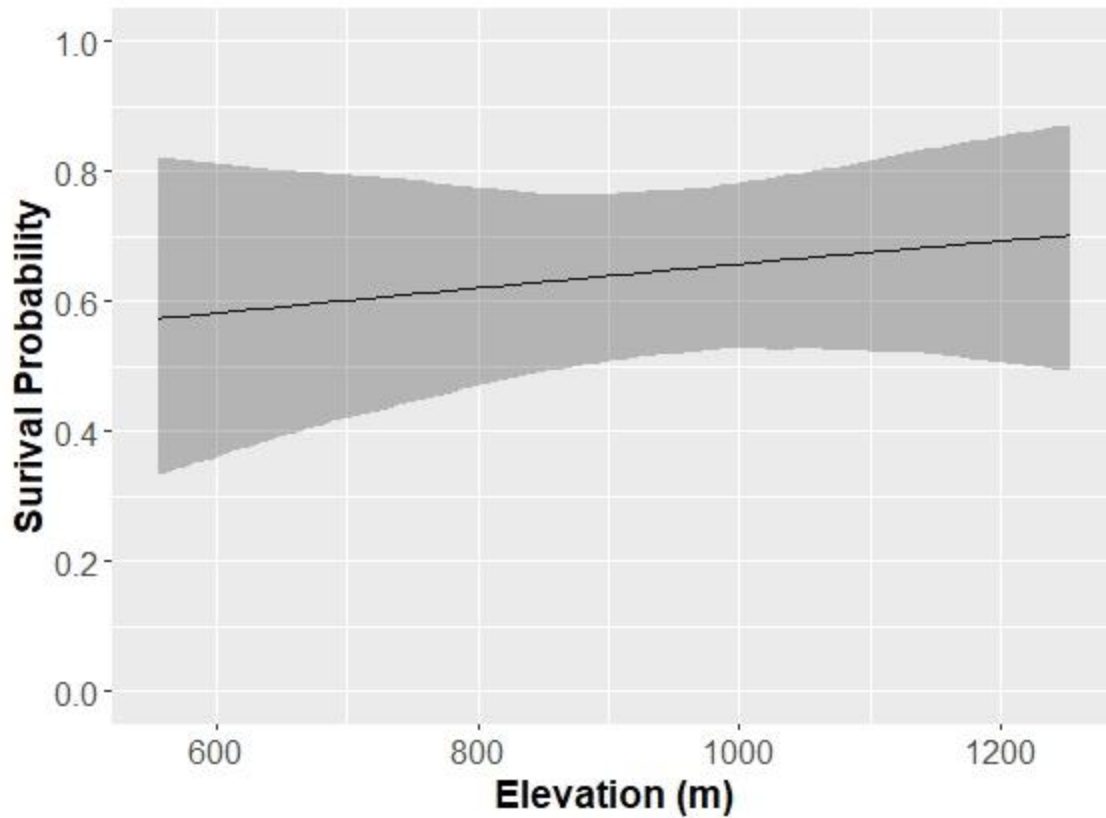
**Figure 1.9** Schematic of 1m x 3 m belt transects (Goodnow and Reitsma 2011) used to calculate rhododendron (*Rhododendron maximum*) and other shrub cover around Canada Warbler (*Cardellina canadensis*) nests in the Monongahela National Forest, WV, USA. Percent coverage within each belt was visually estimated and then averaged for the nest to generate a single value each for both rhododendron and other shrub cover.



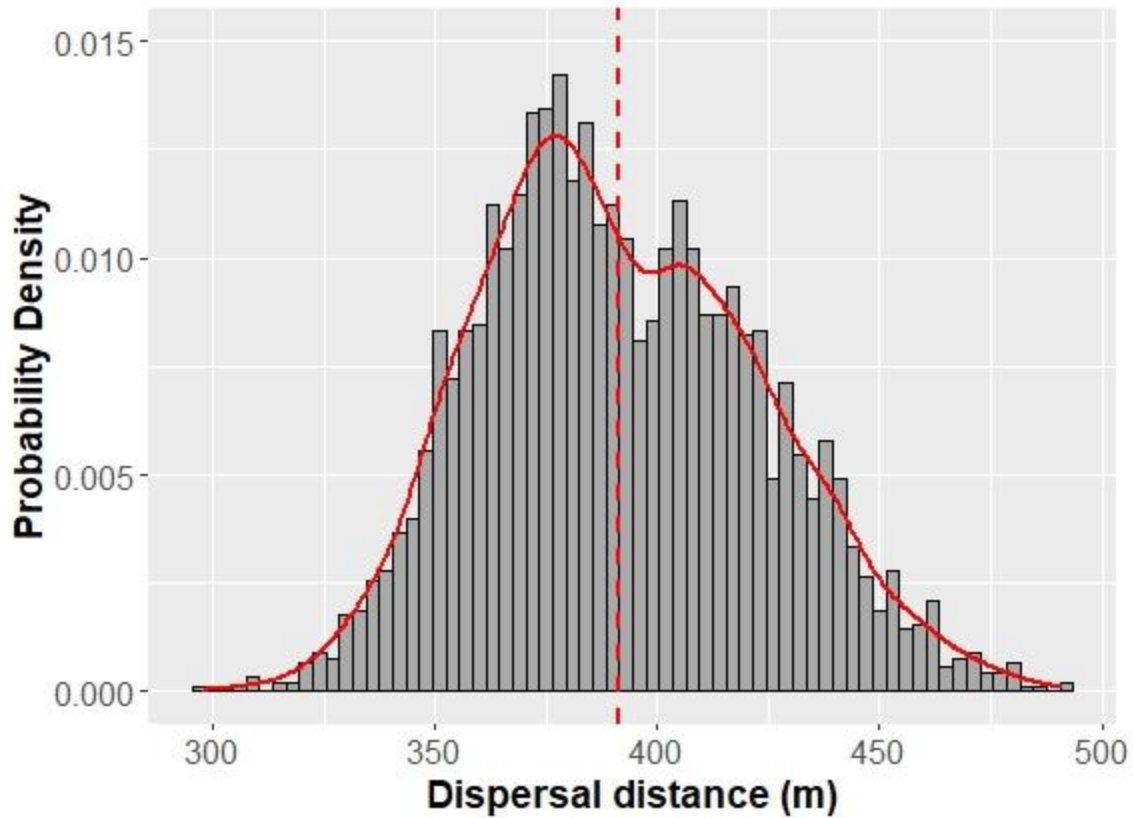
**Figure 1.10** Distribution of annual number of observations of marked Canada Warblers (*Cardellina canadensis*) throughout the full three years of the mark-resight study in the Monongahela National Forest, WV, USA. Most birds were only recorded once within a given year.



**Figure 1.11** Observed interannual dispersal distances by all Canada Warblers (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA detected in at least two different years of the mark-resight study. Dashed red lines mark 80% of movements were < 140 m, and 8.4% were > 500 m.



**Figure 1.12** Expected annual survival probability of male Canada Warblers (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA, with 95% credible intervals in the grey ribbon, resulting from the spatial Cormack-Jolly-Seber model which incorporated a linear effect of elevation on survival.



**Figure 1.13** Posterior distribution of expected interannual dispersal distance by male Canada Warblers (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA, generated by the random walk submodel of the spatially explicit survival model. The dashed red line marks the mean expected interannual dispersal distance of 391 m.



**Figure 1.14** Images of Canada Warbler (*Cardellina canadensis*) nest predation events in the Monongahela National Forest, WV, USA by: (A) Broad-winged Hawk (*Buteo platypterus*) at a nest in site Dogway and a squirrel (*Sciurus sp.*) at a nest in site Glade. Nests are just out of frame due to the camera shifting, and the actual image date of B is 06-14-2021.



**Table 1.1** Summary of six study sites with boundaries defined by 210 m buffer around all bird locations in 2020 within the Monongahela National Forest, WV, USA, in order of mean elevation of all DEM grid cells within site boundaries (standard deviation in parentheses). Grid points spaced 150 m apart within study site boundaries were visited at least once each year; the number of grid points per site in the 2021 field season is shown in the table since the sites incorporated locations from both 2019 and 2020. Marked birds is the total number of males color-banded in 2019 and 2020.

<b>Site Name</b>	<b>Mean elevation (m)</b>	<b>Elevation range (m)</b>	<b>Site area (ha)</b>	<b>Grid points</b>	<b>Marked birds</b>
Losh	629 (38)	527-724	71.8	53	13
Red Run	729 (68)	546-870	160.8	71	48
Kennison	971 (53)	905-1143	174.6	77	28
Falls	1087 (61)	1006-1235	180.3	76	49
Dogway	1132 (56)	1027-1293	208.9	92	38
Glade	1153 (28)	1100-1247	177.1	76	35

**Table 1.2** Published mean size of territory core area defended by male Canada Warblers (*Cardellina canadensis*) based on 50% kernel density estimate where *n* is the sample size of birds mapped and included in analysis.

<b>Core area (ha)</b>	<b><i>n</i></b>	<b>Study Area</b>	<b>Source</b>
0.468 ± 0.251	30	Alberta, Canada 2012-2013	(Flockhart et al. 2016)
0.15 ± 0.02*	32	Canaan, NH 2005-2006	(Hallworth et al. 2008a)
0.29 ± 0.03**	37		
0.169 ± 0.021	92	Canaan, NH 2003-2006	(Hallworth et al. 2008b)

\*In red maple swamp habitat \*\*in second growth forest habitat

**Table 1.3** Summary statistics of environmental covariates within known Canada Warbler (*Cardellina canadensis*) location buffer areas incorporated as predictors of survival across all study sites. Elevation and Topographic Position Index (TPI – unitless) are the mean values calculated within 50-m buffer used to summarize environmental variables for each bird. Aspect is calculated as the mean of the cosine of the aspect value within the buffer. Rhododendron is the area of mapped polygons within the buffer. Streams is the total length of streams within the buffer.

<b>Variable</b>	<b>Mean</b>	<b>Median</b>	<b>Min</b>	<b>Max</b>
Elevation (m)	957	1037	555	1255
Streams (m)	56	61	0	233
Rhododendron (m <sup>2</sup> )	3049	2999	0	7854
TPI	-2.24	-2.00	-10.66	4.38
Aspect	-0.53	-0.73	-1.00	0.88

**Table 1.4** Spatial Cormack-Jolly-Seber model selection DIC values for each of nine combinations of environmental predictors of Canada Warbler (*Cardellina canadensis*) annual survival in the Monongahela National Forest, WV, USA indicate elevation as a linear predictor was the most explanatory variable. The parameters for detection probability  $p$ , and  $X$ - and  $Y$ -variance of dispersal kernel ( $\sigma^2$ ) were held constant.

<b>Model</b>	<b>K</b>	<b>DIC</b>	<b><math>\Delta</math> DIC</b>
Elevation	5	2966.300	0.000
Elevation + Elevation <sup>2</sup>	6	3065.117	98.817
Intercept-only	4	3093.897	127.597
Rhododendron	5	3484.409	518.109
Elevation + Aspect	3	3566.419	600.119
TPI	5	3635.252	668.952
Aspect	5	3663.747	697.447
Stream	5	3734.297	767.997
Elevation + TPI + Aspect	7	4120.254	1153.954

**Table 1.5** Model selection DIC values for each of six environmental predictors of daily nest survival by Canada Warbler (*Cardellina canadensis*) nests observed in the Monongahela National Forest, WV, USA, indicated no measured variables were a strong predictor of nest survival.

<b>Model</b>	<b>K</b>	<b>DIC</b>	<b><math>\Delta</math> DIC</b>
Intercept-only	1	25.64974	0.000
TPI	2	26.91873	1.268985
Elevation	2	27.23961	1.589867
Shrub	2	27.27751	1.627764
Rhododendron	2	27.32291	1.673163
Aspect	2	27.35488	1.705138

**Table 1.6** Encounter history summary of adult (AHY) male Canada Warbler (*Cardellina canadensis*) over three years of mark-resight study conducted in the Monongahela National Forest, WV, USA. Encounters with three digits were first marked in 2019, and those with a dash preceding two digits were first marked in 2020. A 1 denotes that the bird was seen in that year, whereas a 0 denotes the bird was not observed. Of 101 birds captured in the first year, 14% were seen in all three years. All histories begin with 1 to mark their first encounter, when they were captured and marked.

Encounters	# Birds
111	14
110	19
101	0
100	68
-11	48
-10	54

## ***Chapter 2: Potential population connectivity and loop migration by Canada Warblers (*Cardellina canadensis*) revealed by light-level geolocators***

### **INTRODUCTION**

Populations are influenced by events occurring throughout the annual cycle of a species, and conclusions drawn from only one period may be confounded by carryover effects from previous periods (Sherry and Holmes 1996, Sillett and Holmes 2002, Norris et al. 2006, Faaborg et al. 2010, Marra et al. 2015a). The annual cycle of a migratory bird consists of a breeding season, nonbreeding season, and two migration periods; events in one stage of the cycle may impact the population in subsequent stages (Faaborg et al. 2010, Rushing et al. 2017, Schuster et al. 2019). For example, changes in parameters measured in breeding populations such as abundance, density, and individual fitness may be caused by environmental conditions experienced during the nonbreeding season rather than on the breeding grounds (Wilson et al. 2011, Marra et al. 2015b, Briedis and Bauer 2018). Determining population-specific migratory routes and nonbreeding season distribution is crucial to comprehensively model factors that may limit population growth occurring across the full annual cycle.

Although the temporal duration of transit between breeding and nonbreeding habitat is typically shorter than the residency period in either locale for neotropical migrant passerines, migration is a high-risk event that subjects individuals to multiple stressors (Sillett and Holmes 2002, Newton 2006, Klaassen et al. 2014, Rushing et al. 2017). Crossing large bodies of water, resource competition in stopover habitat, predation risk in novel surroundings, and anthropogenic influences such as light pollution, building collisions, and stopover habitat loss are just a few of the hazards a migratory songbird must survive (Sillett and Holmes 2002, Newton 2006, Horton et al. 2019). Mortality rates have been estimated in some species to be 6 – 15 times higher during migration than during stationary periods and may account for more than half of

annual mortality (Sillett and Holmes 2002, Klaassen et al. 2014). Nonfatal consequences of migration stressors such as reduced body condition upon arrival to breeding territories may also impact demographic rates (Newton 2006). Post-breeding and pre-breeding migration routes are not always identical, which may be driven by underlying weather patterns, seasonal differences in resources, or other factors which subsequently influence birds on their breeding or nonbreeding grounds (McKinnon et al. 2013). Avian migration is challenging to study but can elucidate the carryover effects from exposure to stressors encountered en route through a key portion of the full annual cycle.

Migratory connectivity describes the extent of cohesion between groups of individuals throughout the full annual cycle (Webster et al. 2002, Marra et al. 2011, McKinnon et al. 2015, Kramer et al. 2017, Cohen et al. 2019). Strong population connectivity between the breeding and nonbreeding season causes the individuals of a population to be exposed to similar environmental conditions year-round (Webster et al. 2002, Norris et al. 2006, Marra et al. 2011, McKinnon et al. 2013). Connectivity strength influences the degree in which seasonal carryover effects are evident between breeding and nonbreeding populations and may exacerbate or mediate the effect of stochastic events. For instance, if a hurricane destroys a portion of nonbreeding season habitat in a population with strong connectivity, the demographic rates of the linked breeding population may be severely adversely affected. In the case of weak connectivity, the carryover effects are diffused across some individuals of multiple breeding populations (Webster et al. 2002, Briedis and Bauer 2018). In the long-term, species with weaker population connectivity would also have higher genetic variation to evolve beneficial traits that respond to changing selective pressures, such as climate change or anthropogenic impacts (Webster et al. 2002). Conservation action for declining species can be informed by assessment of population



connectivity. In Golden-winged Warblers, identifying strongly linked breeding and nonbreeding populations improved the allocation of conservation funding to sites of greatest need, prioritizing protection of wintering habitat used by the most steeply declining breeding populations (Kramer et al. 2017, Larkin et al. 2017).

Determining migration routes and population connectivity of small (< 20 g) songbirds has become possible over the past decade with the miniaturization of light-level geolocator tags (McKinnon et al. 2013, McKinnon and Love 2018). Tracking individual birds with geolocators has offered unprecedented insight into the migratory ecology of many passerine species (e.g., Heckscher et al. 2011, Ryder et al. 2011, Beason et al. 2012, Cormier et al. 2013, McKinnon et al. 2013, Hallworth et al. 2015, Wolfe and Johnson 2015, Cooper et al. 2017, Kramer et al. 2017, Larkin et al. 2017). While the accuracy and precision of location estimates from light-level geolocation are affected by the time of year, bird behavior, and environmental factors (Lisovski et al. 2012), these data are more robust than previously used alternatives such as band recovery or stable isotope analysis and enable inference at the scale of populations rather than vast regions (Norris et al. 2006, McKinnon et al. 2013, Kramer et al. 2017). The capability of tracking individual birds across seasons is a fundamental step toward incorporating full annual cycle effects into demographic research (Hostetler et al. 2015, Marra et al. 2015a). As numerous neotropical migrant species decline (Rosenberg et al. 2019), there is an urgent need to understand all factors that ultimately influence population dynamics.

The Canada Warbler (*Cardellina canadensis*) is a neotropical migrant songbird exhibiting substantial population declines in recent decades (Sauer et al. 2020). Breeding populations are distributed across Canada and through the northeast US, with a trailing edge south through the Appalachian corridor to northern Georgia. The nonbreeding season distribution

includes Panama through northern South America and central Peru. While distributions are known, the population-specific migratory ecology of this species is not well understood (Reitsma et al. 2009). Within the breeding range, West Virginia, USA, is one of few regions with a trend of increased abundance at 2.4% (95% confidence interval: -0.4% – 5.9%) annually (Sauer et al. 2020), but the southern populations of the Canada Warbler breeding distribution are largely unstudied (but see Weakland et al. 2002, Becker et al. 2012, Dimmig et al. 2022). Modeling population dynamics through the full annual cycle necessitates filling the knowledge gap of this southern population's migratory routes, nonbreeding season distribution, and connectivity strength.

The migratory ecology of Canada Warblers has predominately been described at a broad regional scale, with limited population-level assessment. During the post-breeding migration route in autumn, birds appear to travel west from the Appalachian corridor and continue overland through Central America, with a few records in Florida and the Yucatán Peninsula that may be vagrants or trans-Caribbean movements (Reitsma et al. 2009, Cárdenas-Ortiz et al. 2017). The only other published study, to my knowledge, to use geolocators, reported that the post-breeding routes of multiple populations breeding throughout Canada crossed part of the western Gulf of Mexico and continued overland through Central America. During the nonbreeding season, all birds wintered in Colombia or western Venezuela and appeared to exhibit crosswise connectivity (birds from the west wintered in the east and vice versa) but limited samples from each of the widely distributed breeding populations precluded conclusive evidence of migratory connectivity strength or pattern (Roberto-Charron et al. 2020). Pre-breeding migration in the spring was only described by one functional geocator but followed a similar route to the post-breeding migration (Roberto-Charron et al. 2020). Previously, stable isotope analyses suggested the

presence of regional parallel connectivity, with eastern and western breeding populations segregated across the Colombian Andes (González-Prieto et al. 2017). Connectivity assessment may also be hampered by the comparatively smaller nonbreeding distribution relative to the breeding range; it is estimated that > 50% of the nonbreeding distribution is within the Colombian Andes, where Canada Warblers occupy a narrow elevation band (Céspedes and Bayly 2019). With such limited and sometimes conflicting data, further efforts to understand Canada Warbler migratory ecology will be critical to inform full annual cycle models and determine the sensitivity of populations to environmental changes and management efforts (Hallworth et al. 2015, Larkin et al. 2017, Briedis and Bauer 2018).

In this project, I used light-level geolocators to track adult male Canada Warblers breeding in the Monongahela National Forest, West Virginia, USA, through their annual cycle. The study objectives were: (1) estimate the post-breeding and pre-breeding migratory routes, (2) determine the nonbreeding season sites of the population of Canada Warblers breeding in central Appalachia and (3) assess the potential for migratory connectivity by quantifying the probability of nonrandom geographic clustering. My novel assessment of the migration ecology of this largely unstudied population elucidates the post-breeding and pre-breeding migratory routes, nonbreeding season distribution, and describes the potential for population connectivity.

### *Hypotheses and Predictions*

1. If Canada Warblers that breed in the central Appalachian Mountains of West Virginia use similar migratory routes as birds that breed in Canada, then I predict migratory routes will proceed south through Central America, with the possibility of trans-Gulf of Mexico movements.

2. If Canada Warblers that breed in the central Appalachian Mountains of West Virginia spend the nonbreeding season where highest abundances have been documented, I predict this population will winter in the eastern Colombian Andes.
3. If Canada Warblers that breed in the central Appalachian Mountains of West Virginia exhibit population migratory connectivity, then I predict the geolocator-tagged birds will winter in a distinct geographic cluster relative to potential nonbreeding sites.

## **METHODS**

### *Study Area*

I conducted fieldwork on public lands in the Monongahela National Forest (MNF), West Virginia, USA. The MNF was established in 1920 and encompasses almost 371,000 hectares of federally protected land across the central Appalachian Mountains, with elevations ranging 300 – 1500m (USDA 2011). My study sites are distributed across the Allegheny Highlands Section of the Appalachian Plateau Physiographic Province in the west of the MNF. The region is characterized by the complex topography resulting from mixed flats, folds, and faults (WV Geological & Economic Survey 2020). More than 70 tree species comprise the diverse forest types that vary across the elevation gradient of the MNF (USDA 2011). Below 900 m, mixed oak and mixed mesophytic forest types are dominant, transitioning to northern hardwood between 900 m and 1,150 m, with remnant boreal red spruce forests predominant above 1,150 m (USDA 2011, Dimmig et al. 2022).

### *Site Selection*

I studied the migratory ecology of a population of Canada Warblers within the MNF, West Virginia, USA. I established six study sites throughout the MNF as part of my concurrent demography research on the same population. Sites were selected from data collected previously

that indicated locations of high relative occurrences of Canada Warblers across a range of elevations (Dimmig et al. 2022). The six sites spanned an approximately 130 km north-south geographic range (Figure 1.1), had areas of 72 – 209 ha, and encompassed elevations of 527 – 1293 m (Table 1.1). Dimmig et al. (2022) rarely detected Canada Warblers above 1,158 m, the lower cutoff of the highest elevation stratum. As such, mean elevations of each total high-elevation site search area were all < 1,158 m, with portions of the sites above the cutoff. Sites were generally characterized by lack of recent timber harvest (Dimmig et al. 2022), high density of rhododendron, and were typically bisected by non-ephemeral streams (Figure 1.2). Higher latitude and lower elevation sites consisted chiefly of mixed mesophytic forest transitioning to dry oak and oak-pine mesic forest upslope; southern sites contained predominantly northern hardwood and red spruce forests, with mixed mesophytic patches. Four of the sites were bordered or bisected by gravel roads only accessible with a US Forest Service key and thus subject to minimal vehicular travel, and two were accessed with marked hiking trails.

#### *Study Design: Geolocators*

To investigate the migratory patterns of Canada Warblers, I deployed archival light-level geolocator dataloggers (hereafter geolocators) on birds across the six study sites. Geolocators record light intensity at predetermined intervals and must be retrieved from the bird to access the data. Transitions between light and dark periods mark sunrise and sunset, used to calculate day length and the timing of solar noon, which subsequently allow estimation of longitude and latitude (Sumner et al. 2009, Lisovski et al. 2012). Shading of the light sensor as a result of weather, vegetation, topography or other factors can reduce the precision of the estimate, potentially leading to imprecise or erroneous location estimates. Latitudinal estimates are prone to increased error around the spring and fall equinox, due to the global similarity of day length

(Lisovski et al. 2012). Despite these limitations, light-level geolocation offers the most robust global positional data to date for small songbirds due to their compact size and light weight.

I deployed FL6057 fLight Lotek Wireless geolocators on adult (after-hatch-year) male Canada Warblers. The geolocators recorded light intensity at four-minute intervals, with an expected battery life of 12 months. This model was stemless to minimize size and mass (17 x 6.3 x 3 mm; 0.30 g), but contour feathers may have shaded the light sensor. Geolocators were mounted with superglue onto figure-eight leg loop harnesses made from 0.5 mm Stretch Magic elastic cord (Figure 2.1) (Rappole and Tipton 1991, Streby et al. 2015). Guidelines indicate that attachments to banded birds must be  $\leq 3\%$  of the individual's total body mass (Patuxent Wildlife Research Center 2020), thus the bird had to weigh at least 10.7 g at the time of capture to carry a geocator, harness, and bands.

### *Capture Protocol*

I attached geolocators to 32 Canada Warblers between May and July of 2020. To locate male birds to capture, I first surveyed each study site by listening for territorial songs. When I located a bird, I attempted capture using an audio lure of a speaker broadcasting Canada Warbler song placed near two mist nets (6m x 2.6 m; 30 mm mesh) deployed in an "L" formation parallel and perpendicular to understory growth as structure permitted. Once captured, I first weighed the bird to ensure it met the minimum threshold to carry the geocator. I then attached the tag using a figure-eight harness following Rappole and Tipton (1991) and Streby et al. (2015) and released the bird with a USGS-issued aluminum band and a unique combination of plastic color bands. Eight birds were second-year (SY), 21 were after-second-year (ASY) and three were undetermined and aged as after-hatch-year (AHY).

In 2021, I systematically searched each study site for marked birds. At each site, I created a 210 m buffer around all locations of marked birds recorded in the previous years (see Chapter 1 for details of mark-resight study) to form a search area boundary, and overlaid grid points spaced 150 m apart within the search area boundary to guide search effort (53 – 92 per site) (Figure 1.4A). I selected the 210 m buffer to define the search area boundary by approximating the radius of three home ranges, based on literature reporting the largest defended area by a singing male as 1.5 h which corresponds to a circle with a radius of ~70 m (Hallworth et al. 2008a, Reitsma et al. 2009). This set reasonable borders for re-sighting individuals and enabled me to search the entire site while allowing for territory shifts to occur between years. The 150 m grid point spacing allowed me to account for aural detection limits of Canada Warblers which are estimated to range 60-200m (Matsuoka et al. 2012, Hunt et al. 2017). Furthermore, visiting each grid point at least once ensured search coverage even in challenging terrain. Field personnel walked slowly between grid points listening for singing males, and broadcasting Canada Warbler song at each grid point for up to three minutes to elicit a response if no birds were otherwise detected. If a marked bird was located that had been deployed with a geolocator, I recaptured the bird using the previously described capture protocols and retrieved the geolocator tag.

### *Data Analysis*

I estimated geographic coordinates using guidelines published by Lisovski et al. (2020) and I draw heavily from their methodology in the description below. Analysis consisted of four fundamental steps: (1) determining the threshold value which identified twilight events based on light transitional periods; (2) editing or excluding outlying and likely erroneous twilight events following replicable criteria; (3) generating initial estimates of longitude and latitude from day length and timing of solar noon indicated by the twilight threshold timing; and (4) refining the

estimates through a Bayesian statistical model with semi-informative priors. I performed all analyses in R 4.1.2 (R Core Team 2021) using packages *TwGeos*, *Geolight* and *SGAT* (Sumner et al. 2009, Lisovski and Hahn 2012, Lisovski et al. 2016).

#### ANNOTATING TWILIGHTS

The timing of sunrise and sunset is integral to estimating coordinates from the recordings of light intensity, or light level. To estimate twilight transition times, I defined a light-level threshold; I assumed values below the threshold constituted night readings, and values above constituted daytime readings. I determined the threshold for each tag by first summarizing which low light levels were most frequently repeated sequentially as would be expected in consistent overnight darkness. I then used the most frequently repeated low light value to identify twilights using the *preprocessLight* function in package *TwGeos* (Lisovski et al. 2016). The function determines the timing of twilight by identifying pairs of times surrounding a period when light-levels are consistently below the threshold, which is assumed to be night. In some cases, the initially selected threshold value could not define twilights, potentially due to overnight noise from moonlight or anthropogenic light sources creating  $> 2$  twilight events within a 24hr period. When this occurred, I increased the threshold incrementally by 0.5 lux (metric of light intensity) until twilights were identified throughout the entire year (Figure 2.2). The twilight output was a sequence of dates and times, two readings per date, and whether the time was a sunrise (dark to light) or sunset (light to dark) transition.

The resulting twilights were then filtered to edit and exclude erroneous values following a replicable set of rules. Each focal twilight was contextualized by the surrounding four twilights, two before and two after, in a moving window. If the focal twilight was 45 min earlier or later than the surrounding twilights, and the four surrounding twilights were within 25 min of each



other (which is defined as likely stationary behavior), then the focal twilight time was adjusted to the median of the four surrounding twilight times. If the focal twilight was 45 min different from the surrounding twilights but the surrounding twilights were more variable than within 25 min of each other, the focal twilight was deleted (Lisovski et al. 2020).

#### TWILIGHT CALIBRATION

I used the stationary period on the breeding grounds between geolocator deployment and onset of migration as the calibration period to account for two error sources: individual device accuracy and shading effects while the bird is in its normal habitat. Canada Warblers are documented departing the breeding grounds in mid- to late August (Reitsma et al. 2009) so I conservatively estimated the calibration period to include capture dates through 1 August 2020 (Figure 2.2).

The time of twilight events during the calibration period allow calculation of the zenith angle at apparent twilight because the bird's location is known. The zenith is the point directly above the observer at any point on the planet and thus the zenith angle is the angular distance from that central point. Sunrise and sunset occur when the zenith angle is approximately  $90^\circ$ , or parallel with the horizon. Twilight, the first or last detection of light, occurs when the zenith angle is  $> 90^\circ$  because of the refraction of light through the atmosphere. Comparing the estimated time of twilight with known time of twilight for the calibration site, I generated two zenith angles: the zero angle is the lowest zenith angle at which twilight could be detected at the calibration site; and the median angle is the zenith angle at the median of the error distribution between estimated and actual twilight. The errors are fit to a gamma distribution, of which the shape and scale inform the Bayesian model (Figure 2.3).

#### INITIAL GEOGRAPHIC COORDINATES

After calibration, I generated two initial location estimates per day (sunrise and sunset) as initial values for the Bayesian model. I used the National Oceanic and Atmospheric Administration (NOAA) Solar Position Calculators (National Oceanic & Atmospheric Administration [NOAA] 2022) implemented through the *thresholdPath* function in *SGAT* (Sumner et al. 2009, Lisovski and Hahn 2012) to convert twilight times into initial location estimates for each twilight event (Figure 2.4). Given two sequential twilight times, a sunrise and sunset, the function computes the apparent time of solar noon (halfway between the twilights). The time of solar noon determines the longitude. The length of the day, or the amount of time between the sunrise and sunset twilights, determines the latitude.

Longitude is reliably estimated throughout the year, but latitude is prone to increased error under certain conditions, when solar declination approaches 0. The solar declination is the angle between the sun and the plane of the equator, and equals 0 at the autumn and spring equinox, where the length of day and night are similar across the planet. Because latitude is determined from day length, latitudinal estimates are unreliable with increased error around the equinox. The *thresholdPath* function allows a user-defined tolerance on the solar declination, where it will replace latitude values estimated when the sine of the solar declination was  $\leq$  the specified tolerance with the previous acceptable latitude value (when the sine of the solar declination was  $>$  the specified tolerance). Too low of a tolerance value results in numerous large latitudinal shifts due to equinox error as solar declination approaches 0; too high, and the location estimates around the equinox are constrained to longitudinal movements only, resulting in unrealistic horizontal paths. I specified the tolerance as 0.075 based on trial runs.

## MODELING LOCATIONS

I estimated geographic locations with the Estelle model in package *SGAT* (Sumner et al. 2009, Lisovski and Hahn 2012) using Bayesian methods, implemented in R 4.1.2 (R Core Team 2021). The model proposes a location estimate  $x_i$  and calculates the error between the actual twilight at that location and the twilight time the geolocator light levels estimate. I denote  $t_i$  as the difference between twilight at proposed location  $x_i$  and geolocator-observed twilight. I assume  $t_i$ , conditional on location  $x_i$ , is a gamma random variable:

$$t_i|x_i \sim \text{Gamma}(\alpha, \beta)$$

with parameters shape  $\alpha$  and scale  $\beta$  as determined during the twilight calibration step.

I assumed  $x_i$  was uniformly distributed over geographic space with the following prior constraints to incorporate known spatial information. Because Canada Warblers are largely known to be overland migrants, and their nonbreeding season grounds are in northern South America (González-Prieto et al. 2017, Céspedes and Bayly 2019, Roberto-Charron et al. 2020), I expected no location estimates would be within the Pacific Ocean. Therefore, I set the prior probability of a point occurring within the Pacific Ocean to 0. Canada Warblers breed throughout Canada, with occurrences up to the Northwest Territories, below 60 degrees latitude. Nonbreeding distribution extends through southern Peru, to north of -19 degrees latitude. I set the prior probability of a point occurring outside of these latitudinal constraints to 0. To limit points occurring over the Gulf of Mexico and the Atlantic Ocean, points in these bodies of water were assigned a prior weight of  $\log(0.05)$ . To constrain points to within the documented geographical distribution of the species (Figure 2.5), points on land that were within the Canada Warbler range were assigned a prior weight of  $\log(5)$ . The weights were selected based on preliminary trials to ensure the prior did not wholly drive the final modeled location estimates. Locations within the known range had the highest prior weight, followed by terrestrial locations

outside the known range, with the lowest prior weight over the Gulf of Mexico or Atlantic Ocean.

To incorporate biologically reasonable distances between successive locations, I defined a prior for flight speed. Canada Warblers spend most of the breeding and nonbreeding season stationary, excepting migration periods, so most expected movements should be extremely small. I assumed the orthodromic distances between location estimates  $x_i$  and  $x_{i+1}$  was a gamma random variable with a shape parameter of 0.7 and a scale parameter of 0.08. This set a maximum speed of ~50 km/hr with the most common speed <1km/hr, following parameters used for Kirtland's Warblers (Cooper et al. 2017).

I sampled from posterior distributions of location estimates  $x_i$  using three independent chains. The Bayesian models were fit using Metropolis-Hastings Markov Chain Monte Carlo, which required tuning before the final posterior draw. Initially, I drew 1000 samples for each of three tuning runs. After tuning was complete, I continued to draw samples, keeping every 20<sup>th</sup> sample, until the Brooks-Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998) indicated all chains converged (i.e.,  $R_{hat} < 1.1$ ).

#### DETERMINING MIGRATORY ROUTES

I estimated the post-breeding (fall) migratory routes for each tag using the posterior median of each location and linking successive points. Latitude estimates around the autumn equinox, which I defined as the period  $\pm 20$  days from 22 September 2020 (2 September 2020 – 12 October 2020) (Wolfe and Johnson 2015), were unreliable and often exhibited erratic successive long distance north-south movements. In this case, I manually adjusted the latitude of a point by visually estimating between the preceding and following locations, keeping the model posterior longitude unchanged because it is unaffected by the equinox, and ensuring the new

latitude value fell within the 95% credible intervals. For example, in several birds, sequential points would alternate between the Gulf Coast of the US and the Yucatán Peninsula of southern Mexico, as if the bird had completed multiple trans-Gulf flights. To infer a more reasonable route estimate, I linked the locations before and after the erratic jumps. Pre-breeding (spring) migration consisted of fewer location estimates, and large latitudinal shifts were not clearly preceded and followed by points demarcating the migration route. Therefore, I could not plot the pre-breeding route without introducing considerable subjectivity into what constituted a reliable location estimate. So, to determine if post-breeding and pre-breeding migration routes differed, I compared the minimum (most negative, or westernmost) longitude reached during post-breeding and pre-breeding migration for each bird with a paired t-test.

#### ASSESSING POPULATION CONNECTIVITY

I defined the nonbreeding season location for each bird as the median coordinates of all points between 16 November 2020 – 28 Feb 2021. This date range was defined based on the eBird definition of the nonbreeding season (Fink et al. 2021) with dates within the spring equinox period,  $\pm 20$  days from 20 March 2021 (Wolfe and Johnson 2015), subtracted. To determine the probability that nonbreeding season locations were randomly distributed within the nonbreeding season range of Canada Warblers, I first used kernel density estimation, implemented in R package *ks* (Tarn Duong 2021), to define the boundaries of the winter distribution of the tagged birds using the 99% contour. Next, I drew ten random points (equal to the number of tagged birds), assuming a uniform distribution within the eBird polygon boundary (Fink et al. 2021) of the non-breeding distribution I used to define prior distributions for  $x_i$ . I counted the number of random points located within the winter distribution of the tagged birds

and iterated the test 1000 times, estimating the probability all 10 random locations would fall within the estimated winter distribution of tagged birds.

Finally, I compared the size of the 99% contour of the kernel density estimate between the breeding and nonbreeding season. As with the non-breeding season, I defined the breeding season locations from the model posterior, using the median coordinates of all points from deployment until 1 August 2020, which was the duration of the geolocator calibration period. Following the same methods as for the nonbreeding season, I generated a polygon around the 99% contour of the kernel density estimate.

## **RESULTS**

### *Geolocator Retrieval*

I recovered 13 geolocators (40.1%) from Canada Warblers that returned in 2021 (Table 2.1); return rate by age was not significantly different (SY = 0.37, ASY = 0.48; Fisher's Exact Test: odds ratio= 0.669,  $p=0.697$ ). All marked individuals carrying geolocators that were detected were successfully recaptured. Of the 13 retrieved geolocators, 11 recorded usable light-level data to generate location estimates; one geolocator battery failed during the breeding season, and one light sensor malfunctioned throughout the year, resulting in indeterminable twilights. A third tag was excluded from analyses because modeled location estimates were consistently skewed east, including during the breeding season when the modeled estimates were contradicted by observed locations in the field (Appendix I). One tag battery failed 3 April 2021, while the rest recorded data until retrieval. In total, 10 geolocators provided data on post-breeding migration routes and overwintering sites, and nine geolocators provided data on pre-breeding migration.

### *Population Connectivity*

All 10 birds appeared to winter in north-central Colombia, based on the median coordinates from within the nonbreeding season stationary period (Figure 2.6). The 99% kernel density estimate around the breeding season points was 33,339 km<sup>2</sup>, while the nonbreeding season points distribution covered an area of 80,528 km<sup>2</sup>. While the locations appeared to be more dispersed during the nonbreeding season than the breeding season, they occupied an area < 10% of the potential nonbreeding season range (nonbreeding season range defined as 931, 235 km<sup>2</sup> per data from Fink et al. 2021). The 10 overwintering locations of Canada Warblers from West Virginia were clustered nonrandomly ( $p < 0.001$ ) within the possible nonbreeding season distribution.

### *Post-breeding Migration*

Post-breeding migration routes from geolocator location estimates indicated initial travel west-southwest through the US to Mexico, circumventing the majority of the Gulf of Mexico (Figure 2.7). While latitude estimates were unreliable during most of migration movements due to the equinox, longitude estimates suggested some overwater flights were possible (Figure 2.8 and Appendix I: A.2 – A.9). Not all birds departed the breeding grounds at the same time; three birds appear to have entered Mexico or Central America before the equinox period began (2 September 2020), where several other birds had only traveled a few hundred kilometers from the breeding grounds by the same date (Figure 2.7).

### *Pre-breeding Migration*

The nine geolocators which continued recording data through pre-breeding (spring) migration indicated that the pre-breeding migration route was further east than the post-breeding

migration route. On average, the minimum (furthest west) longitude during spring was 232 km further east than the minimum fall longitude, following a pattern of anticlockwise loop migration (Figure 2.9). A post-hoc two-sample t-test revealed the difference in minimum longitude between the two seasons was significant ( $t = -4.75$ ,  $df = 8$ ,  $p = 0.001$ ) and suggests a higher probability of pre-breeding migration routes crossing the Gulf of Mexico than post-breeding migration routes.

## **DISCUSSION**

This is the second known study to track Canada Warblers throughout the annual cycle, the first from the southern portion of the breeding range, and provides novel insight into the migration ecology of this declining species. I found that male Canada Warblers breeding in West Virginia, USA, spent the nonbreeding season in the Colombian Andes. The relatively small area within which birds were observed wintering is consistent with a pattern of strong population migratory connectivity. The location of the cluster is not consistent with a pattern of chain connectivity (in which the southern breeding populations would spend the winter at the southern end of the nonbreeding range), which Roberto-Charron et al. (2020) had hypothesized as an explanation for the preponderance of birds tracked from Canada spending the nonbreeding season in the northern portion of the nonbreeding range, and lack of migration further south.

Evidence defining the spatial pattern of connectivity in Canada Warblers is inconsistent. Stable isotope analyses suggested parallel connectivity where eastern and western breeding populations segregated on corresponding sides of the Andean cordillera, whereas the geolocators deployed across Canada exhibited low levels of crosswise connectivity, where western breeding populations wintered to the east of the eastern breeding populations (González-Prieto et al. 2017, Roberto-Charron et al. 2020). The cluster of nonbreeding season locations may also be due to



multiple breeding populations converging at high densities into a small spatial area. An estimated 50% of the nonbreeding season distribution is within the Colombian Andes, where Canada Warblers are most likely to occupy a narrow elevation band of 1,000 – 2,200 m in humid native forest (Céspedes and Bayly 2019), and Roberto-Charron et al. (2020) observed Canada Warblers wintering in this region. Tracking birds from multiple geographically distinct populations would provide better insight into the extent of population connectivity.

The post-breeding (fall) routes used by the West Virginia population of Canada Warblers appear to exhibit strong westward movement preceding any notable southward movements, but the uncertainty associated with the equinox limits the power of inference of the latitudes during this time, however, longitude is unaffected (Lisovski et al. 2018). The estimated flight paths along the Gulf Coast of Mexico with potential evidence of partial trans-Gulf flights were consistent with findings reported by Roberto-Charron et al. (2020), wherein 61.1% of geolocator-tagged Canada Warblers partially or fully crossed the Gulf. I did not find evidence of trans-Caribbean movements through islands south of Florida, as the longitudinal estimates were likely too far west to support this hypothesis. This result is also consistent with previous geolocator and mist-netting data, suggesting Canada Warbler records in the Caribbean are likely vagrants (Cárdenas-Ortiz et al. 2017, Roberto-Charron et al. 2020).

My results are the first to report multiple pre-breeding (spring) migration routes used by Canada Warblers. In contrast to the single bird with sufficient battery life through spring migration reported by Roberto-Charron et al. (2020) to use the same general path as the post-breeding migration, I observed pre-breeding routes were > 200 km further east than the post-breeding route used by each bird. The longitudinal difference suggests this population exhibits anticlockwise loop migration. There are several hypothesized drivers of a loop migration pattern,

such as seasonal wind patterns and stopover habitat resource availability (McKinnon et al. 2013, Bradley et al. 2014, Briedis et al. 2018). However, many neotropical species appear to follow a clockwise loop, with pre-breeding routes further west than post-breeding routes (Callo et al. 2013, Jahn et al. 2013, McKinnon et al. 2013), suggesting the evolutionary drivers of the differing routes may be species-specific. The anticlockwise loop traveled by Canada Warblers from West Virginia may reflect a strategy which minimizes flight distance and time. While migration timing and duration were not explicitly tested here, pre-breeding migration is typically shorter than the post-breeding migration for many species (McKinnon et al. 2013) including Canada Warblers (Reitsma et al. 2009, Roberto-Charron et al. 2020). Furthermore, the 2020 hurricane season (1 June – 30 November) consisted of a record-breaking number of storms and increased rainfall (Reed et al. 2022), which may have induced fall migration routes to proceed nearer the coast; however, multiple years of data would be necessary to assess a causative relationship.

As Canada Warbler abundance continues to decline (Sauer et al. 2020), a better understanding of the factors limiting populations throughout the full annual cycle is critical to their conservation. The nonbreeding season locations estimated here and from previous geolocator data (Roberto-Charron et al. 2020) is indicative of the conservation importance of the Colombian Andes, which has been estimated to contain > 50% of the nonbreeding distribution of Canada Warblers (Céspedes and Bayly 2019). A global biodiversity hotspot, the region provides habitat for > 1,500 bird species (Franco et al. 2007). An estimated 90% loss of the montane forest used by overwintering Canada Warblers has resulted from deforestation for both crops and livestock (Etter et al. 2006, Céspedes and Bayly 2019, Clerici et al. 2019). While overwinter survival by Canada Warblers in shade-grown coffee was comparable to native forest, only 10%

of Colombian coffee was grown in agroforest systems in 2013, down from 23% in 1997 (González et al. 2020). Approximately 3.5 million ha of Colombian native montane forest falls within protected areas, but the value to Canada Warblers is uncertain, with different protected areas of various sizes hosting a wide range of 3%-72% of overwintering migratory species found in the region (Franco et al. 2007). Even in protected areas, insufficient resources are available to adequately monitor these biodiversity reserves which are encroached by illegal cropping of high-value coca and opium, a situation further complicated by the often-extreme political climate and decades of social unrest (Etter et al. 2006, Clerici et al. 2019). The Colombian Andes serve as nonbreeding season habitat for Canada Warblers from several distinct populations, but this does not preclude the existence of strong population connectivity, with potentially major conservation implications. In the long-term, strongly connected populations of Canada Warblers will be more vulnerable to anthropogenic effects and stochastic events, such as the documented losses of montane forest; in weakly connected populations, negative effects on individuals such as reduced survival, body condition, and subsequent reproductive success will be diffused across multiple breeding populations (Webster et al. 2002).

Given that Canada Warblers across the breeding distribution seem to converge within the Colombian Andes, it raises the question of where Canada Warblers wintering elsewhere in the nonbreeding distribution spend the breeding season. Migratory birds, including warblers, have been known to segregate during the nonbreeding season, with females often found in lower quality habitat or even migrating further than males (Cristol et al. 1999, Catry et al. 2005, 2006, Briedis and Bauer 2018). In Colombia, a greater proportion of Canada Warblers in native forest tended to be male, and the inverse was true in shade-grown coffee, with some statistical uncertainty (González et al. 2020). It is also possible the southern latitudes of the Canada

Warbler nonbreeding distribution are occupied by a preponderance of female birds, but to my knowledge this is unstudied. Failing to account for segregation by sex may bias models of population dynamics with conservation implications; Golden-winged Warbler female-preferred habitat has incurred greater losses than male-preferred habitat (Briedis and Bauer 2018, Bennett et al. 2019). Tracking female Canada Warblers may provide more conclusive insight into factors in the nonbreeding season influencing breeding populations.

Factors outside of the breeding season affecting population growth may also occur during migration. The trend of increased abundance in West Virginia (Sauer et al. 2020) could be explained by the geographically shorter migration route from the southern extent of the breeding range to the nonbreeding grounds. Migration is a high-risk period in the annual cycle, and longer distances increase the opportunities for mortality events (Sillett and Holmes 2002, Newton 2006, Klaassen et al. 2014). Building full annual cycle demographic models across the breeding range for Canada Warblers will help elucidate the drivers of population dynamics.

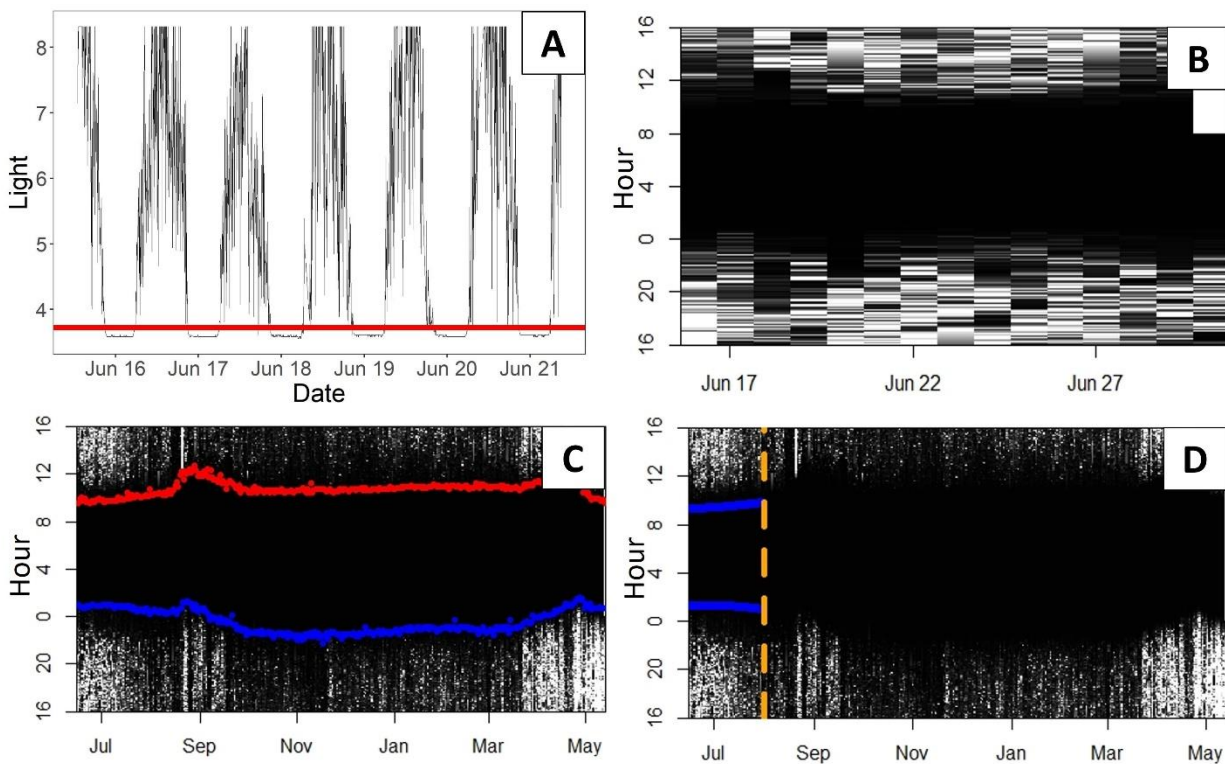
My study is the first to track the migration of Canada Warblers from the southern portion of their breeding range and my findings reinforce published data emphasizing the importance of the Colombian Andes as nonbreeding season habitat for this species. Whether the clustering of nonbreeding locations is due to strong population connectivity, multiple breeding populations converging due to higher habitat quality, or latitudinal segregation by sex, continued habitat loss and degradation in the region could have negative consequences on multiple breeding populations (González-Prieto et al. 2017, Céspedes and Bayly 2019, González et al. 2020, Roberto-Charron et al. 2020). As the species continue to decline across most of their breeding range (Sauer et al. 2020), this project will provide essential baseline data to construct full annual cycle population models. Incorporating environmental conditions associated with the stationary

nonbreeding season and migratory stopover locations in addition to breeding season dynamics will be critical to inform habitat management to aid in the conservation of the Canada Warbler.

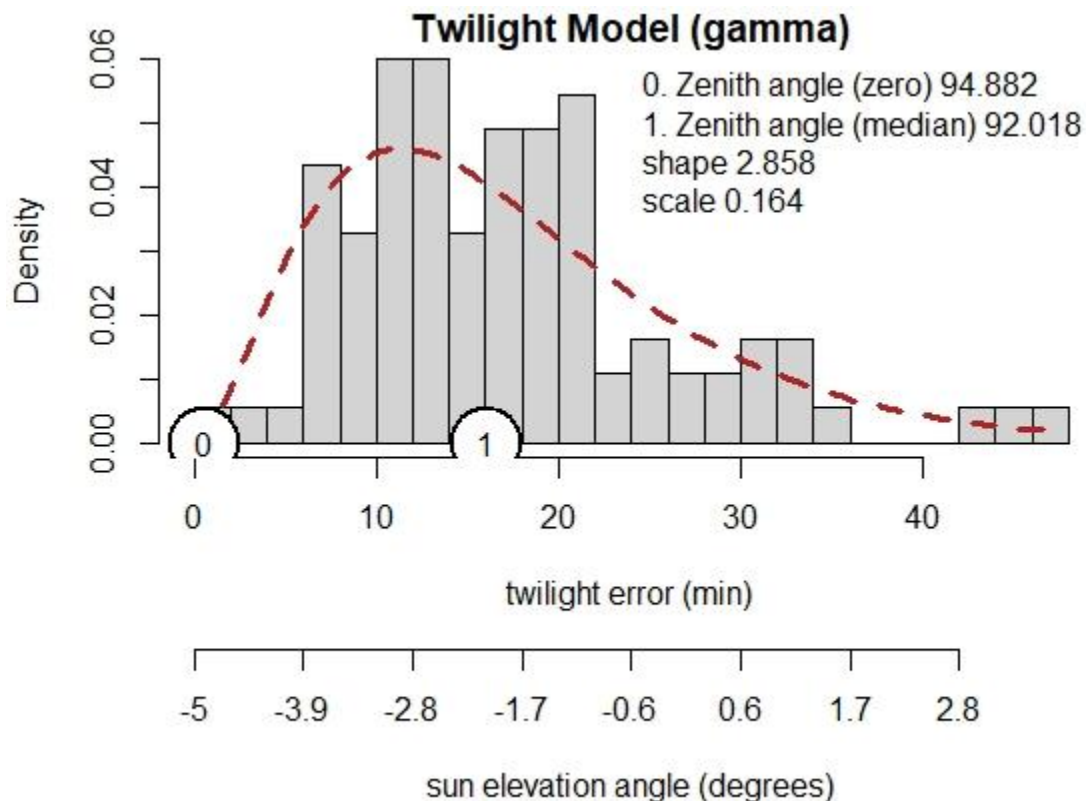
## CHAPTER 2: FIGURES AND TABLES



**Figure 2.1** Leg-loop harness method used to deploy 32 FL6057 fLight Lotek Wireless geolocator tags to on adult male Canada Warblers (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA. Main photo shows Geo ID 475 attached to an adult male Canada Warbler at initial capture in June 2020, and the inset shows a closeup of Geo ID 473 with the harness made from made of 0.5 mm Stretch Magic elastic cord.

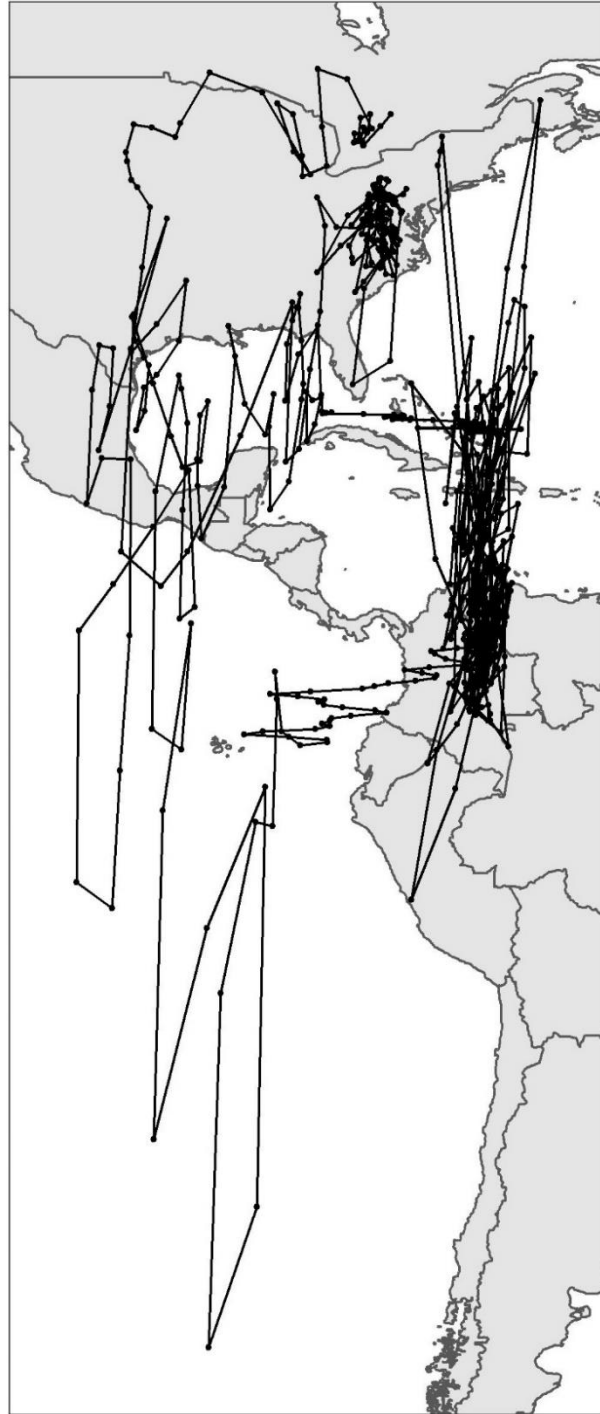


**Figure 2.2** Light-level data recorded by Geo ID 452 deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA on 15 June 2020 and retrieved 13 May 2021. In (A) light levels recorded across 6 days with the threshold value used to define night as a horizontal red line, shown on the log scale. In (B) – (D), pixels represent a single light level reading with darker pixels representing lower light levels, and Hour in GMT, with night period at the center of each figure. (B) is a close-up of the first 2000 light readings (the white bar beginning at hour 8 on the last day is no data at the end of the 2000 readings); (C) shows the twilight annotated with sunrise times in red and sunset in blue; and (D) shows the end of the calibration period as an orange dashed line and actual twilight time for the known location indicated with blue horizontal lines.

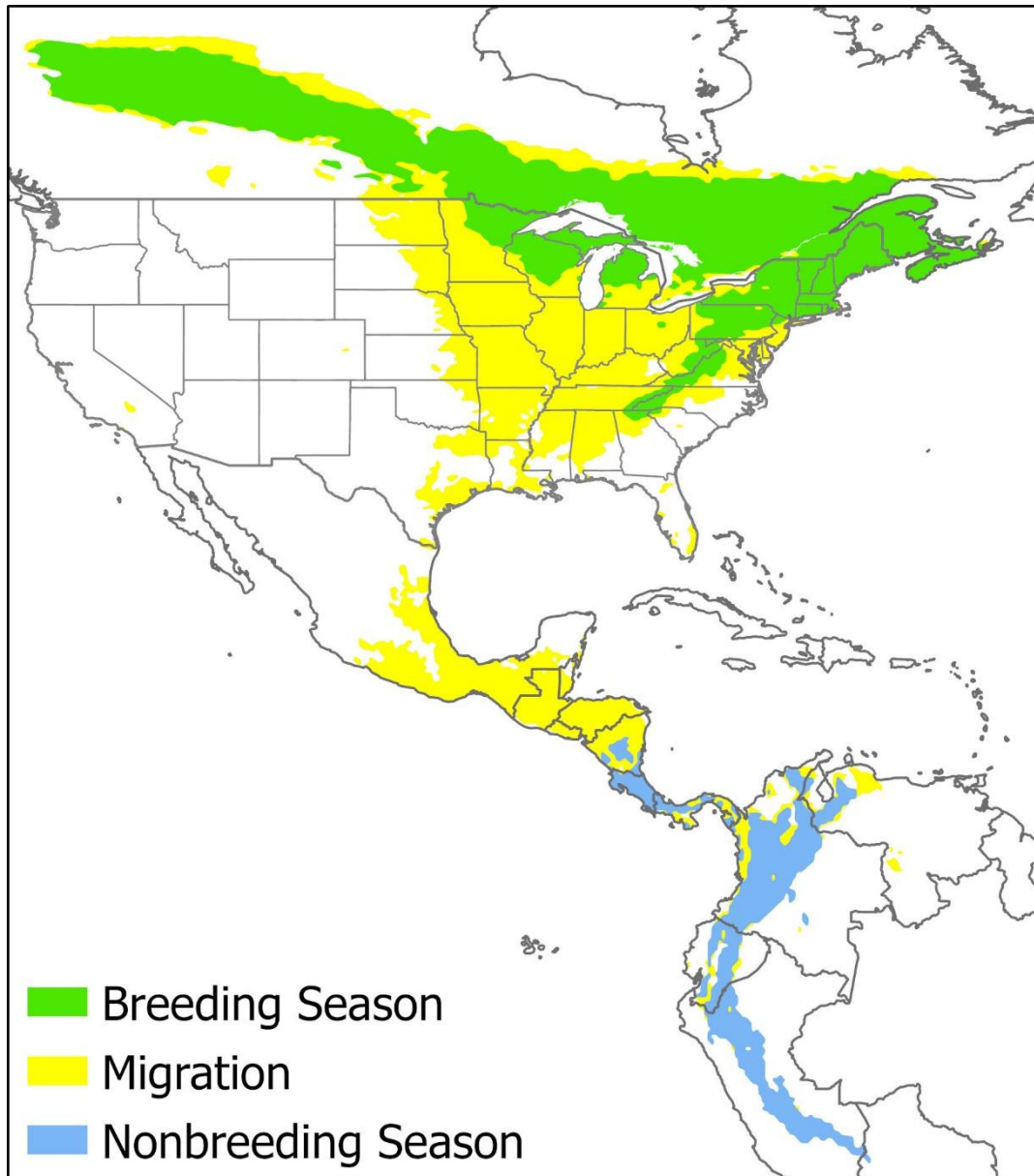


**Figure 2.3** Error distribution of twilight times fit to a gamma curve (red dashed line) recorded by Geo ID 452 deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA. Calibration period was from deployment on 15 June 2020 to 1 August 2020. The twilight error is the number of minutes between actual twilight for the known coordinates (zenith angle 0) and the time of twilight estimated by the device from the light level data in the twilight annotation step (Figure 2.2A). The zenith angle (median) notes the angle of the sun at the median deviation of device annotated twilight from true twilight and is used to generate initial location estimates. The final two parameters are the shape and scale of the gamma distribution which are used as a prior distribution in the Bayesian model.

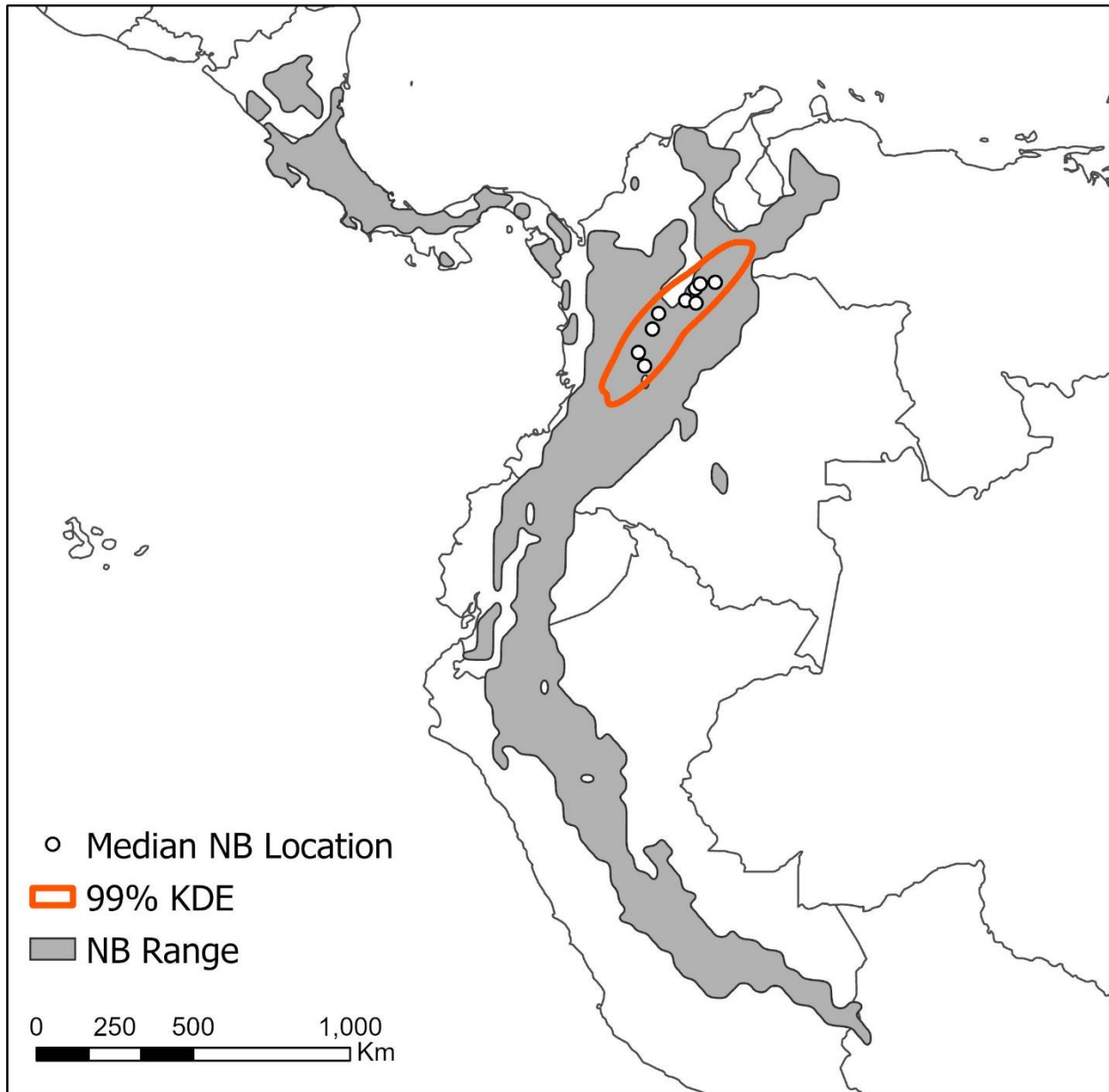




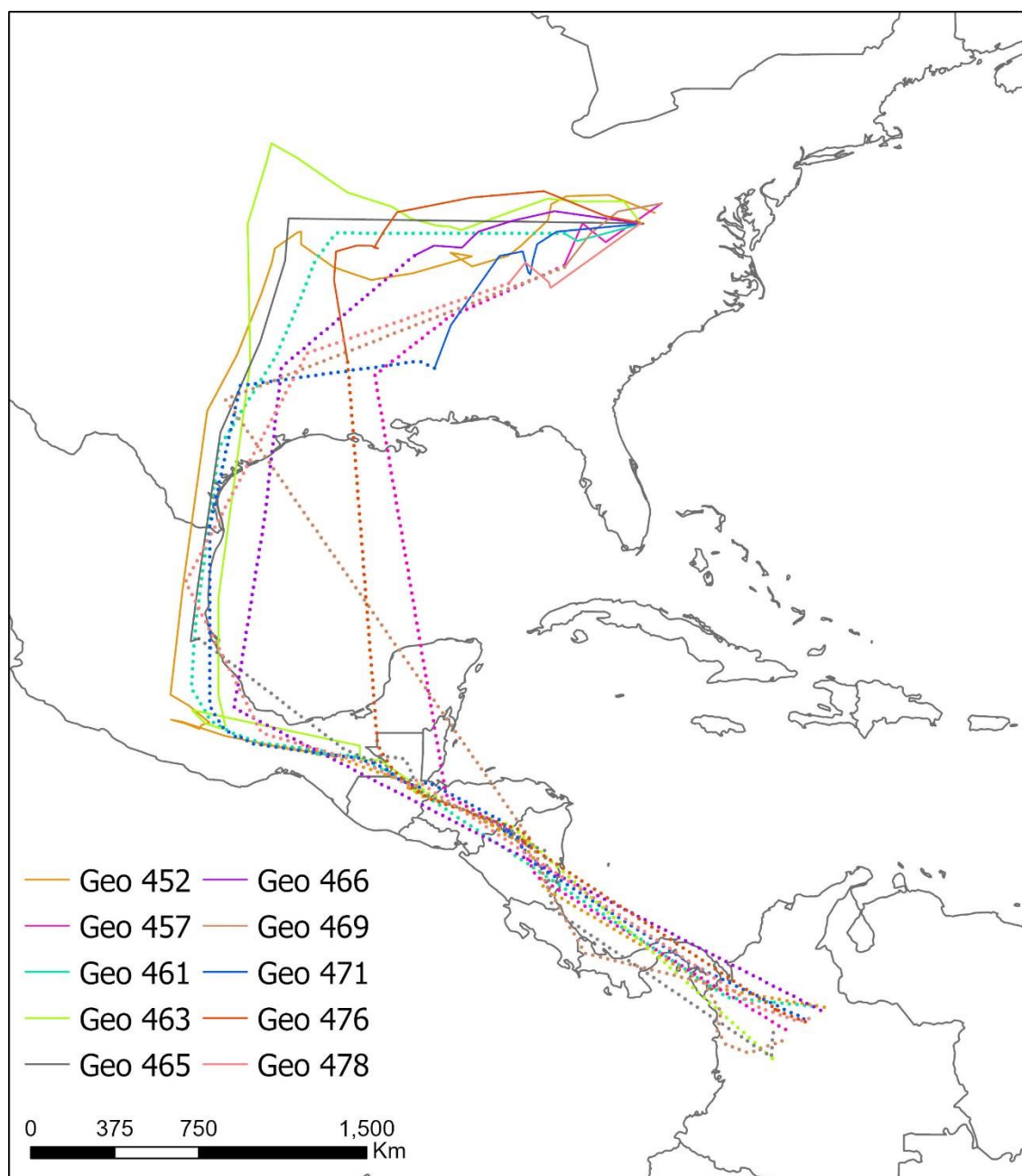
**Figure 2.4** Initial location estimates calculated from twilight times of Geo ID 452 deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA on 15 June 2020 and retrieved 13 May 2021. Locations are estimated using twilight times (Figure 2.2A) and median twilight error (Figure 2.3) using *thresholdPath* function in package *GeoLight* (Lisovski and Hahn 2012).



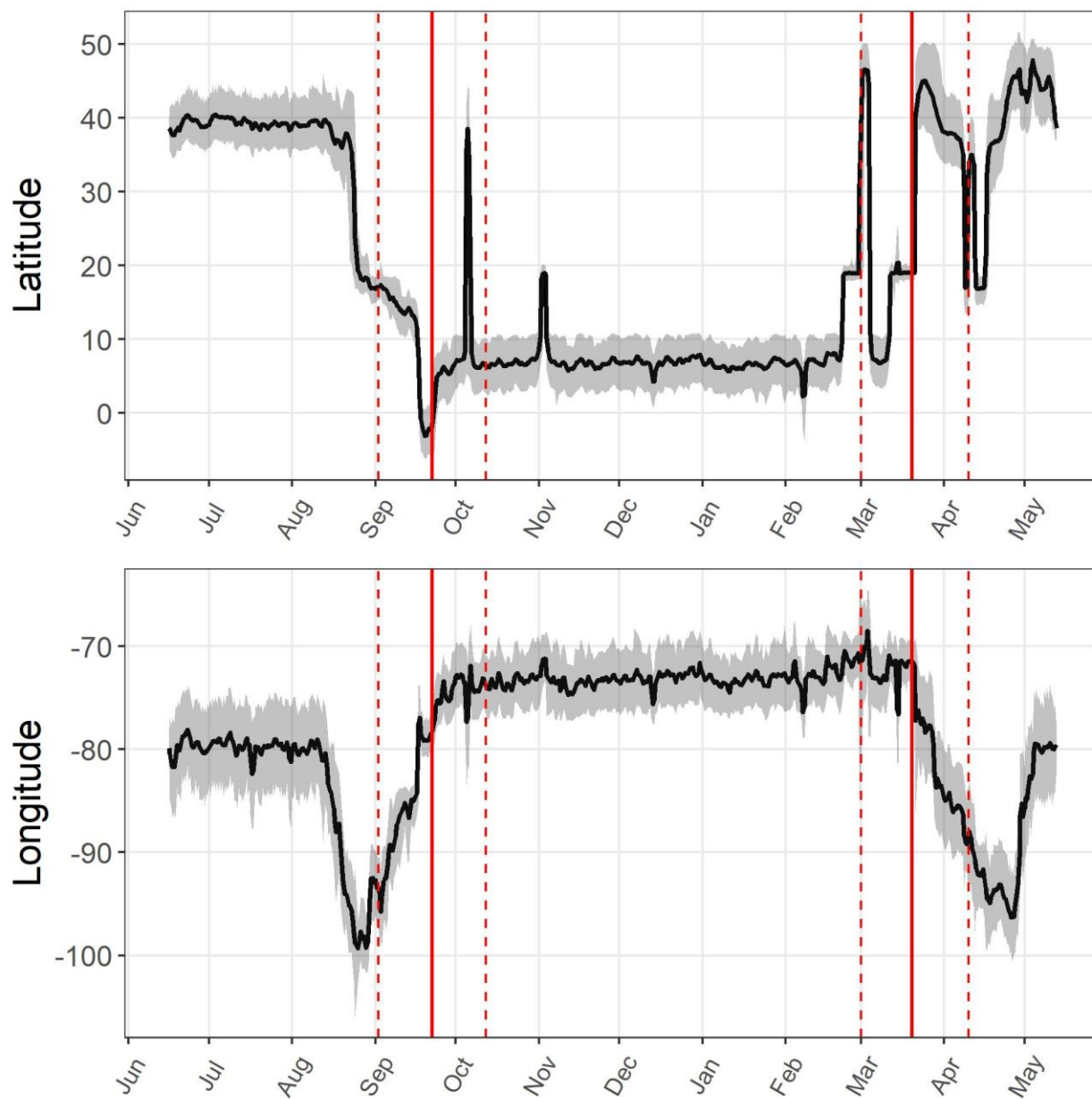
**Figure 2.5** Range map of Canada Warbler (*Cardellina canadensis*) created with the ‘low-resolution’ data from eBird (Fink et al. 2021). Range data were used as a spatial prior for the Bayesian model of geolocator location estimates where occurrence anywhere within any season’s range was more likely than terrestrial locations outside of the range.



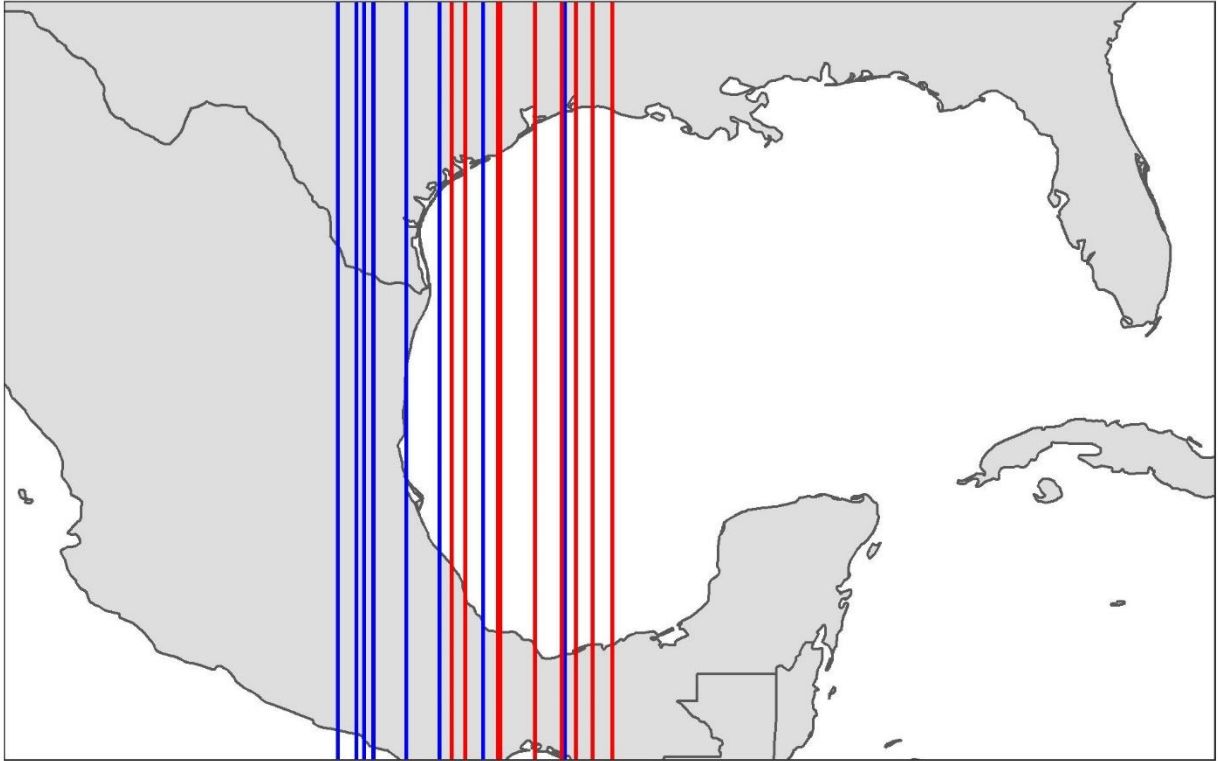
**Figure 2.6** Median nonbreeding season (16 November 2020 – 1 March 2021) location estimates, (white circles) of Canada Warblers breeding in the Monongahela National Forest, WV, USA based on geolocator tag data. The 99% kernel density estimate, in red, for the ten individual locations encompasses 80,528 km<sup>2</sup>, while the dark grey represents the documented nonbreeding range of Canada Warblers, an area of 931,235 km<sup>2</sup> (Fink et al. 2021). Median nonbreeding season locations were clustered nonrandomly ( $p = 0.001$ ) relative to the total available nonbreeding distribution.



**Figure 2.7** Estimated post-breeding migration routes used by adult male Canada Warblers (*Cardellina canadensis*) in fall 2020 from their breeding sites in the Monongahela National Forest, WV, USA, obtained from light-level geolocators. Routes were inferred by linking successive location estimates. Each color is a different bird with unique geolocator identifier, and the routes are dashed when point estimates fell during the defined equinox period of  $\pm 20$  days from the autumnal equinox (22 September 2020). Erratic north-south movements during the equinox period were discarded and therefore equinox routes are interpolated from longitude and latitudes recorded before or after the equinox period.



**Figure 2.8** Latitude and longitude estimates throughout the year from light-level geolocator (Geo ID 452) deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA on 15 June 2020. Posterior median is the solid black line, with 95% credible intervals defined by the grey ribbon. Spring and fall equinox dates are indicated by the solid red lines, with the equinox period of  $\pm 20$  days indicated by the dashed red lines. Latitude estimates are particularly unreliable during the equinox, while longitude is unaffected.



**Figure 2.9** Posterior median of westernmost longitude reached by Canada Warblers (*Cardellina canadensis*) during post-breeding (fall; blue) and pre-breeding (spring; red) migration between breeding sites in the Monongahela National Forest, WV, USA, and nonbreeding season sites in Colombia. Post-breeding routes are further east than pre-breeding routes, resulting in apparent anticlockwise loop migration, and indicating most birds likely took trans-Gulf flights during the pre-breeding migration.

**Table 2.1** Summary of 13 recovered light-level geolocators from 32 deployed on male Canada Warblers during the breeding season in the Monongahela National Forest, WV, USA in 2020 and successfully retrieved in 2021, in order of deployment date. Geo ID is the unique identifier for the geocator, age indicates bird age at geocator deployment determined from plumage characteristics, with dates the geocator was deployed and then retrieved the following year, and study site indicates which of the six sites within the study area the bird was captured (more study site details in Figure 1.1 and Table 1.1). Of the 13 retrieved tags, 10 provided usable data to mark the fall migration and nonbreeding season locations, and 9 continued recording data through spring migration as well.

<b>Geo ID</b>	<b>Age</b>	<b>Deployed 2020</b>	<b>Retrieved 2021</b>	<b>Study Site</b>
476	ASY	29 May	16 May	Dogway
478	ASY	31 May	20 May	Kennison
482 <sup>a</sup>	SY	3 June	26 May	Red Run
457	ASY	4 June	12 May	Red Run
458 <sup>b</sup>	ASY	9 June	25 May	Losh
459 <sup>c</sup>	SY	9 June	9 June	Losh
461	ASY	10 June	15 May	Falls
463 <sup>d</sup>	ASY	11 June	6 May	Falls
465	ASY	12 June	17 May	Dogway
466	SY	12 June	30 May	Dogway
452	ASY	15 June	13 May	Glade
469	ASY	25 June	9 June	Red Run
471	ASY	27 June	15 May	Falls

<sup>a</sup>Battery failure 30 July 2020; discarded from analyses

<sup>b</sup>Light sensor malfunctioned throughout entire year; no usable data recorded

<sup>c</sup>Location estimates biased east during known location periods; discarded from analyses

<sup>d</sup>Battery failure 1 April 2021; used in fall migration and nonbreeding season analyses

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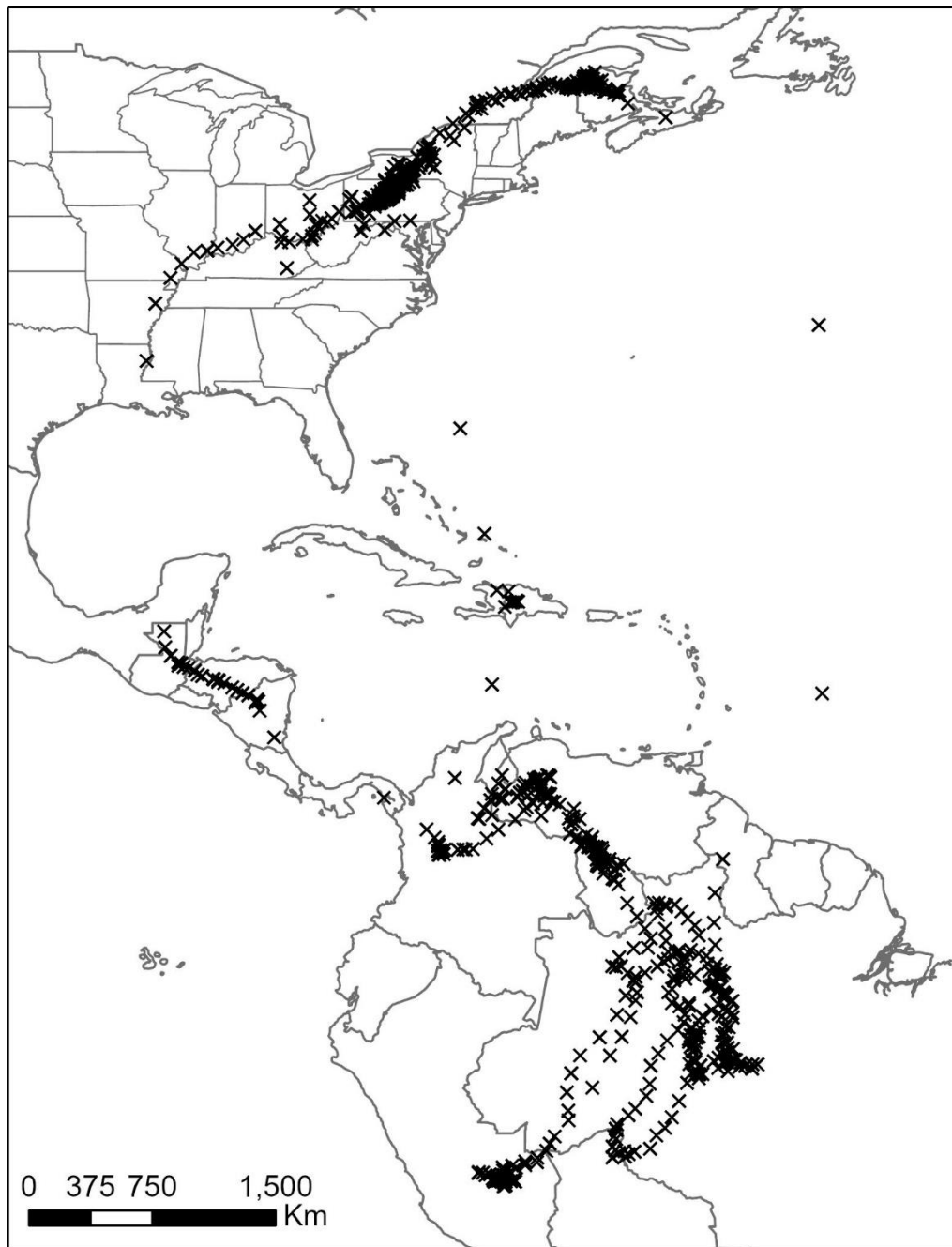
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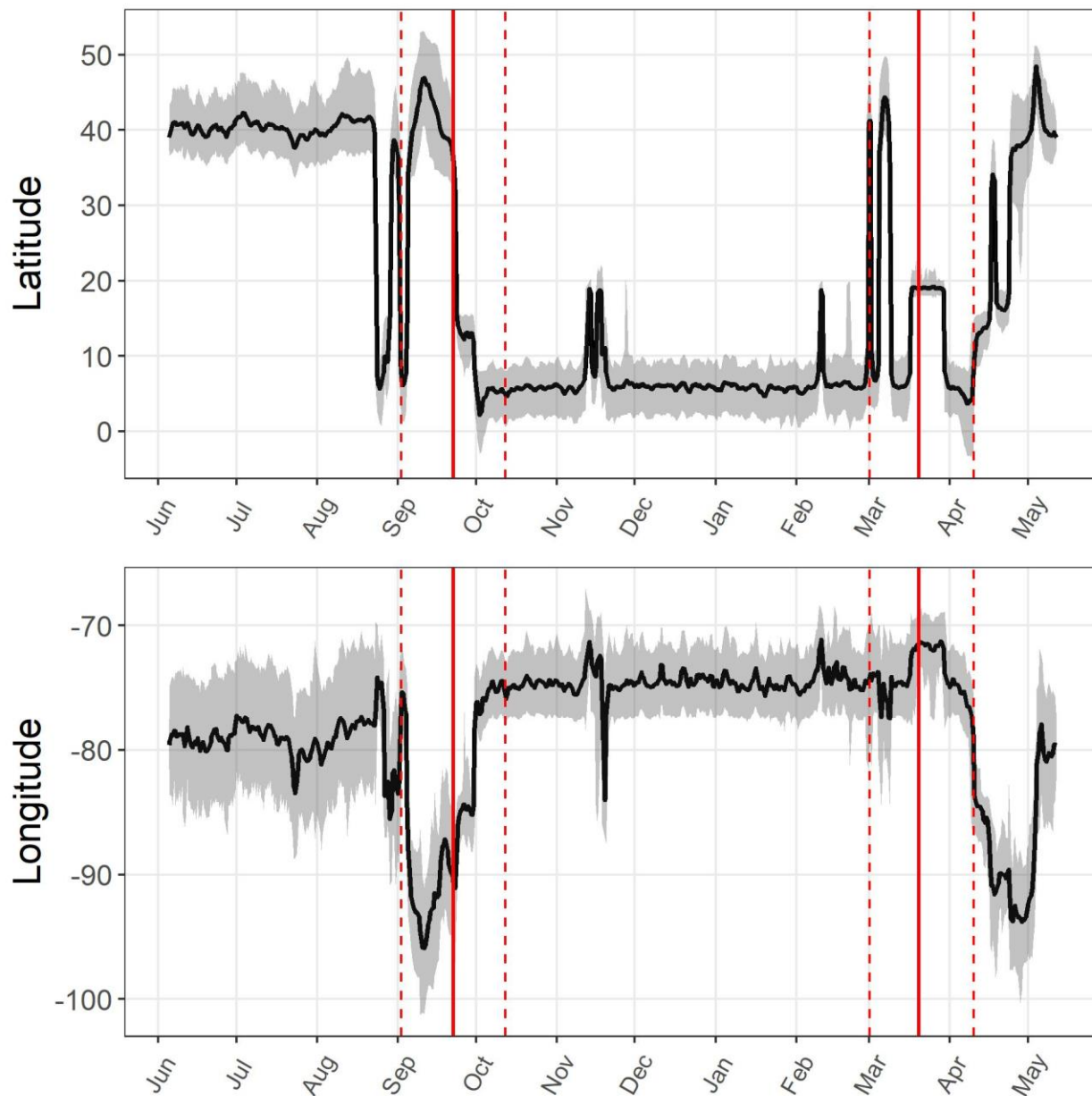


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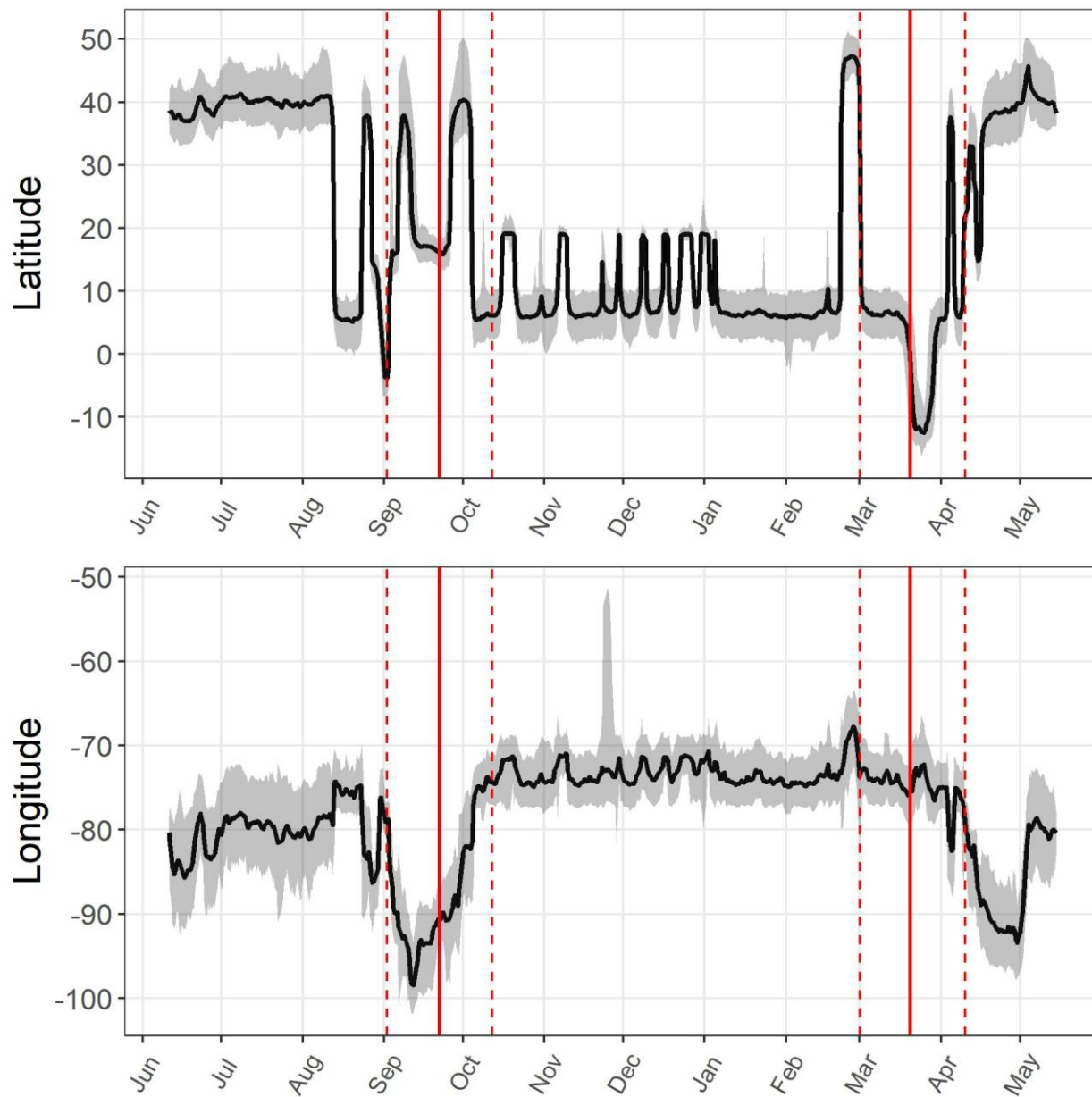
*Appendix I: Supplemental Figures*



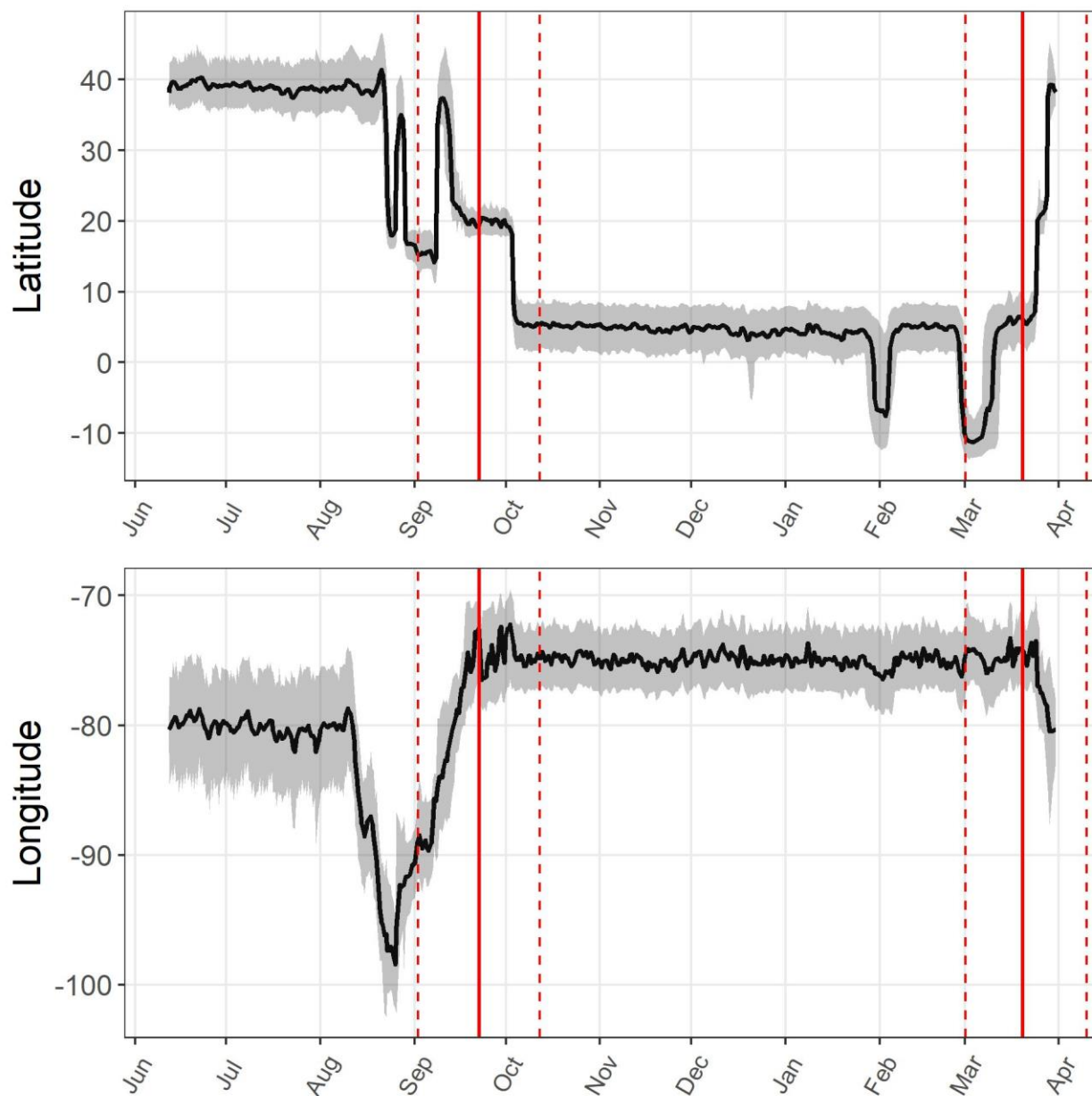
**Figure A.1** Bayesian model posterior median location estimates for Canada Warbler (*Cardellina canadensis*) deployed with light-level geolocator Geo ID 459 in the Monongahela National Forest, WV, USA on 9 June 2020. Data were discarded from analyses due to erroneous northeastward movement while the bird was confirmed to be still on the breeding grounds that indicate a strong eastward bias in the locations, in addition to movement well outside the recorded nonbreeding distribution of the species.



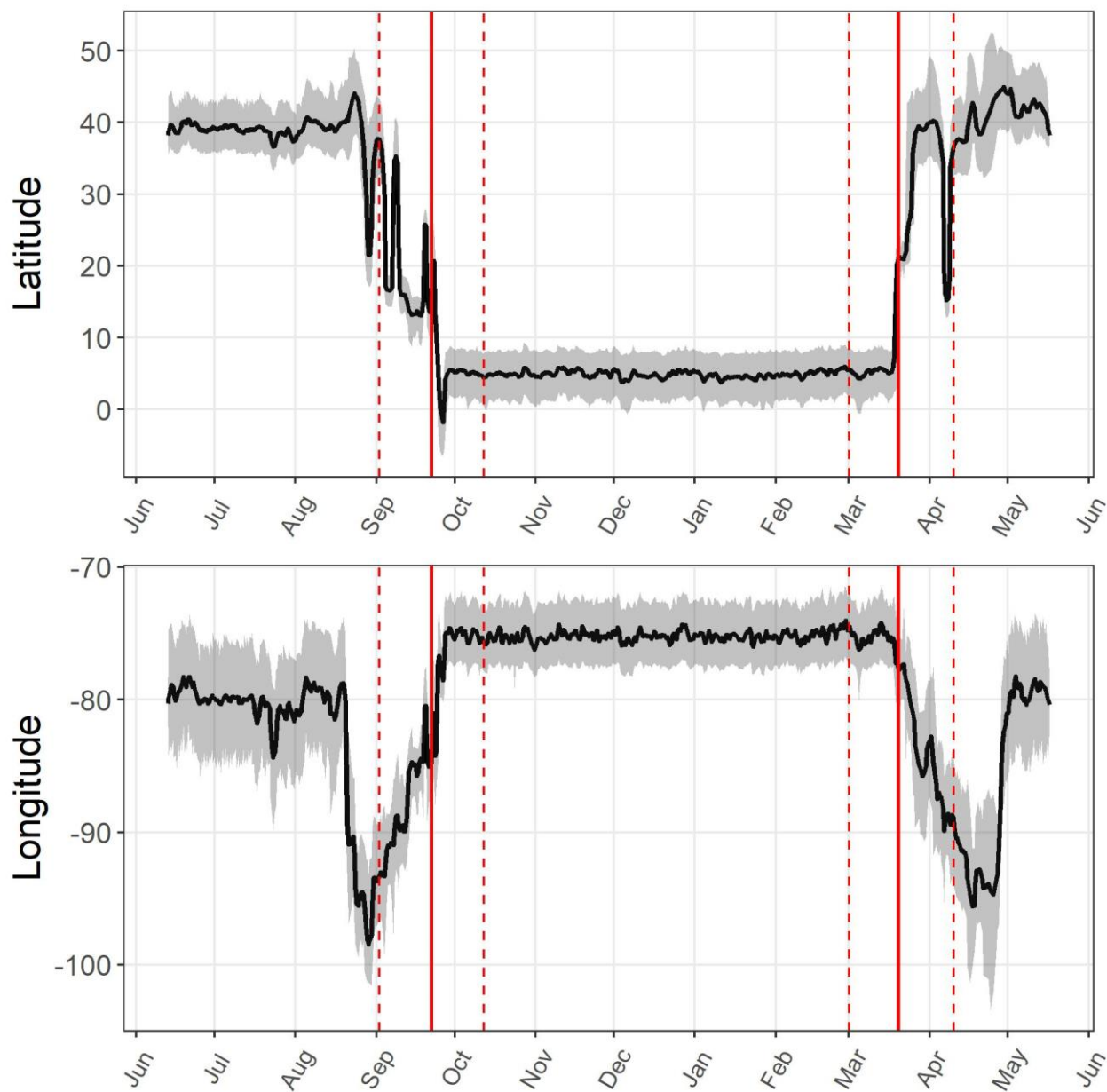
**Figure A.2** Latitude and longitude estimates throughout the year from light-level geolocator (Geo ID 457) deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA on 4 June 2020. Posterior median is the solid black line, with 95% credible intervals defined by the grey ribbon. Spring and fall equinox dates are indicated by the solid red lines, with the equinox period of  $\pm 20$  days indicated by the dashed red lines. Latitude estimates are particularly unreliable during the equinox, while longitude is unaffected.



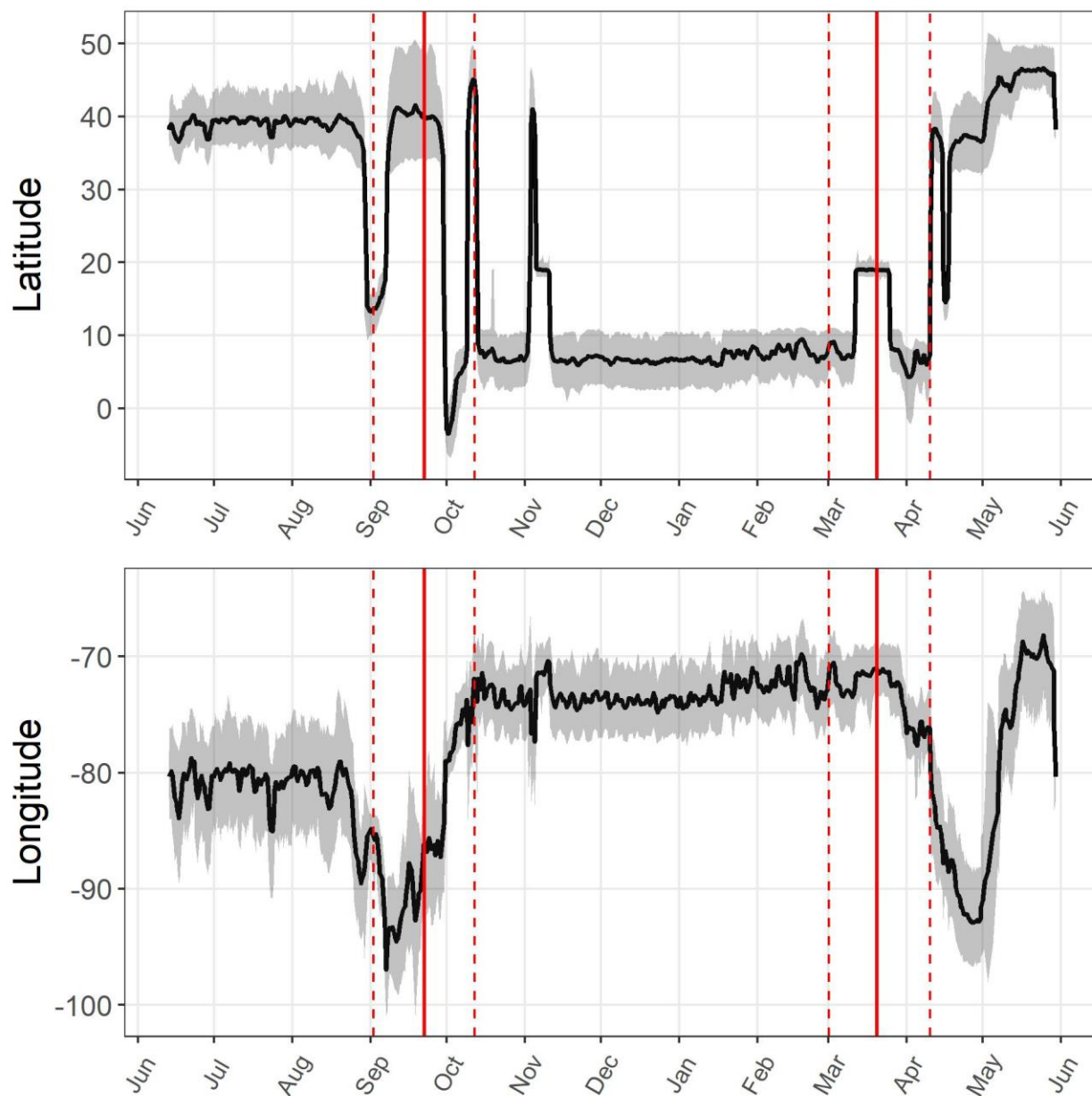
**Figure A.3** Latitude and longitude estimates throughout the year from light-level geolocator (Geo ID 461) deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA on 10 June 2020. Posterior median is the solid black line, with 95% credible intervals defined by the grey ribbon. Spring and fall equinox dates are indicated by the solid red lines, with the equinox period of  $\pm 20$  days indicated by the dashed red lines. Latitude estimates are particularly unreliable during the equinox, while longitude is unaffected.



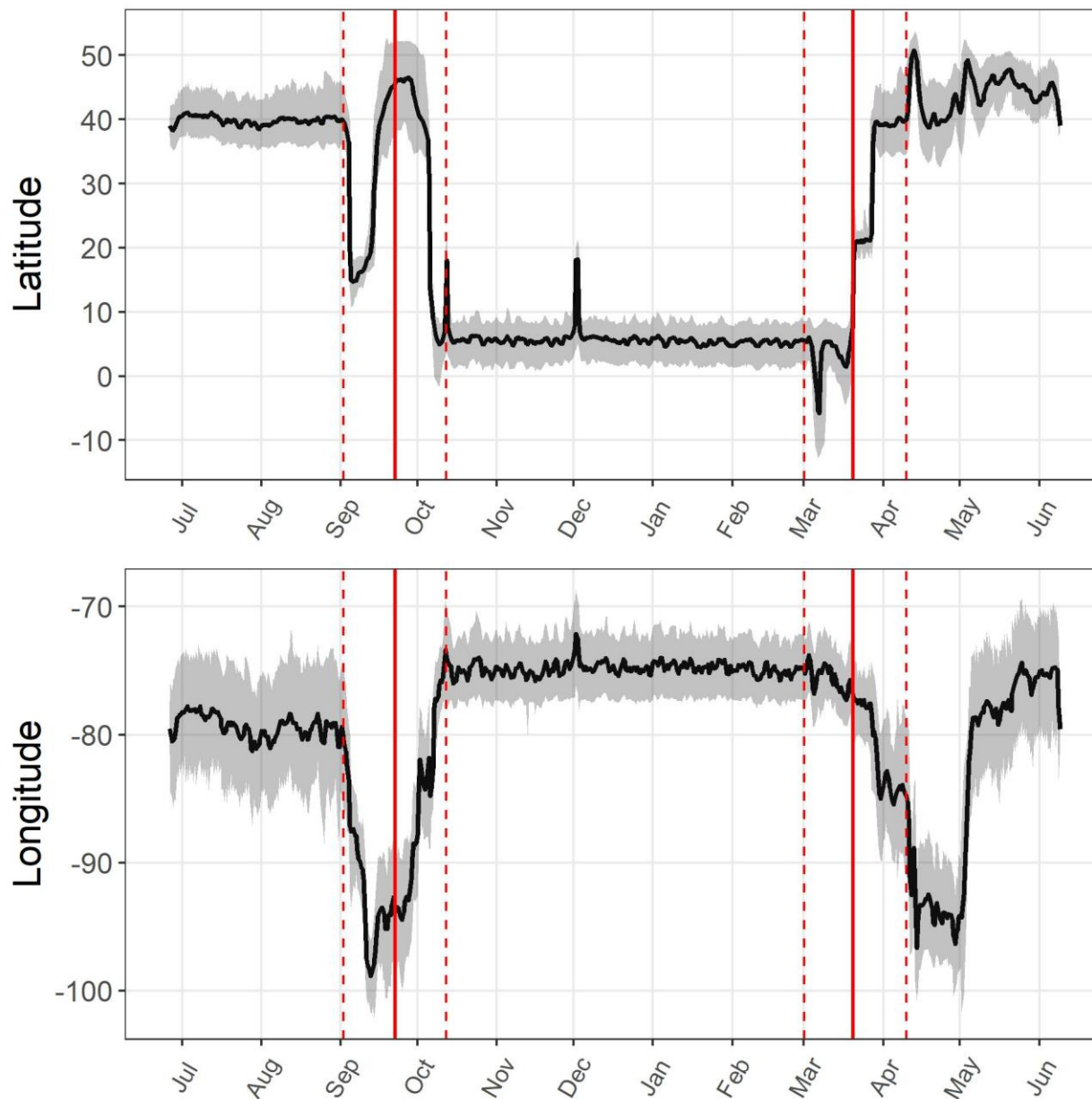
**Figure A.3** Latitude and longitude estimates throughout the year from light-level geolocator (Geo ID 463) deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA on 11 June 2020. Posterior median is the solid black line, with 95% credible intervals defined by the grey ribbon. Spring and fall equinox dates are indicated by the solid red lines, with the equinox period of  $\pm 20$  days indicated by the dashed red lines. Latitude estimates are particularly unreliable during the equinox, while longitude is unaffected. Geolocator battery failed 1 April 2021.



**Figure A.4** Latitude and longitude estimates throughout the year from light-level geolocator (Geo ID 465) deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA on 12 June 2020. Posterior median is the solid black line, with 95% credible intervals defined by the grey ribbon. Spring and fall equinox dates are indicated by the solid red lines, with the equinox period of  $\pm 20$  days indicated by the dashed red lines. Latitude estimates are particularly unreliable during the equinox, while longitude is unaffected.

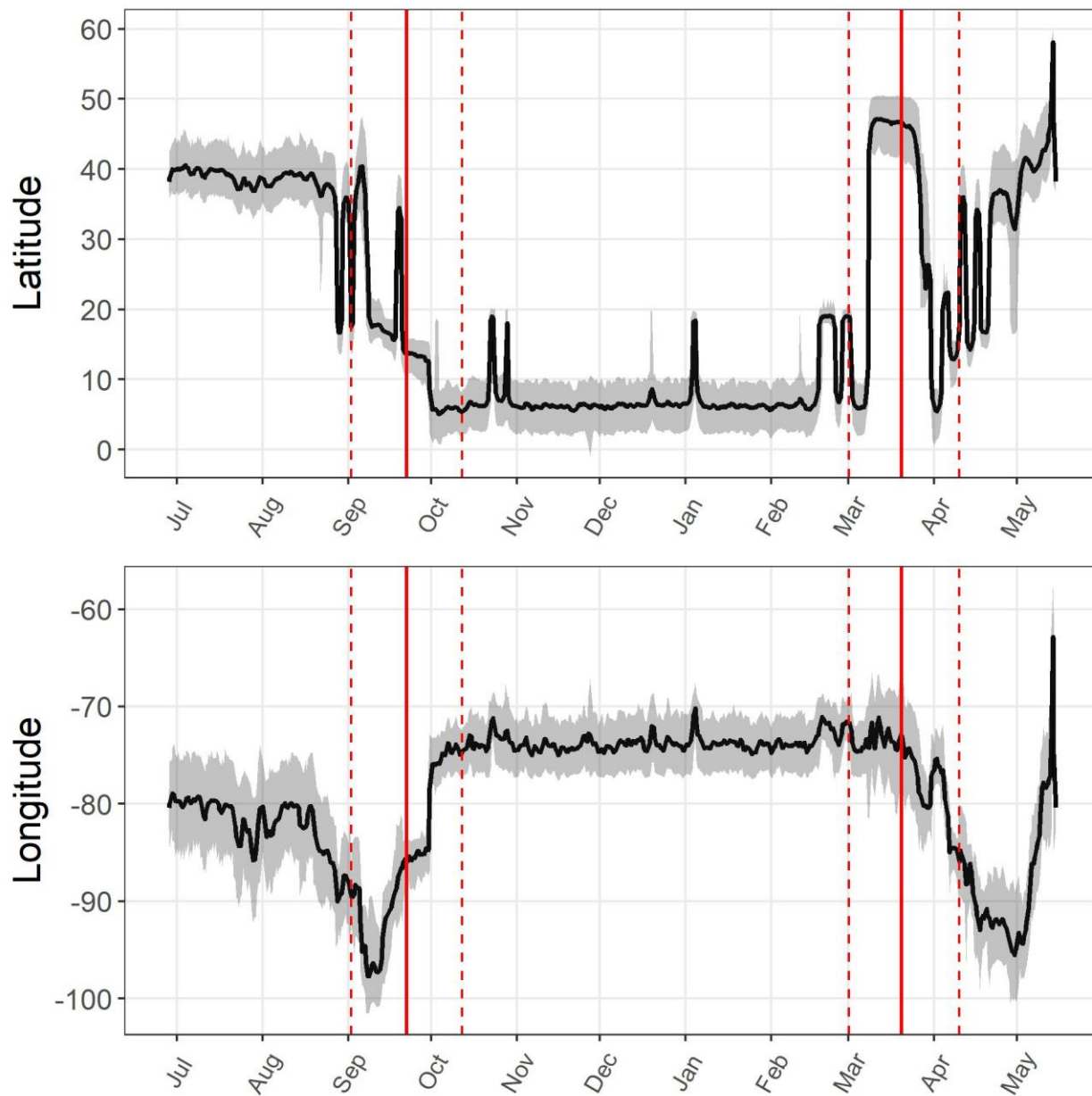


**Figure A.5** Latitude and longitude estimates throughout the year from light-level geolocator (Geo ID 466) deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA on 12 June 2020. Posterior median is the solid black line, with 95% credible intervals defined by the grey ribbon. Spring and fall equinox dates are indicated by the solid red lines, with the equinox period of  $\pm 20$  days indicated by the dashed red lines. Latitude estimates are particularly unreliable during the equinox, while longitude is unaffected.

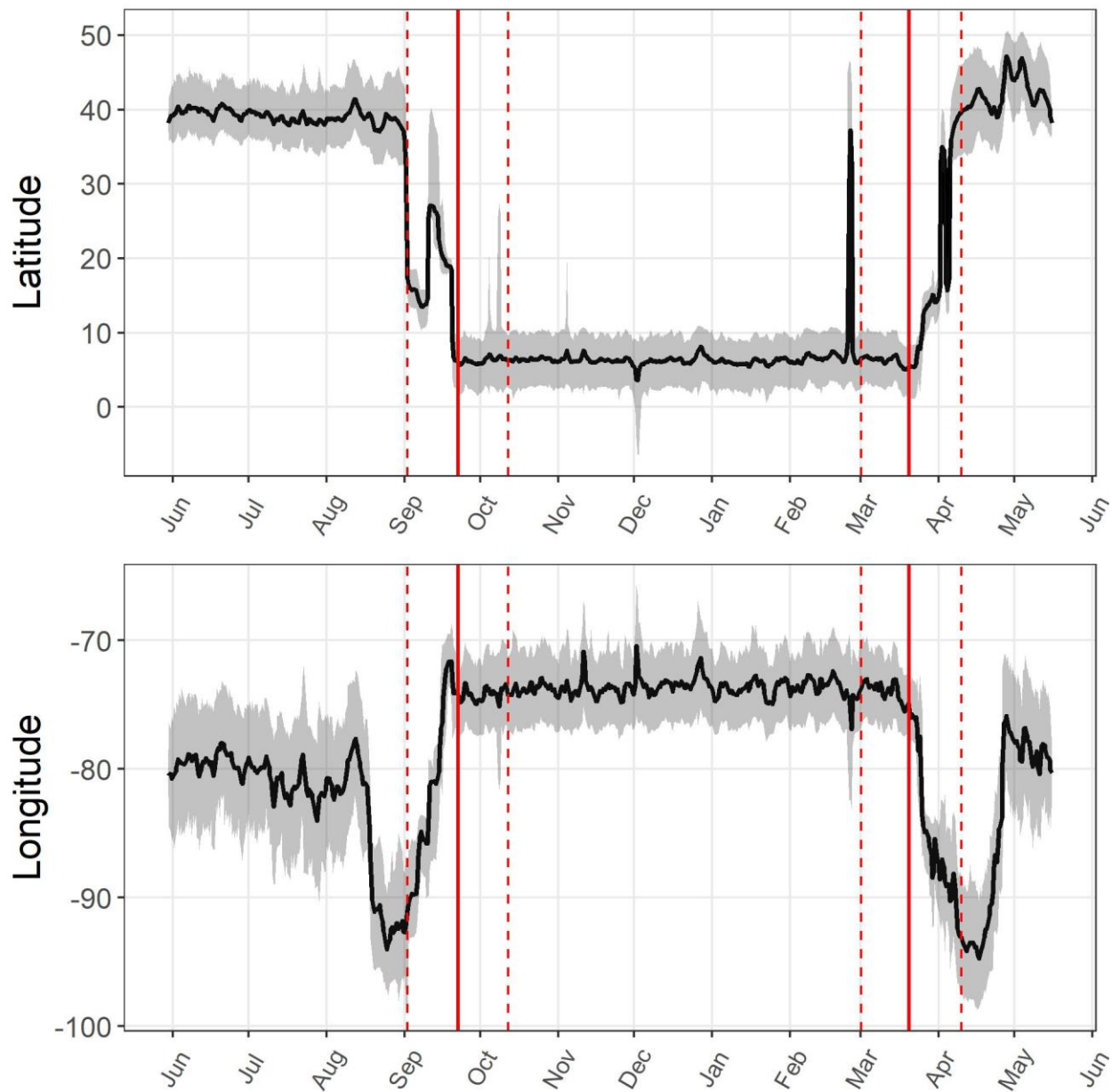


**Figure A.6** Latitude and longitude estimates throughout the year from light-level geolocator (Geo ID 469) deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongahela National Forest, WV, USA on 25 June 2020. Posterior median is the solid black line, with 95% credible intervals defined by the grey ribbon. Spring and fall equinox dates are indicated by the solid red lines, with the equinox period of  $\pm 20$  days indicated by the dashed red lines. Latitude estimates are particularly unreliable during the equinox, while longitude is unaffected.

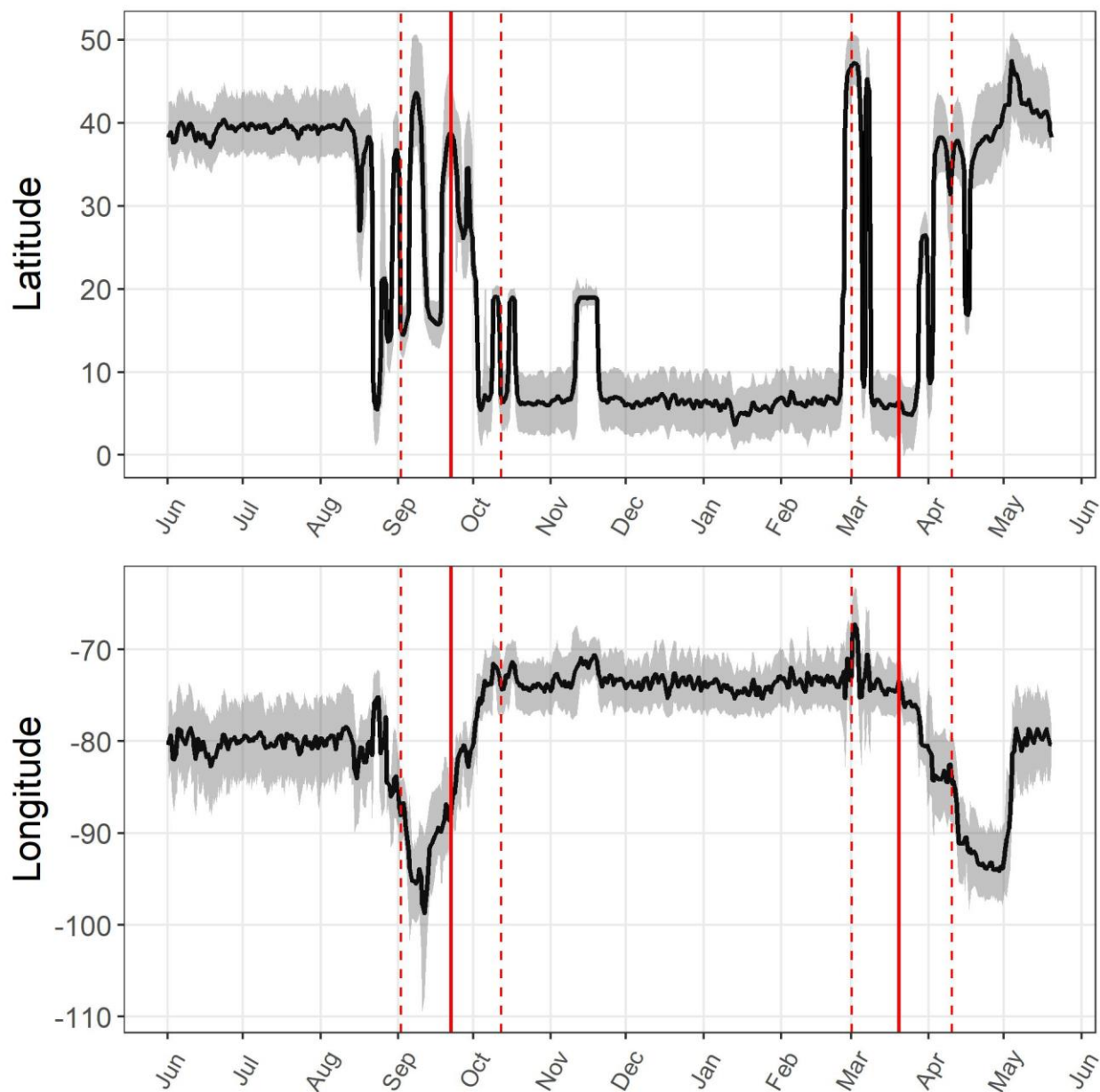




**Figure A.7** Latitude and longitude estimates throughout the year from light-level geolocator (Geo ID 471) deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongehela National Forest, WV, USA on 27 June 2020. Posterior median is the solid black line, with 95% credible intervals defined by the grey ribbon. Spring and fall equinox dates are indicated by the solid red lines, with the equinox period of  $\pm 20$  days indicated by the dashed red lines. Latitude estimates are particularly unreliable during the equinox, while longitude is unaffected.



**Figure A.8** Latitude and longitude estimates throughout the year from light-level geolocator (Geo ID 476) deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongehela National Forest, WV, USA on 29 May 2020. Posterior median is the solid black line, with 95% credible intervals defined by the grey ribbon. Spring and fall equinox dates are indicated by the solid red lines, with the equinox period of  $\pm 20$  days indicated by the dashed red lines. Latitude estimates are particularly unreliable during the equinox, while longitude is unaffected.



**Figure A.9** Latitude and longitude estimates throughout the year from light-level geolocator (Geo ID 478) deployed on an adult male Canada Warbler (*Cardellina canadensis*) in the Monongehela National Forest, WV, USA on 31 May 2020. Posterior median is the solid black line, with 95% credible intervals defined by the grey ribbon. Spring and fall equinox dates are indicated by the solid red lines, with the equinox period of  $\pm 20$  days indicated by the dashed red lines. Latitude estimates are particularly unreliable during the equinox, while longitude is unaffected.