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COVER: A male Harlequin Duck (*Histrionicus histrionicus*) in the Rocky Mountains of Alberta. This small sea duck winters in coastal marine waters and breeds on fast-moving mountain streams in western North America. A 25-year roadside monitoring study in Banff National Park, Alberta has revealed a declining population trend. See Smith *et al.* (pages 358–366). Photo: Mark Bradley.

The Canadian Field-Naturalist

Limited evidence for the influence of the physical structure and floristics of habitat on a boreal forest bird community

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Abstract

Studies conducted at regional and continental scales show that avian richness, community composition, and abundance are associated with variation in the vegetation physical structure and community composition (floristics) within broad habitat types. The relative contributions of physical structure and floristics are contested, and relationships are often taxon-specific. We used 110 microphone arrays deployed across 90 sampling locations and two breeding seasons to survey an avian community in the boreal forest in Labrador, Canada. Our objectives were (1) to describe the avian community of an underrepresented portion of the boreal forest, (2) to estimate the relationships between avian species richness and habitat characteristics, (3) to estimate if species detection at a given location was related to local habitat characteristics, and (4) to investigate the spatial and temporal patterns of the avian community composition. We detected 32 species at our sampling locations; physical structure and floristics were not related to avian species richness, although estimates of richness were higher on warmer days and lower on windier days. Habitat characteristics were associated with the detection of Boreal Chickadee (*Poecile hudsonicus*), Yellow-rumped Warbler (*Setophaga coronata*), American Robin (*Turdus migratorius*), and Black-throated Green Warbler (*Setophaga virens*). Finally, avian community composition was only moderately consistent among three categorical forest types and between audio sampling periods in two consecutive breeding seasons. Overall, we show that the structural and floristic traits measured at our study site are not related to the detection of most avian species or to species richness.

Key words: Behaviour; boreal forest; conservation; habitat selection

Introduction

Avian community characteristics, such as species diversity and community composition, are influenced by several environmental factors. Changes in avian community composition, species abundance, and presence/absence patterns across a landscape have been correlated with aspects of the physical structure of the habitat, including foliage height diversity, mean tree height, stem density, and canopy cover (MacArthur *et al.* 1962; Lee and Rotenberry 2005; McElhinny *et al.* 2005; Lemaître *et al.* 2012), as well as with aspects of the community composition of vegetative species (i.e., floristics), including the richness and diversity of vegetative species (Gillespie and Walter 2001; Poulsen 2002; Lee and Rotenberry 2005) and the densities of particular tree species (Willson and Comet 1996; Thompson *et al.* 1999). These relationships are often complex and the direction of any correlation is often specific to an avian species, population, or foraging guild. Avian communities also are influenced by abiotic factors, such as local weather conditions. For example, interannual variation in avian abundance and community composition during the breeding season is related to variation in temperature and rainfall, which affects the distribution and availability of food, resources, and shelter across the landscape (Şekercioğlu *et al.* 2012; Zellweger *et al.* 2016; Grima *et al.* 2017; Bradley *et al.* 2022). It is therefore important to consider not only the relationship between habitat and avian communities, but also how the communities change over time and in relation to abiotic factors such as weather (Sparks *et al.* 2002).

Many bird-habitat relationships that incorporate physical structure and floristics of habitat are conducted at large spatial scales that include several environmental gradients throughout North America (MacArthur *et al.* 1962; Willson and Comet 1996; Thompson *et al.* 1999; Lee and Rotenberry 2005; Lemaître *et al.* 2012) and Europe (Poulsen 2002; Honkanen *et al.* 2010). Relatively few studies have investigated if the bird-habitat relationships observed at large-scales are consistent at the local or stand scale (Rotenberry 1985; Berg 1997; Seavy and Alexander 2011), or how local weather conditions might influence these relationships. The Boreal Shield Ecozone in Canada is an important breeding location for more than 240 North American bird species (Blancher and Wells 2005; Downes *et al.* 2011), yet most surveys in this ecozone have been conducted in southern Ontario and Quebec, with poor coverage outside these regions in areas such as Labrador (Downes *et al.* 2011). We used acoustic surveys to study bird-habitat relationships across two breeding seasons and multiple locations at a local scale in Labrador, Canada. Because each bird species produces a unique vocalization and vocalizes regularly throughout the breeding season, acoustic surveys can be a reliable method of determining which species are present at a given location (Blumstein *et al.* 2011; Shonfield and Bayne 2017). Compared to point counts that are conducted by human listeners and often last only minutes, acoustic surveys can record continuously for hours or days and thus detect species that vocalize infrequently or at unusual times, such as at night (e.g., owls) when human point counts are rarely conducted (Shonfield and Bayne 2017). A concern with acoustic surveys, however, is that multiple factors affect the range over which vocalizations can be heard, including weather, species, and an individual's behaviour (Hobson *et al.* 2002; Blumstein *et al.* 2011). Using a single audio recorder or human listener to conduct acoustic surveys can thus confound the probability of detecting a species with the audible range of that species' vocalizations. Microphone arrays resolve this issue because they allow researchers to localize vocalizing birds in two- or three-dimensional space and therefore to standardize the area sampled at each location (Stevenson *et al.* 2015; Pérez-Granados and Traba 2021). The method is tantamount to using a fixed-radius point count, but with the added benefit of allowing users to determine objectively if birds are located within the fixed radius of the sampling location (Stevenson *et al.* 2015; Pérez-Granados and Traba 2021). By surveying birds with microphone arrays, we correlated species richness and presence, as inferred through acoustic detection, with the physical structure and floristics of the habitat at each sampling location.

We had four objectives. First, we described the avian community of Labrador, an underrepresented portion of the boreal forest in avian ecological studies. Second, we determined the relationships between avian species richness and three environmental factors, including weather and the physical structure and floristics of the habitat. Consistent with previous studies, we hypothesized that local avian species richness would increase with greater diameter at breast height (DBH; McCarthy and Weetman 2006; Klein *et al.* 2020) and greater vegetative species richness (Gahbauer and Rashleigh 2021). We also hypothesized that avian species richness would increase at later dates in the breeding season and on warmer days (DesGranges and LeBlanc 2012). Third, we tested whether the detection of individual species was related to either the physical structure or floristics of a location. Based on previous findings in the boreal forest (Seavy and Alexander 2011; Lemaître *et al.* 2012; Ralston *et al.* 2019) and the expectation that each bird species differs in its food and shelter requirements (Johnson 1980), we hypothesized that any associations between habitat characteristics and if a species was detected would vary among species. Fourth, we compared the avian community composition between two consecutive breeding seasons and among three categorical forest types identified at the study site. Because many bird species show site fidelity to breeding locations (Schlossberg 2009), we predicted that the avian community composition would not be significantly different between breeding seasons unless a dramatic change such as a Spruce Budworm (*Choristoneura fumiferana*) infestation occurred between seasons. Conversely, we predicted that avian community composition would differ among forest types, because each type differs in physical structure and floristics.

Methods

Study area

Boreal forest bird communities are underrepresented in bird-habitat studies, and Labrador, Canada in particular is understudied (Lewis and Starzomski 2015). The current study focussed on an ~50 × 50 km area (250 000 ha; centred at 666550 m E, 5921190 m N, UTM Zone 20U [53.413°N, 60.494°W]) within the Lake Melville Ecoregion in Labrador, Canada (Riley *et al.* 2013; Figure 1). Houses and cottages are distributed sparsely throughout the entire area, but most of the human population is concentrated in the towns of Happy Valley-Goose Bay to the south, and North West River and Sheshatshiu to the north. This region is relatively unpopulated compared to other portions of Canada, with an estimated human population of 8040 in Happy Valley-Goose Bay as of the 2021 census (Statistics Canada 2022). The study area falls within the provincial Forest Management District 19A, which is ~2.27 million ha (Forsyth *et al.*

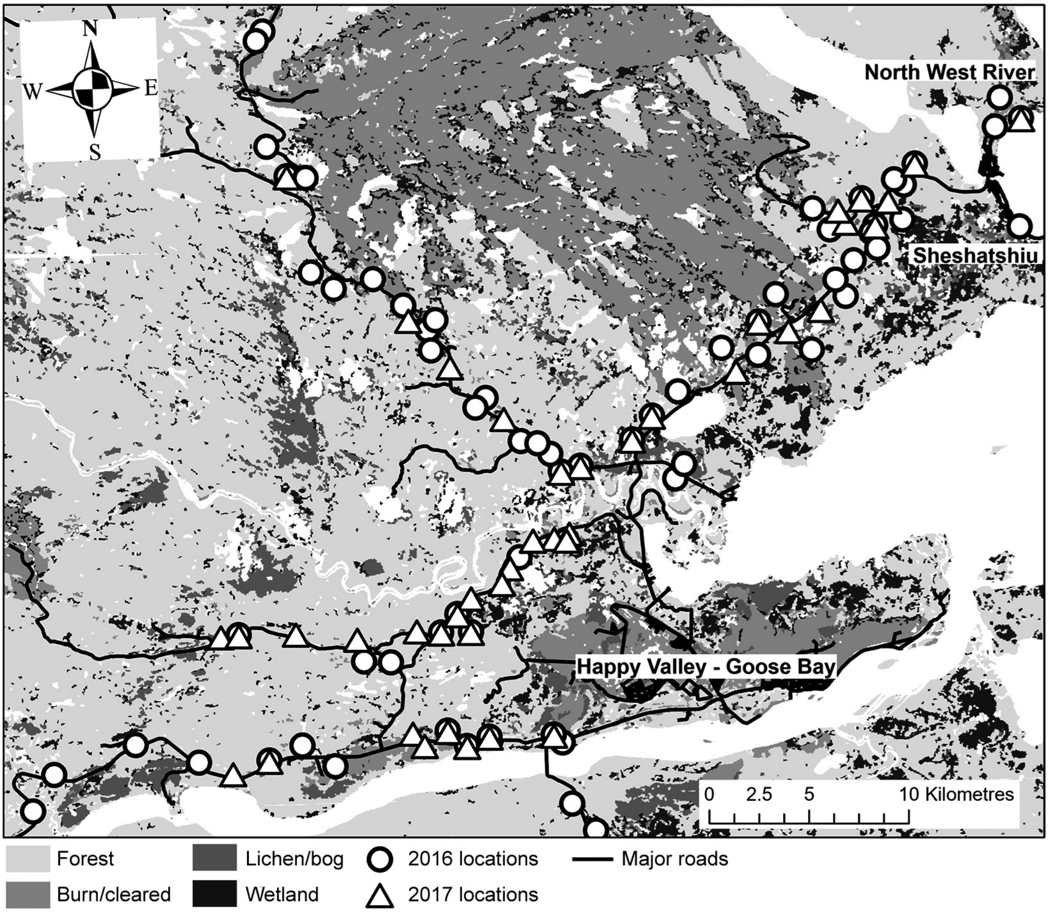

FIGURE 1. Map of locations sampled in District 19A in Labrador, Canada, where aspects of the avian community were compared to the physical structure and floristics of the habitat. Sites were sampled during the avian breeding season (May–July) in 2016 (*n* = 68) and 2017 (*n* = 42). Note: some points overlap because 20 locations from 2016 were resampled in 2017. The large area identified as "Burn/cleared" represents the 1985 wildfire that destroyed 340 km^2 of forest. Base map and 2017 land cover dataset (10 m resolution) provided by Impact Observatory and ESRI (Karra *et al.* 2020).

2003), or ~0.4% of the 552 million ha boreal forest in Canada. The area has a history of forest harvesting and other disturbances, including natural wildfire, drought, and disease. The most recent large-scale burns occurred in 1972, 1985, and 1994 (Simon and Schwab 2005). Most notably, a large portion of the study area (~34 000 ha or 13.6%) was burned by wildfire in 1985 (Notzl *et al.* 2013). During the same years, several portions of the forest were clearcut (Simon and Schwab 2005).

Forest stands in the area are dominated by Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh) and Balsam Fir (*Abies balsamea* (L.) Miller). Other species in the upper canopy, in order of decreasing prevalence within study locations, are Tamarack (*Larix laricina* (Du Roi) K. Koch), White Birch (*Betula papyrifera* Marshall), Heart-leaved Birch (*Betula cordifolia* Regel), and Trembling Aspen (*Populus tremuloides* Michaux). The woody vegetation in the understorey includes Speckled Alder (*Alnus incana* (Du Roi) R.T. Clausen), American Mountain-ash (*Sorbus americana* Marshall), Squashberry (*Viburnum edule* (Michaux) Rafinesque), willow (*Salix* spp.), serviceberry (*Amelanchier* spp.), and Skunk Currant (*Ribes glandulosum* Grauer). The most common ericaceous species in the understorey are Labrador Tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd), Sheep Laurel (*Kalmia angustifolia* L.), Swamp Laurel (*Kalmia polifolia* Wangenheim), and Leatherleaf (*Chamaedaphne calyculata*

(L.) Moench). Vegetation layers below the canopy layer were largely homogenous, with all stands being dominated by lichen in the ground cover layer, Labrador Tea in the herbaceous layer, and Speckled Alder in the shrub/understorey layer.

Microphone arrays

Between 16 May and 10 July of the 2016 avian breeding season, we deployed microphone arrays at 68 locations for a minimum of 24 h each. During the 2017 avian breeding season, we deployed microphone arrays between 17 May and 30 June at 42 locations, including 22 new locations and 20 locations sampled during 2016 to allow for analyses of temporal species similarity. All locations that were resampled in 2017 were sampled within three days of the year of when they were sampled in 2016. We chose to conduct our study over this wide range of dates to maximize our sample size and to capture the breeding seasons and periods of peak vocal activity of diverse avian species. In some species, such as Ruby-crowned Kinglet (*Regulus calendula*), vocal activity peaks as early as mid-May and decays precipitously thereafter (Fahmy and Wilson 2020). In other species, such as Swainson's Thrush (*Catharus ustulatus*) and Tennessee Warbler (*Leiothlypis peregrina*), individuals do not even arrive at our study site until mid-June (e-bird [ebird.org] checklist data for the Happy Valley-Goose Bay area). There are no known publications on arrival dates in these remote regions; however, several experts of the Newfoundland and Labrador birding community based in Happy Valley-Goose Bay regularly post to eBird.

Array locations were selected at random, but with the constraints that they were within 1 km of road access (either a two-lane highway or a gravel road) and a minimum distance of 500 m from each other. We chose a maximum distance from road access of 1 km because hiking beyond this distance through dense forest while carrying a microphone array would have been difficult and would have reduced our sample size. We chose to separate array locations by a minimum of 500 m because this reduced the risk of detecting the same birds at multiple locations (Wilson and Mennill 2011). Global positioning system (GPS) coordinates for locations were generated using a random integer set generator that creates non-repeating integers within confined boundaries (RANDOM.org). These random coordinates were then plotted on 1:50 000 scale topographic maps (National Topographic System, Series A771, Edition 4 MCE, Map 13 F/7 – 13 F/10) and discarded if they violated the inclusion criteria or were within a delineated swamp, bog, or water body based on provincial forest inventory maps. We chose to randomly select locations to sample rather than intentionally sample locations of high species richness identified by previous researchers and birders. Random sampling produces unbiased estimates of the probability of detecting a given species at a given location, which can then be used in future research to model species richness and species occupancy throughout the general study area. We navigated to array locations using a survey-grade global navigation satellite systems (GNSS) unit with 10 cm accuracy (model: Geo7X; Trimble, Sunnyvale, California, USA).

Each array was left recording for 24 h, beginning two hours after setup to minimize potential disturbance effects associated with setup. An array consisted of four autonomous recorders (SongMeter 3; Wildlife Acoustics, Concord, Massachusetts, USA) placed at the corners of an ~40 m × 40 m square that was centred on a predetermined array location. Each recorder had two channels: one built-in omnidirectional microphone (frequency response: 20–20 000 Hz ± 10 dB) was positioned ~1 m above the ground, and a second external omnidirectional microphone (model: SMM-A2; frequency response: 20–20 000 Hz ± 10 dB; Wildlife Acoustics, Concord, Massachusetts, USA) was positioned in the understorey or lower canopy ~2–3 m above the first. All microphones were pointed towards the centre of the array, and their exact positions were determined with the survey-grade GNSS described above. Each recorder was programmed to record continuously and to produce a new stereo audio file every two hours (WAVE format, 24 kHz sampling rate, 16 bit amplitude encoding). In 2016, we had enough recorders to construct two arrays per day (i.e., eight recorders). We therefore deployed these arrays at two of our randomly determined locations, left them to record for at least 24 h, then redeployed them at two different locations the next day. Given the logistical challenges of accessing many of our array locations, the two arrays deployed on the same day were deployed at locations that were within a few kilometers of each other (1–4 km). In 2017, we only had enough recorders to construct one array per day (i.e., four recorders).

We recorded weather variables by placing a portable weather station (Kestrel 5500; Kestrel Instruments, Boothwyn, Pennsylvania, USA) 0.5–1.0 m above the ground in the middle of every second array during 2016 and at every array during 2017. Arrays were always deployed in pairs within a few kilometers (1–4 km) of each other during 2016, so weather conditions should have been sufficiently similar between the locations to justify obtaining weather data from only one of them. The weather station provided data at 20 min intervals throughout the 24 h recording period, including temperature (± 0.1°C), wind speed (± 0.1 km/h), relative humidity

(± 0.1%), and barometric pressure (± 0.1 mb). Temperature, in particular, affects the speed of sound and was required for the sound localization process. Wind can also affect the signal-to-noise ratio of audio recordings and thus the probability of detecting distant signals. However, wind speed, as measured with the portable weather stations, was always low (mean ± SD = 0.7 ± 1.0 km/h; range 0.0–4.6 km/h) and thus was not considered further. We note, however, that wind speeds in and above the canopy were likely higher than those measured at ground-level by our portable weather stations. We therefore obtained hourly wind speeds measured throughout the 24 h recording period by Environment and Climate Change Canada (ECCC) in an open environment at the nearby Canadian Forces Base in Goose Bay (671845 m E, 5910973 m N, UTM Zone 20U [53.320°N, 60.420°W]; elevation 49 m), and used these in all subsequent analyses. The Canadian Forces Base in Goose Bay was a mean (± SD) distance of 17.3 ± 8.1 km from array locations. Because precipitation can affect avian vocal activity and the signal-to-noise ratio on recordings, we obtained precipitation data for Happy Valley-Goose Bay, Labrador from ECCC. If the first 24 h of recording included more than 10 mm of rain, we left the array recording until at least 24 h after the rainfall had decreased to below the threshold, and then used only the audio recordings from the final 24 h period in subsequent acoustic analyses. Only 23 arrays had any precipitation during their recording period and the mean (± SD) rainfall among them was only 2.8 ± 2.0 mm over 24 h (range 0.6–8.4 mm). We therefore did not consider precipitation in subsequent analyses.

General habitat characterization

The general habitat was characterized at each array by assessing vegetation cover at five standardized habitat sampling points, including midway between each pair of recorders and in the centre of the array. At each point, we measured canopy cover (%) with a spherical densiometer held pointing north. We determined stem density by holding a 2 m pole horizontally by one end at breast height (1.4 m) and then counting the number of trees touched by the pole while making a full rotation (i.e., a circle with a radius of 2 m; Avery and Burkhart 2015). The standard definition of a tree in monitoring protocols is any woody species with a height exceeding 2 m and a diameter at breast height (DBH) exceeding 4 cm (EMAN 2004). However, with several locations being dominated by wetlands with stunted tree growth, we defined a "tree" as any woody species with a minimum height of 1.5 m and a minimum DBH of 1 cm. The number of trees was divided by the area of the circle (12.57 m^2) to determine stem density in trees/m^2 (Avery and Burkhart 2015). Using a standard diameter tape, we measured the DBH of the three trees nearest to the sampling point. We determined vegetative species richness within the array by recording the total number of species of trees, shrubs, and ericaceous plants encountered within 1 m of the observer while walking slowly along the perimeter of the array, then from the SW corner to the NE corner of the array, and then from the NW corner to the SE corner of the array (~1 h of effort). We found that the ground layer among arrays was consistently a combination of *Sphagnum* moss and lichen, and thus omitted it from further consideration. Using the data from the five habitat sampling points, we calculated the mean value/array for stem density and canopy cover and the maximum value/array for DBH. We calculated maximum DBH instead of mean DBH because we expected that the presence of birds would be influenced more by a few large trees than by many trees of average size (Kebrle *et al.* 2021).

Although all locations were dominated by Black Spruce and Balsam Fir, we identified three distinct forest types within the general coniferous forest habitat type on the basis of species that were secondarily dominant. Although we did not quantify the prevalence of each tree species, these three forest types appeared to us to be discrete in nature. The "spruce/fir type" contained only Black Spruce and Balsam Fir in the canopy layer, or also contained a smaller portion (we estimate ≤20% of stems) of Jack Pine (*Pinus banksiana* Lambert). The "birch/poplar type" was distinguished by the secondary prominence (we estimate 5–50% of stems) of birch and/or poplar species in the canopy layer. The "tamarack type" was distinguished by secondary prominence (we estimate 5–50% of stems) of Tamarack in the canopy layer and greater ericaceous plant species richness.

Acoustic analysis

We used Kaleidoscope software (Version 4.3.2, Wildlife Acoustics, Maynard, Massachusettes, USA, https://www.wildlifeacoustics.com) to automatically detect avian vocalizations and to group them into clusters of similar sounds. The settings used in the program included: maximum distance from the cluster centre = 2.0, fast-Fourier transform size = 256 points (5.33 ms), maximum number of states = 12, maximum distance to cluster centre for building clusters = 0.5, and maximum clusters created = 500. These settings ensure that all detections are assigned to a cluster. The clusters approximate species, but, sometimes, multiple clusters were associated with a single species. We therefore inspected sample detections from each cluster and manually renamed clusters according to the species they represented. Species identities were determined by listening to recordings of vocalizations and reviewing their associated spectrograms and comparing these to the species accounts on the Birds of North America (Rodewald 2015), Xeno-Canto (www.xeno-canto.org), and Macaulay Library (https://www.macaulaylibrary.org) websites. Detected vocalizations were localized using a custom MATLAB program (details of the localization algorithm are in Ethier and Wilson 2019; Hennigar *et al.* 2019; Fahmy and Wilson 2020). The program uses waveform cross-correlation to measure the latencies of when a vocalization reaches each microphone in the array, relative to when that same vocalization reaches the closest microphone in the array (speed of sound through air is approximately 343 m/s). Separate sets of theoretical latencies are then calculated for all possible origins in the array and the origin that produces theoretical latencies closest to the observed latencies is selected as the most likely origin of the vocalization. The program produces UTM coordinates in two- and three-dimensions, and a localization error value that reflects the certainty of the estimated location.

We applied several exclusion criteria to the initial vocalization dataset. Previous studies (e.g., Mennill *et al.* 2012; Wilson *et al.* 2014) demonstrated that localization becomes less reliable when analysing sounds produced outside the array. Additionally, we wanted to limit the sampling area to that which was assessed for general habitat characteristics and to an area that was small enough to ensure that quieter species would still be within the detection range of the microphones. Using the "rgeos" package (Bivand and Rundel 2017) in R (Version 3.0.1; R Core Team 2017), we created a 2-dimensional spatial polygon of the array based on the UTM coordinates of the array microphones. We then determined the minimum distance of each localized vocalization from the edge of the polygon (0 m if inside the polygon). The list of vocalizations was reduced to include only those that originated from inside the microphone array or from within 5 m of its edge. This filtering step reduced the number of vocalizations considered for statistical analysis by ~60%, from 4 879 624 to 1 928 312 vocalizations. This reduction is substantial, but not surprising. Based on localization estimates in our study, and on previous research (e.g., Dawson and Efford 2009), microphones can detect some birds that are up to 90 m away. Therefore, the vast majority of the active "listening" space of the array fell outside the target area.

We further reduced the vocalization dataset to include only those vocalizations that occurred during the targetted 24 h period of the recordings and that had a localization error value of 0.02 or less, which reduced the dataset from 1 928 312 to 470 761 vocalizations (i.e., to 10% of the original). We considered these localizations to be accurate because, based on a "ground-truthing" speaker playback experiment, 90% of vocalizations with an error value ≤0.02 are within 3.55 m of their true locations (Ethier 2018). This error value strikes a balance between including vocalizations that are localized with a relatively high accuracy and retaining a large enough dataset that still reflects the local avian community. Next, although the localization procedure relies on vocalizations being detected in multiple channels, it is necessary to remove duplicate detections when counting the number of vocalizations produced. Whenever the same species was detected in multiple channels within 250 ms of each other, we retained only the first instance of the vocalization. This reduced the dataset from 470 761 to 89 242 unique vocalizations (i.e., to 2% of the original). Finally, we excluded vocalizations produced by non-target sources, such as Red Squirrel (*Tamiasciurus hudsonicus*) and humans, which reduced the dataset from 89 242 to 49 155 vocalizations (i.e., to 1% of the original). The remaining 49 155 vocalizations were manually reviewed in Kaleidoscope using visual scanning and by listening to audio clips to confirm species identity. This step was important because vocalizations from the same species were sometimes incorrectly assigned by the software to other species.

Statistical analysis

All statistical analyses were performed in R (Version 4.2.1; R Core Team, Boston, Massachusetts, USA). For all analyses, data from the 2016 and 2017 breeding seasons were combined. After applying the exclusion criteria described above, two array locations from the 2017 breeding season yielded no detections, and thus were removed from analysis. For locations that were sampled in both years, only data from 2017 were included in statistical models, to yield a similar number of samples from each year (2016 = 48 locations, 2017 = 40 locations). All descriptive statistics are mean ± (SD), unless stated otherwise. Taxonomy follows the American Ornithological Society's checklist (Chesser *et al.* 2021; Table 1). We provide our R script (R script 1) and two data files (Data file 1 and Data file 2) as supplemental material.

Species richness—Species richness was the total number of species detected at a location during the 24 h sampling period. First, we used a general linear model (GLM) to determine if species richness was related to habitat characteristics and abiotic factors. Predictor variables were three physical structure variables: mean canopy cover (%), mean stem density (stems/m^2), and maximum DBH (cm); two floristic variables: vegetative species richness and forest type; and three abiotic variables: mean daily temperature, day within year, and mean daily wind speed. For

TABLE 1. Family, scientific name, common name, and nomenclature authority of avian species detected in Labrador, Canada. Taxonomy follows the American Ornithological Society's checklist (Chesser *et al.* 2021).

Family	Scientific name	Common name	Authority
Anatidae	*Branta canadensis*	Canada Goose	Linnaeus, 1758
Scolopacidae	*Gallinago delicata*	Wilson's Snipe*	Ord, 1825
Gaviidae	*Gavia immer*	Common Loon	Brünnich, 1764
Caprimulgidae	*Chordeiles minor*	Common Nighthawk	Forster JR, 1771
Picidae		Woodpecker sp.*†	
Tyrannidae	*Empidonax flaviventri*	Yellow-bellied Flycatcher	Baird and Baird, 1843
Vireonidae	*Empidonax alnorum*	Alder Flycatcher	Brewster, 1895
Corvidae	*Vireo philadelphicus*	Philadelphia Vireo*	Cassin, 1851
	Perisoreus canadensis	Canada Jay	Linnaeus, 1766
	Corvus brachyrhynchos	American Crow	Brehm, 1822
	Corvus corax	Common Raven	Linnaeus, 1758
Paridae	*Poecile hudsonicus*	Boreal Chickadee	Forster JR, 1772
Regulidae	*Regulus calendula*	Ruby-crowned Kinglet	Linnaeus, 1766
	Regulus satrapa	Golden-crowned Kinglet*	Lichtenstein MHC, 1823
Bombycillidae	*Bombycilla garrulus*	Bohemian Waxwing	Linnaeus, 1758
Sittidae	*Sitta canadensis*	Red-breasted Nuthatch	Linnaeus, 1766
Certhiidae	*Certhia americana*	Brown Creeper	Bonaparte, 1838
Troglodytidae	*Troglodytes hiemalis*	Winter Wren	Vieillot, 1819
Turdidae	*Catharus ustulatus*	Swainson's Thrush	Nuttall, 1840
	Catharus guttatus	Hermit Thrush	Pallas, 1811
	Turdus migratorius	American Robin	Linnaeus, 1766
Fringillidae	*Pinicola enucleator*	Pine Grosbeak	Linnaeus, 1758
	Acanthis flammea	Common Redpoll*	Linnaeus, 1758
	Spinus pinus	Pine Siskin	Wilson A, 1810
Passerellidae	*Passerella iliaca*	Fox Sparrow	Merrem, 1786
	Junco hyemalis	Dark-eyed Junco	Linnaeus, 1758
	Melospiza lincolnii	Lincoln's Sparrow	Audubon, 1834
	Zonotrichia leucophrys	White-crowned Sparrow*	Forster JR, 1772
	Zonotrichia albicollis	White-throated Sparrow	Gmelin JF, 1789
Parulidae	*Parkesia novaboracensis*	Northern Waterthrush	Gmelin JF, 1789
	Leiothlypis peregrina	Tennessee Warbler	Wilson, 1811
	Oreothlypis celata	Orange-crowned Warbler	Say, 1822
	Setophaga ruticilla	American Redstart	Linnaeus, 1758
	Setophaga tigrina	Cape May Warbler	Gmelin JF, 1789
	Setophaga magnolia	Magnolia Warbler	Wilson A, 1811
	Setophaga striata	Blackpoll Warbler	Forster JR, 1772
	Setophaga palmarum	Palm Warbler*	Gmelin JF, 1789
	Setophaga coronata	Yellow-rumped Warbler	Townsend, 1837
	Setophaga virens	Black-throated Green Warbler	Gmelin JF, 1789
	Cardellina pusilla	Wilson's Warbler*	Wilson A, 1811

*Detected by one or more audio recorders but fell outside the boundary of the microphone array(s) and thus was not included in formal analyses.
†Species identity could not be determined with certainty.

each location, mean daily temperature was calculated by averaging values recorded by the portable weather station at 20 min intervals across the 24 h recording session; mean daily wind speed was calculated by averaging hourly measurements from the weather station at Goose Bay for the same period. The statistical significance of individual predictor variables and the statistical significance and adjusted R^2 of the overall model were assessed using the summary function in base R. Variance inflation factors (VIF) >5 indicate potential problems associated with collinearity (Quinn and Keough 2002); our greatest VIF was 2.73, so all variables remained in the model. Second, we calculated the intraclass correlation coefficient (ICC) to test if species richness was repeatable between the 2016 and 2017 breeding seasons across the 20 locations that were sampled in both years (Wolak *et al.* 2012; Koo and Li 2016). The ICC was calculated with a 95% CI in the R package "irr" using a two-way consistency type model (Gamer *et al.* 2019).

Species-specific detection—We used GLM (family = binomial, link = logit) to test for relationships between habitat characteristics, abiotic factors, and the presence/absence of each species that was detected in at least 10% of the array locations (i.e., ≥9/88 locations) to have sufficient sample size for statistical analysis. As predictor variables, we included three physical structure variables (mean canopy cover, mean stem density, and maximum DBH), two floristic variables (vegetative species richness and forest type), and three abiotic factors (mean daily temperature, day of the year, and mean daily wind speed). The statistical significance of individual predictor variables was assessed using the "summary" function of base R, and *post-hoc* pairwise comparisons between forest types were conducted using a Tukey procedure in the "multcomp" package (Hothorn *et al.* 2008). Regression coefficients were calculated using the "summary" function in base R, adjusted odds ratios and their 95% CI were estimated using the "logistic.display" function in the "epiDisplay" package (Chongsuvivatwong 2022), and pseudo R^2 was calculated according to McFadden (1974) in the "pscl" package (Jackman 2020).

Spatial and temporal consistency in avian community composition—We used the Sorensen index (C_S), which is widely used in pairwise comparisons (Sorensen 1948; Southwood and Henderson 2000; Lennon *et al.* 2001; Magurran 2004) to compare the avian community composition in a given location from one forest type to the avian community composition in a given location from another forest type (spatial species similarity). We limited this analysis to species that were detected in at least 10% of the array locations (i.e., ≥9/88 locations). The index is defined as:

$$C_S = \frac{2a}{2a + b + c}$$

where a is the number species found at both locations, b is the number of species found at the first location and not the second, and c is the number of species found at the second location but not the first. C_S values near one indicate that the two locations are very similar in community composition, whereas C_S values near zero indicate that the two locations are very different. To compare the average similarities in avian community composition among the birch/poplar, spruce/fir, and Tamarack forest types, we calculated C_S between all possible combinations of array locations for each pair of forest types. For example, we compared each of the 34 locations of the birch/poplar type to each of the 24 locations of the Tamarack type, which resulted in 816 C_S values. We then calculated the mean of these C_S values to quantify the average (± SD) similarity for the two forest types. We also calculated the average (± SD) *Cs* between all possible pairwise combinations of array locations within a given forest type as a way of assessing if avian community composition differed more between forest types than within forest types. Rather than using a different index, we adjusted the variables of the Sorensen index to calculate temporal species similarity (C_t) for each of the 20 arrays that were deployed in the same locations in both 2016 and 2017. Temporal species similarity at a given location was defined as the proportion of species that were detected at the location at both time points (Magurran 2004):

$$C_t = \frac{2a}{2a + b + c}$$

where a = number of species found at both points in time, b = number of species at time point 1 but not time point 2, and c = number of species at time point 2 but not time point 1. C_t was calculated separately for each of the 20 array locations sampled in both 2016 and 2017, and then averaged among the 20 locations. Again, we limited this analysis to species that were detected in at least 10% of the array locations (i.e., ≥9/88 locations) to have sufficient sample size for statistical analysis.

Results

Based on the 49 155 detections composing our final dataset, we detected 32 species across the 88 microphone array locations (Table 1, Figure 1). The three most common species, as determined by the proportion of locations in which they were detected, were Ruby-crowned Kinglet, Dark-eyed Junco (*Junco hyemalis*), and Yellow-rumped Warbler (*Setophaga coronata*; Figure 2). Most species (26/32, or 81%) were detected at fewer than half of the locations. Common Nighthawk (*Chordeiles minor*) was detected at a single location and is the only federally or provincially listed species-at-risk (SARA Public Registry 2023; https://www.gov.nl.ca/ffa/wildlife/endangeredspecies/birds) we detected. Although not considered forest birds, Canada Goose (*Branta canadensis*) and Common Loon (*Gavia immer*) were

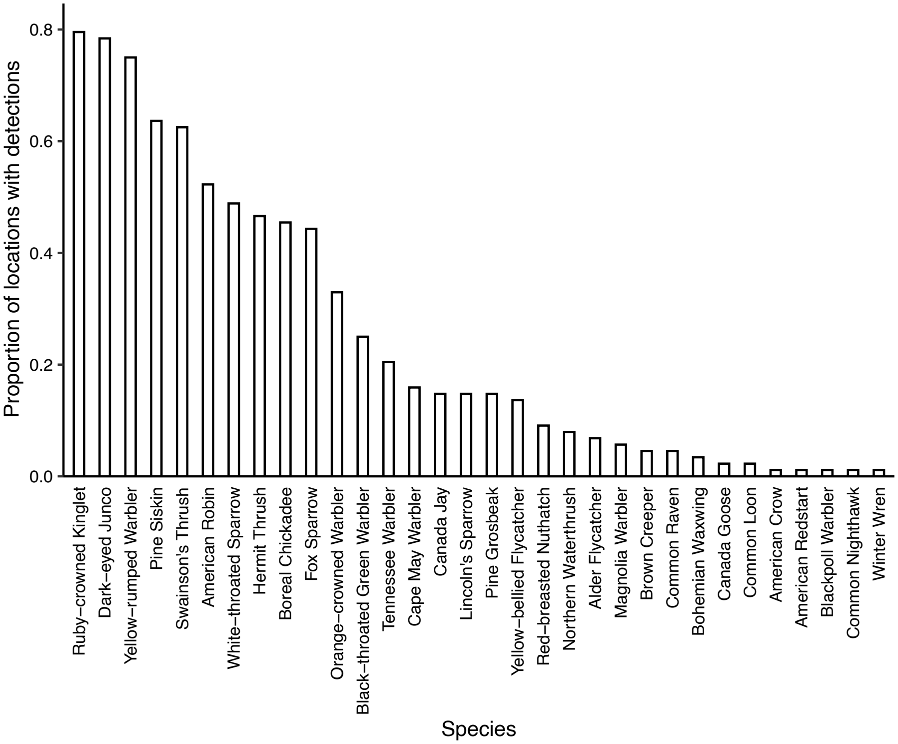

Figure 2. The proportion of 88 locations sampled in Labrador, Canada where bird species were detected. Locations were sampled during the 2016 (n = 48) and 2017 (n = 40) avian breeding seasons. See Table 1 for common name, scientific name, and nomenclature authority for listed species.

detected at two locations that included a small pond/lake edge within the boundaries of the array. Finally, we note that our recorders detected 40 species during the 2016 and 2017 breeding seasons, but that eight species did not meet our inclusion criteria and were thus excluded from statistical analyses. We include those eight species in Table 1 to provide a more comprehensive description of the species present at our overall study site.

Among the 88 microphone array locations, we detected an average (± SD) of 8.0 ± 3.3 avian species/location (range 1–17). The locations had an average mean canopy cover of 48.1 ± 23.9% (0.2–91.5%), average mean stem density of 0.8 ± 0.4 trees/m^2 (0.0–2.3 trees/m^2), average maximum DBH of 13.2 ± 7.3 cm (1.0–41.0 cm), and an average vegetative species richness of 4.8 ± 1.4 species (2–10 species). On average, arrays were set up 160.1 ± 14.0 days after the start of the year (136–188 days). The average mean daily temperature was 10.0 ± 4.6°C (0.9–20.7°C) and the average mean daily wind speed was 15.6 ± 5.4 km/h (6.2–35.2 km/h).

Species richness

Avian species richness was predicted by the model containing habitat characteristics, including mean canopy cover, mean stem density, maximum DBH, vegetative species richness, and forest type, and abiotic factors, including mean daily temperature, day of the year, and mean daily wind speed ($F_{9,78}$ = 3.31, P = 0.002, adjusted R^2 = 0.19; Table 2). However, the only significant variables in the model were mean daily temperature and mean daily wind speed (Figure 3). On average, species richness (model coefficient ± SE) increased by 0.2 ± 0.1 species/1°C increase in temperature and decreased by 0.1 ± 0.1 species/1 km/h increase in wind speed (Table 2, Figure 3).

Species richness was compared among 20 locations sampled in both 2016 and 2017 (Table S1). Among those 20 locations, avian species richness was 9.1 ± 2.3 species (range 5–14 species) in 2016, and 6.5 ± 3.7 species (range 0–15) in 2017. Species richness among locations was moderately consistent between years, with an intraclass correlation coefficient of 0.559 (95% CI of ICC = 0.17–0.80; $F_{19,19}$ = 3.53, P = 0.004; Table S1).

Species-specific detection

We tested the relationship between the detection of a given species at a location and the habitat

TABLE 2. Summary of the general linear model of avian species richness regressed against mean canopy cover (%), mean stem density (trees/m^2), maximum diameter at breast height (DBH [cm]), vegetation species richness, forest type (spruce/fir, birch/poplar, Tamarack), mean daily temperature (°C), day of the year, and mean daily wind speed (km/h) across 88 locations in Labrador, Canada during the 2016 and 2017 avian breeding seasons. Statistically significant ($\alpha = 0.05$) variables are shown in bold. The reference level for forest type is "birch/poplar".

Variable	Coefficient	SE	*t* value	*P*-value
Intercept	4.26	4.69	0.91	0.367
Mean canopy cover	−0.03	0.02	−1.27	0.209
Mean stem density	1.45	1.05	1.39	0.169
Max DBH	0.07	0.06	1.07	0.289
Vegetation species richness	0.06	0.28	0.22	0.827
Mean daily temperature	**0.20**	**0.10**	**2.10**	**0.039**
Day of the year	0.02	0.03	0.74	0.464
Wind speed	**−0.14**	**0.06**	**−2.37**	**0.020**
Forest type (birch/poplar)				
Tamarack	−1.30	0.90	−1.45	0.152
Spruce/fir	−1.57	0.85	−1.84	0.069
Overall model: $F_{9,78} = 3.31$, $P = 0.002$, adjusted $R^2 = 0.19$.				

characteristics and abiotic factors at that location for the 18 species that occurred in at least 10% of locations (Table 3). General habitat characteristics were significantly associated with species detection for 4/18 species (22%). Boreal Chickadee (*Poecile hudsonicus*) was more likely to be detected at array locations with greater stem density (adjusted odds ratio [OR] and 95% CI = 6.01 [1.03–34.97]) and Yellow-rumped Warbler was more likely to be detected at locations with larger diameter trees (OR = 1.27 [1.05–1.53]) and less canopy cover (OR = 0.95 [0.91–1.00]; Table 3). American Robin (*Turdus migratorius*) was less likely to be detected in the spruce/fir forest type than in the birch/poplar forest type (OR = 0.13 [0.04–0.48]), and Black-throated Green Warbler (*Setophaga virens*) was less likely to be detected in either the spruce/fir (OR = 0.06 [0.01–0.40]) or Tamarack forest types (OR = 0.05 [0.01–0.49]) than in the birch/poplar forest type (Table 3, Table S2). Abiotic factors were significantly associated with species detection for 9/18 species (50%; Table 3). Warmer days were associated with a greater probability of detecting Boreal Chickadee (OR = 1.25 [1.06–1.48]), Ruby-crowned Kinglet (OR = 1.28 [1.021.59]), Pine Siskin (*Spinus pinus*, OR = 1.23 [1.03–1.48]), Orange-crowned Warbler (*Oreothlypis celata*, OR = 1.22 [1.04–1.45]), and Yellow-rumped Warbler (OR = 1.45 [1.10–1.91]), whereas cooler days were associated with a greater probability of detecting Pine Grosbeak (*Pinicola enucleator*, OR = 0.72 [0.54–0.97]; Table 3). Boreal Chickadee and Ruby-crowned Kinglet were more likely to be detected earlier in the season (Boreal Chickadee, OR = 0.90 [0.85–0.96]; Ruby-crowned Kinglet, OR = 0.91 [0.85–0.98]), whereas Swainson's Thrush (OR = 1.08 [1.02–1.14]) and Tennessee Warbler (OR = 1.10 [1.03–1.18]) were more likely to be detected later in the season (Table 3). Lincoln's Sparrow (*Melospiza lincolnii*, OR = 0.80 [0.65–0.97]) and Tennessee Warbler (OR = 0.84 [0.72–0.98]) were less likely to be detected on windier days.

Spatial and temporal consistency in avian community composition

Based on the 18 species that were detected in at least 10% of locations, we found that avian community composition was moderately consistent among the three forest types: birch/poplar and Tamarack: mean $C_S = 0.496 \pm 0.183$, birch/poplar and spruce/fir: mean $C_S = 0.487 \pm 0.203$, Tamarack and spruce/fir: mean $C_S = 0.495 \pm 0.192$. The degree of similarity in avian community composition among the three forest types is comparable (within 1 SD) to the degree of similarity in avian community composition among locations within forest types (birch/poplar: mean $C_S = 0.534 \pm 0.209$, spruce/fir: mean $C_S = 0.485 \pm 0.208$, Tamarack: mean $C_S = 0.556 \pm 0.184$). These values indicate a moderate level of similarity within and among forest types, with ~50% of species being found in both forest types on average in pairwise comparisons. Avian community composition was also moderately consistent between 2016 and 2017 (mean ± $C_t = 0.543 \pm 0.244$; range 0.000–0.889; Table S1), with the community composition ranging among locations from very similar between years to complete species replacement. The temporal species similarity at a given site was not related to the day of

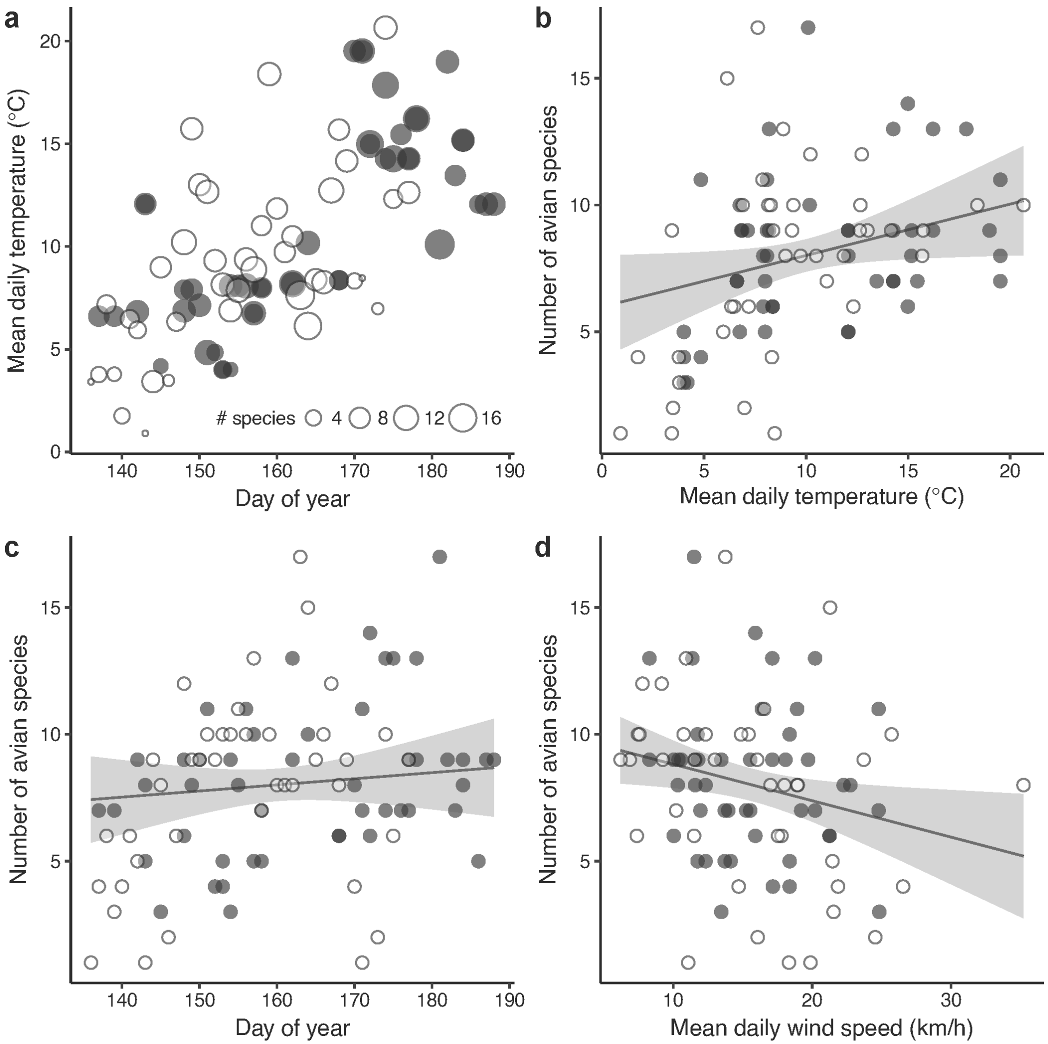

FIGURE 3. Abiotic predictors of avian species richness. Mean daily temperature and day of the year were positively correlated with each other (a) but mean daily temperature (b) was also correlated with the number of avian species detected on a given day, whereas day of the year (c) was not. The number of avian species detected was negatively associated with mean daily wind speed (d). Data points represent 24 h recording periods at 88 array locations in 2016 (filled circles, $n = 48$) or 2017 (open circles, $n = 40$) in Labrador Canada. The number of avian species detected during the 24-hour recording period are depicted by the size of the data points in a and on the y-axis in b–d. Regression lines and their 95% CI (grey shading) are based on estimated marginal means derived from the statistical model described in the text.

the year when the site was sampled (linear regression: $F_{1,18} = 0.27$, $P = 0.608$, $R^2 = 0.01$).

Discussion

Species richness

Several studies have shown a relationship between avian species richness at different sampling locations within a single forested habitat type and the DBH, stem density, and canopy cover at those locations (i.e., Berg 1997; Warren *et al.* 2005; Deppe and Rotenberry 2008; Lemaître *et al.* 2012). However, those studies were conducted in more heterogeneous habitats and across larger spatial extents (i.e., ≥100 × 100 km). At the smaller spatial scale used in our study (50 × 50 km or 250 000 ha), DBH, tree height, and stem density were not significantly associated with avian species richness, which is consistent with previous studies that found that physical structure characteristics better explain differences in avian assemblages

TABLE 3. Regression coefficients and pseudo R^2 of logistic regression models comparing presence/absence versus habitat characteristics and abiotic factors for 18 bird species across 88 locations in Labrador, Canada during the 2016 and 2017 avian breeding seasons. Coefficients represent the change, per one-unit increase in the predictor variable, in the log odds of the species being present (versus absent). Only those species that were present in at least 10% of the locations (i.e., ≥9/88 sites) were analysed. Pseudo R^2 was calculated using McFadden (1974). Coefficients of statistically significant continuous predictors are in bold ($\alpha = 0.05$). For the categorical variable forest type, only statistically significant pairwise comparisons are shown (e.g., BIR>TAM indicates that the probability of a species being present is higher in the birch/poplar compared to the Tamarack forest type). Order of species reflects taxonomy according to the American Ornithological Society's checklist (Chesser *et al.* 2021).

Species	Intercept	Mean canopy cover	Mean stem density	Max DBH	Vegetative species richness	Mean temp	Day of year	Wind speed	Forest type*	Pseudo R^2
Yellow-bellied Flycatcher	−11.75	−0.01	0.11	0.01	0.25	0.08	0.05	0.06	·	0.23
Canada Jay	**−10.79**	−0.03	1.61	0.04	0.01	0.03	0.05	0.01	·	0.17
Boreal Chickadee	**12.99**	−0.01	**1.79**	0.04	−0.09	**0.23**	**−0.10**	0.02	·	0.22
Ruby-crowned Kinglet	**14.40**	0.01	0.08	0.09	−0.17	**0.24**	**−0.09**	−0.04	·	0.21
Swainson's Thrush	**−11.43**	−0.01	1.10	0.04	−0.01	0.05	**0.07**	−0.04	·	0.23
Hermit Thrush	3.23	−0.03	1.30	−0.03	−0.14	0.09	−0.02	−0.02	·	0.12
American Robin	8.58	−0.01	−1.12	−0.04	−0.21	0.08	−0.03	−0.09	**BIR > SPF**	0.16
Pine Grosbeak	−11.63	0.03	0.28	−0.03	0.37	**−0.33**	0.07	−0.10	·	0.15
Pine Siskin	−4.86	0.00	1.38	0.03	−0.16	**0.21**	0.02	−0.04	·	0.21
Fox Sparrow	1.57	−0.01	1.04	0.02	0.02	0.05	−0.01	−0.08	·	0.07
Dark-eyed Junco	−3.27	−0.01	−0.43	−0.03	0.15	0.19	0.02	−0.03	·	0.18
Lincoln's Sparrow	2.38	0.02	−2.78	−0.20	0.12	0.05	0.01	**−0.23**	·	0.31
White-throated Sparrow	−3.17	−0.03	−0.52	−0.04	−0.08	0.01	0.03	0.00	.	0.21
Tennessee Warbler	**−15.20**	0.02	0.01	0.00	0.12	−0.04	0.09	**−0.17**	·	0.28
Orange-crowned Warbler	1.88	−0.01	−1.61	−0.01	0.23	0.20	−0.03	−0.02	.	0.25
Cape May Warbler	1.15	0.04	1.06	−0.09	−0.25	−0.04	−0.01	−0.03	.	0.29
Yellow-rumped Warbler	−3.06	**−0.05**	2.31	**0.24**	−0.21	**0.37**	0.00	−0.04	·	0.35
Black-throated Green Warbler	−4.23	−0.01	2.00	0.10	0.25	0.04	0.00	−0.04	**BIR > (SPF, TAM)**	0.38

*Forest type codes: BIR = birch/poplar, TAM = Tamarack, SPF = spruce/fir.

between, rather than within, broad habitat classifications (Rotenberry 1985; Lee and Rotenberry 2005). A possible explanation for the lack of relationships between avian species richness and habitat structure at the smaller spatial scales used in our study is that the three physical structure characteristics that we considered (DBH, stem density, and canopy cover) are closely related to stand age. Stand age correlates with the number of avian species in the boreal forest region (Thompson *et al.* 1999; McCarthy and Weetman 2006) yet appeared to us to be homogeneous throughout our study site, perhaps owing to recent burns and harvesting activity. Limited variation in stand age therefore may have resulted in limited variation in the structural traits measured and, in turn, a lack of relationship between habitat structure and avian species richness.

Previous studies have shown that habitat floristics can affect avian assemblages at various scales (Hewson *et al.* 2011; DesGranges and LeBlanc 2012; Lemaître *et al.* 2012; Gahbauer and Rashleigh 2021) and that this is especially true when comparing assemblages within a single, broad habitat type. A strong, positive correlation between vegetative species richness and avian species richness has been demonstrated previously at the landscape scale (i.e., James and Wamer 1982; Currie 1991; Tews *et al.* 2004). Even at finer spatial scales, a greater diversity of tree species increases the number of niches that different species can exploit for foraging, nesting, and shelter (Lee and Rotenberry 2005). For example, within 1 km² plots, Gillespie and Walter (2001) and Poulsen (2002) both found that the number of bird species and the number of individuals of each species were positively correlated with the number of tree species. However, these studies were conducted in areas of high avian and vegetative species richness and diversity. In Gillespie and Walter (2001), for example, mean forest bird richness was 22 ± 8.4 species (range 12–35) and mean woody vegetation richness was 41 ± 9.2 species (range 27–54). In our study, vegetative species richness was not significantly associated with avian species richness, which may be due to the limited variation in vegetative species richness among the locations where our arrays were deployed (mean vegetative richness = 5 ± 1.4 species; range 2–10 species).

In our study, mean daily temperature was significantly associated with avian species richness after controlling for all other variables in the model (Table 2, Figure 3). DesGranges and LeBlanc (2012) conducted a similar study in the Quebec-Labrador Peninsula region of the Canadian boreal forest and similarly found that species richness was significantly and positively correlated with temperature. One explanation for this relationship is that some avian species were present but remained silent and undetected on cooler days. Indeed, Wiley and Richards (1982) found positive correlations among temperature, the number of vocalizations produced, and the detectability of birds. An alternative explanation is that the relationship between temperature and avian species richness is due to variation in the arrival dates of the various bird species, because departure and arrival dates are known to be affected by weather variables such as precipitation, wind, and temperature (Sparks *et al.* 2002; Deppe *et al.* 2015). In particular, Sparks *et al.* (2002) showed that migratory species arrive on breeding grounds earlier when spring temperatures are warmer. Because our models included day of year, any effect of temperature is in addition to seasonal effects that influence arrival date and the total number of species that are present in the general area on a given date. The positive correlation between avian species richness and temperature in our study might therefore be driven by migratory species that had not yet arrived in early spring when temperatures were cold, but which had arrived days or weeks later when temperatures had increased. Although temperature and day of year are generally positively correlated, exceptions do occur that could explain why temperature but not day of year predicted species richness. In 2016, for example, temperature remained consistently low for the first half of the sampling period but then increased suddenly and remained consistently high for the remainder of the sampling period (Figure 3a). Future research involving longer sampling periods that span a mixture of cooler and warmer days would help determine whether the observed relationship between avian species richness and temperature is due to some species being present but silent on cooler days or to them not arriving on the breeding grounds until temperatures warm.

Avian species richness was moderately consistent between consecutive years among the 20 locations that were sampled in both years (intraclass correlation coefficient of 0.559, 95% CI of ICC 0.166–0.798), suggesting that it may have been influenced by some combination of abiotic and biotic environmental variables that were consistently associated with each location. Given that the physical structure and floristic variables measured in our study were poorly correlated with avian species richness, it is likely that other habitat variables, or perhaps stable microgeographic variation in weather, influence the consistency of species richness. On the other hand, because avian species richness was positively correlated with mean daily temperature, any differences in temperature at a given array location between years may have reduced our estimate of inter-annual consistency. It is also important to note that repeatability in species richness does not necessarily mean that the same species returned to each location the following year, only that a similar number of species returned. We discuss temporal consistency in avian community composition below.

Species-specific detection

For most species (14/18 species that were detected in at least 10% of array locations), the physical structure and floristics of the habitat were not significantly associated with their detection. This is consistent with previous studies (i.e., Rotenberry 1985; Lee and Rotenberry 2005; Seavy and Alexander 2011; Lemaître *et al.* 2012; Ralston *et al.* 2019) that found both the physical structure and floristics of a habitat are potentially important when considering species individually, but that each species responds differently to variation in habitat characteristics, with some species showing little or no response to variation in physical structure and floristics.

Temperature and day of year were significantly associated with species detection for 6/18 species and 4/18 species, respectively. For Ruby-crowned Kinglet, Swainson's Thrush, Pine Siskin, Tennessee Warbler, Orange-crowned Warbler, and Yellow-rumped Warbler, which are migratory at our study site, the patterns are consistent with previous research showing that migrants are more likely to arrive on the breeding grounds during warmer weather, which tends to occur later in the year (Sparks *et al.* 2002). Because we used audio recorders to estimate species presence, relationships between species detection and temperature and date may also have been driven by seasonal and temperature-related variation in vocal activity.

For example, Wiley and Richards (1982) showed that birds produce more vocalizations and are more likely to be detected on warmer days, which could explain why five species were more likely to be detected on warmer days. Interestingly, Boreal Chickadee and Ruby-crowned Kinglet were both more likely to be detected on warmer days earlier in the season. In a study conducted at the same time and location as ours, Fahmy and Wilson (2020) found that Ruby-crowned Kinglet had an early breeding season and was most vocal in early June (2016) and late May (2017), which could explain why we were more likely to detect them earlier within our sampling period (16 May to 10 July). However, there are exceptions. Pine Grosbeak were less likely to be detected on warmer days. Pine Grosbeak call throughout the day, from dawn to dusk, but less often during the warmest parts of the day (1000–1600), suggesting a negative relationship between vocal activity and temperature in this species (Young and Adkisson 2020). Finally, wind speed affected the detection of 2/18 species, with Lincoln's Sparrow and Tennessee Warbler both less likely to be detected on windier days. High wind speeds are known to reduce the ability of recorders to detect birds (Thomas *et al.* 2020) but it is unclear why this occurred only for Lincoln's Sparrow and Tennessee Warbler.

The relationship between forest type and detection was also species-specific. American Robin was detected in a higher proportion of birch/poplar stands versus spruce/fir stands, and Black-throated Green Warbler was detected in a higher proportion of birch/poplar stands versus any other forest type. Our findings are consistent with Gahbauer and Rashleigh (2021), who found that Black-throated Green Warbler is associated with hardwood forest in Labrador. The apparent preference for birch/poplar by these species might be explained by previous research conducted in Alberta, Canada, which shows that an increasing deciduous/hardwood component is associated with increased diversity of food resources and potential nest sites in forests previously harvested for timber (Work *et al.* 2004; Buddle *et al.* 2006). Yet, more abundant resources in forests with hardwood tree species does not explain why these patterns emerged for American Robin and Black-throated Green Warbler and not for other bird species. Gahbauer and Rashleigh (2021) suggested that the increased presence of Black-throated Green Warbler in mixed or hardwood stands was associated with their preference for large-diameter trees, but maximum DBH was not significantly associated with the detection of either Black-throated Green Warbler or American Robin in our study, although it was significantly and positively associated with the presence of Yellow-rumped Warbler.

Overall, our findings suggest that, at the local scale used in our study, the composition of avian assemblages is influenced predominantly by factors other than the habitat characteristics measured. Several non-habitat factors affect habitat selection in birds, including competition (Jaakkonen *et al.* 2015), conspecific and heterospecific attraction (Forsman *et al.* 1998; Parejo *et al.* 2005; Campomizzi *et al.* 2008), and physiological constraints (Block and Brennan 1993; Jones 2001). Alternatively, it may be that, as Niemi *et al.* (1998) state, there is an "overabundance of suitable sites" in our study area. Those authors speculated that, while some locations are avoided, the majority of habitat is perceived as being of comparable quality and thus equally exploited.

Spatial and temporal consistency in avian community composition

Avian community composition was moderately consistent among the three forest types categorized in our study (~49% similarity) and was only slightly lower between forest types than within forest types (~53% similarity). Many migratory bird species that depend on boreal forests for breeding tend to have similar requirements (Schmiegelow and Mönkkönen 2002), likely contributing to the comparable results observed among versus within forest types.

Avian community composition among the 20 locations sampled in 2016 and 2017 was moderately consistent between years (mean ± SD C_t: 0.54 ± 0.24; range 0–0.89), suggesting that individuals and species do not always occupy particular patches or territories within the overall area between consecutive years. The moderate C_t values might be attributed to the observation that species richness at these locations was generally lower during 2017 (mean ± SD: 6.5 ± 3.7 species; range 0–15) in comparison to 2016 (9.1 ± 2.3; range 5–14; Table S1). If a small number of species present in the first year do not return the next year, this will increase the temporal species turnover, even if there are no new species that are present only in the second year. Another possible explanation for the moderate C_t values is that individuals may have returned in 2017 to similar locations but just outside the small target area of the array. Whatever the reason, our results are consistent with the meta-analysis by Schlossberg (2009), which found that 64% of adult migratory forest birds do not return to the same location between breeding seasons. Finally, although C_t values varied among the 20 locations, we did not find evidence that they were related to the day of the year when the locations were sampled, suggesting that low C_t values were not an artifact of sampling a particular location early in the season before all the migrants had arrived.

Differences in weather patterns and the arrival dates of individual species potentially influenced the differences in avian community composition observed between years. We also observed that snow in the forest persisted on the ground for a longer period into the breeding season in 2017, and that the daily mean temperature (averaged over 24 h) in 2017 was 3.5ºC (± 4.8ºC) cooler compared to in 2016 when comparing the same dates between years. It is possible that migration in 2017 was delayed one or two weeks. E-bird checklists (ebird.org) for Happy Valley-Goose Bay for these years support this argument. Several migratory warbler species (e.g., Black-throated Green Warbler, Magnolia Warbler [*Setophaga magnolia*], Orange-crowned Warbler, Tennessee Warbler) were first recorded on the checklist approximately one week later in 2017, as compared to 2016. Because locations were sampled within a few days (day of the year) of each other in 2016 and 2017, daily temperature, through its effects on arrival dates, is likely the primary cause for differences in community composition between breeding seasons.

Considerations and implications

We acknowledge the clustering algorithm used by Kaleidoscope is imperfect and its accuracy varies by species. Sometimes, multiple clusters were created for each species (e.g., based on different song types) or vocalizations from the same species were distributed across clusters belonging to two or three different species; our manually reviewing the spectrograms and listening to the sounds resolved these issues. Woodpeckers were the only group for which we did not have the expertise to confidently distinguish among related species based on drumming patterns. Although we did not quantify the rate of correct assignments, we estimate that it ranged from ~40% for species with variable sounds or sounds that are similar to other species, to over 80% for species with simple or stereotyped song structure. The reasonable clustering accuracy made the manual review process much more efficient than it otherwise would have been.

Similarly, we can never be completely confident that our 24 h recording at each site was sufficient to detect every species present. The duration of the monitoring period must always be balanced with the number of sampling locations. The 24 h of continuous recordings allowed us to deploy 110 arrays across two seasons and diverse habitat. For comparison, most conventional point counts used for surveying birds last only 10 min per location and rely on human auditory detection. We doubt that the temperature effect influenced the analysis of the relationship between species richness and habitat because each habitat type was sampled evenly throughout the season and because both temperature and habitat were included in the model (see Table 2). It is possible, however, that interannual variation in temperature affected our estimate of the consistency of avian species richness between years. Given that temperature correlated with our estimate of richness, any difference in temperature at a given array location between the two years could have reduced our consistency estimate.

There also are limitations to the scope of our study. Our findings are likely only applicable to the general area in which the study took place (i.e., the boreal forest of Labrador), because wildlife-habitat relationships inferred from relatively small spatial extents have limited transferability (Tuanmu *et al.* 2011). Regardless, such relationships are important for making local land-use decisions and are often necessary for establishing conservation efforts to protect habitat critical for survival and reproduction (Morrison *et al.* 2006). Furthermore, in our study, inferences based on statistical analysis could only be made for species that were adequately abundant. However, the most common species are generally those with the fewest constraints on habitat selectivity, such as generalists, which are the least likely to show a relationship between presence and habitat characteristics. This presents a potential problem, because those species that are of the greatest interest to conservation efforts are usually uncommon or rare (Cunningham and Lindenmayer 2005).

We only considered a small subset of physical structure and floristic variables that have previously been used to study bird-habitat relationships. Other commonly used variables include percent cover of each vegetative species (Gillespie and Walter 2001; Poulsen 2002; Lee and Rotenberry 2005; DesGranges and LeBlanc 2012), the number and percent cover of vegetative strata/height classes (Hobson and Schieck 1999; Deppe and Rotenberry 2008), total vegetative volume (Lewis and Starzomski 2015), and the number and DBH of snags/standing dead trees and downed woody debris (Imbeau *et al.* 1999; Drapeau *et al.* 2000). Incorporating these habitat variables may explain more variation in species richness and species-specific detection but would also take more time to measure and may thus limit sample size. However, our study was able to produce avian species richness and species-specific models with high adjusted R^2 values (>0.20) with relatively few physical structure and floristic variables. Changes in food abundance and pest infestations, such as Spruce Budworm, could also have drastic effects on the presence and abundance of avian species (Venier and Holmes 2010). Pest infestations often occur in 10–15 year cycles and their impact on avian composition is unlikely to be captured in shorter duration surveys such as our two-year study. Future studies should also include distances to landscape features such as wetlands, waterbodies, and anthropogenic structures (e.g., roads, powerlines), because these features have the potential to significantly influence avian assemblages (e.g., Summers *et al.* 2011; Zlonis *et al.* 2017).

It is important to collect data about habitat selection by common species, because many rare species were once abundant. Indeed, conservation organizations, such as Partners in Flight, emphasize that prevention is more feasible and affordable than recovery (Rosenberg *et al.* 2016), and consequently stress the importance of studying and monitoring all species to keep "common birds common". Overall, our data show that the structural and floristic traits measured at our study site in the boreal forest in Labrador, Canada are not related to the detection of most avian species or to species richness.

Author Contributions

Conceptualization: J.E. and D.W.; Investigation: J.E. and D.W.; Formal Analysis: J.E. and D.W.; Writing – Original Draft: J.E.; Writing – Review & Editing: J.E. and D.W.; Supervision: D.W.; Funding Acquisition: D.W.

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SUPPLEMENTARY MATERIAL:

R SCRIPT 1. The R script for statistical analysis and creation of figures.

DATA FILE 1. Data used to model the relationships between avian species richness and three environmental factors, including weather and the physical structure and floristics of the habitat and to produce species-specific models.

DATA FILE 2. Data used to calculate ICC values for avian richness in 2016 and 2017 to determine the consistency in richness between years.

TABLE S1. Avian species that were detected in 2016 and 2017 for 20 arrays sampled in both years in Labrador, Canada.

TABLE S2. The number of array locations, sampled from each forest type, where a given species was detected.

The Canadian Field-Naturalist

Description of a relict aspen parkland-associated grassland in the Peace River region of British Columbia, Canada

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Abstract

The aspen parkland-associated grasslands of the Peace River region, British Columbia (BC), have been severely reduced in area, primarily because of agricultural and urban development. In this region, the species composition of plant communities is similar to that of prairie grasslands and is topographically influenced, occurring primarily on warm-aspect slopes along the Peace River and some of its tributaries. Historical records show that non-forested grass- and sedge-dominated plant communities occurred on flat and gently rolling terrain in a parkland ecosystem near what are now the communities of Dawson Creek and Fort St. John. The Peace grasslands are not represented in BC's biogeoclimatic ecosystem classification, perhaps leading to their neglect in regional natural resource management and conservation planning. Here, I describe the vascular plant community of a level-terrain relict aspen parkland-associated grassland in the Peace River region. Its species composition differs from nearby warm-aspect grasslands and includes provincially listed plant species. Increased awareness of grassland communities may support conservation, ecosystem restoration, and climate change adaptation in the southern boreal region of BC.

Key words: Aspen parkland; grasslands; Peace River; relict

Introduction

Across the Great Plains of North America, the aspen parkland ecosystem is broadly transitional—in climate and plant species composition—from grasslands to boreal forests (Rowe and Coupland 1984). Aspen parkland extends from Manitoba to western Alberta, with some descriptions including areas in the Peace River region of northeastern British Columbia (BC; Moss 1932, 1952). The biogeoclimatic ecosystem classification system of BC excludes aspen parkland. Plains on the eastern side of the Rocky Mountains are included in its Boreal White and Black Spruce zone (Meidinger and Pojar 1991). Further, although climate and disturbance regimes drive parkland vegetation to the south (Hogg 1994), various soil properties that limit tree growth are an additional factor in maintaining parkland conditions in the Peace River region's boreal climate (Wilkinson and Johnson 1983). Parklands include a mosaic of forested, grassland, and shrubby vegetation. In this study, I focus on the grassland component, and hereafter "grasslands" refers to grassland parts of the parkland mosaic/ecosystem.

In BC's Boreal White and Black Spruce zone, grasslands are limited to steep, warm-aspect slopes of some major river valleys, especially along the Peace River (Pojar 1982; DeLong *et al.* 2011). These topographically influenced grasslands are floristically similar to prairie grasslands, as Coupland (1961) described. Common species include Northern Wheatgrass (*Elymus lanceolatus* (Scribner & J.G. Smith) Gould), Western Wheatgrass (*Pascopyrum smithii* (Rydberg) Barkworth & D.R. Dewey), Western Porcupine Grass (*Hesperostipa curtiseta* (Hitchcock) Barkworth), and Junegrass (*Koeleria macrantha* (Ledebour) Schultes; Moss 1952; Pojar 1982). Considering current landscape patterns, the biogeoclimatic ecosystem classification treatment of grasslands as "non-zonal" because of topographic influences is accurate; grasslands are generally limited to steep, warm-aspect slopes of some major river valleys. However, an early soil survey (Farstad *et al.* 1965), early pre-agricultural descriptions (Dawson 1881; Macoun 1904), and an early account by Raup (1934) of BC's Peace region suggest an aspen parkland ecosystem existed that included level and gently rolling terrain in areas surrounding what are now the communities of Dawson Creek and Fort St. John. The grassland plant communities on the level and gently sloping terrain of this ecosystem have been considered lost to agricultural cultivation and urban development (Wikeem and Wikeem 2004). Native grassland plant communities in the region remain primarily on slopes too steep for cultivation.

In spring 2022, the Province of BC invited me to comment on a resource extraction permit process for the expansion of a gravel quarry in a grassland. The notification included the location of the grassland area in the Peace region, at the confluence of the Pine and Peace rivers, where vegetation is predominantly native grasses. The area is flat, indicating that it may be a relict aspen parkland-associated grassland and perhaps representative of formerly more extensive plant communities in the southern part of BC's Peace region. The grassland area is the site of a large, expanding gravel quarry that is reducing its extent. I surveyed this grassland to characterize its vascular plant biodiversity and inform conservation and management.

Methods

The grassland covers ~200 ha at the confluence of the Pine and Peace rivers in northeastern BC (56.152823°N, 120.766177°W), near the community of Taylor. The area is in the moist warm Boreal White and Black Spruce subzone (DeLong *et al.* 2011); mean annual temperature is 2.3°C and mean annual precipitation is 392 mm, with average temperatures of −14.5°C in January and 16.4°C in July for the 1981–2010 climate normal period (Wang *et al.* 2016). Soils are classified as the Clayhurst type, which consists of Eluviated Eutric Brunisols that have a sandy loam veneer over gravelly and sandy glaciofluvial deposits (Lord and Green 1986). The grassland is in Treaty 8 territory and on the traditional territory of the Dane-Zaa people. The area is mostly provincial Crown land with provincial grazing tenure allocation, and part of the area is private land.

Field sampling was carried out on 27 July 2022. I placed a single 10 m × 10 m plot on a location judged to represent average plant cover conditions. Considering the flat terrain (no ridges or swales), the plot location was representative of the grassland, excluding shrubbier areas bordering forest edges. Within the plot, I estimated vascular plant species cover according to modified Daubenmire (1959) cover classes with the cover-class categories, range (mid-point) for each category as follows: "trace" <1%, 1 = 1–<5% (2.5%), 2 = 5–<25% (15%), 3 = 25–<50% (37.5%), 4 = 50–<75% (62.5%), 5 = 75–<95% (85%), and 6 = 95–100% (97.5%). The sole modification to the Daubenmire cover classes was adding the trace category to better represent the abundance of sparse species (cover class categories and mid-points are described in Mueller-Dombois and Ellenberg [2003]). I also walked through the grassland for ~2 h recording all observed additional species; however, considering the reconnaissance nature of this project, I likely missed some species, especially those not visible in summer, such as spring-flowering forbs. No vouchers were collected because of time limitations and my 20 years of experience in plant ecology work in grasslands. At two locations near the plot, I sampled soil to a depth of 20 cm, recording soil colour and assessing the proportion of soil particle size according to the soil texturing key (Province of British Columbia 2010: 38).

Results

I recorded a total of 48 plant species in the grassland (Table 1): 30 occurring in the plot and an additional 18 found in my survey across the grassland (Figure 1). The plot location was a good representation of average cover values of frequent species throughout the grassland, while additional infrequently occurring species were recorded outside the plot. Richardson's Needlegrass (*Eriocoma richardsonii* (Link) Romaschenko) was the most abundant grass species throughout the grassland, while Slender Wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners), Western Porcupine Grass, Junegrass, Vasey's Oatgrass (*Danthonia intermedia* Vasey), and Spike Oat (*Helictochloa hookeri* (Scribner) Romero Zarco) had lower cover values but were highly frequent. The grassland had high forb cover, with Northern Bedstraw (*Galium boreale* L.) and Prairie Smoke (*Geum triflorum* Pursh) present across the grassland and an additional 28 forb species

TABLE 1. Species composition of the grassland according to modified Daubenmire (1959) coverage classes. The cover class ranges were determined by ocular estimation of a single plot. As the plot was judged to be representative of the average condition of the grassland, the cover values are also an approximation for average cover across the grassland area.

Species	Cover class*	Status†
Grasses and sedges		
Richardson's Needlegrass, *Eriocoma richardsonii* (Link) Romaschenko	25–50	n
Western Porcupine Grass, *Hesperostipa curtiseta* (Hitchcock) Barkworth	1–5	n
Junegrass, *Koeleria macrantha* (Ledebour) Schultes	1–5	n
Vasey's Oatgrass, *Danthonia intermedia* Vasey	<1	n
Spike Oat, *Helictochloa hookeri* (Scribner) Romero Zarco	<1	n
White-scaled Sedge, *Carex xerantica* L.H. Bailey	<1	n

TABLE 1. *Continued.*

Species	Cover class*	Status†
Rough Bentgrass, *Agrostis scabra* Willdenow	t	n
Smooth Brome, *Bromus inermis* Leysser	t	e
Rocky Mountain Fescue, *Festuca saximontana* Rydberg	t	n
Green Needlegrass, *Nassella viridula* (Trinius) Barkworth	t	n
Canada Ricegrass, *Piptatheropsis canadensis* (Poiret) Romaschenko, P.M. Peterson & Soreng	t	n
Kentucky Bluegrass, *Poa pratensis* L.	t	e
Purple Oatgrass, *Schizachne purpurascens* (Torrey) Swallen	t	n
Forbs		
Northern Bedstraw, *Galium boreale* L.	5–25	n
Prairie Smoke, *Geum triflorum* Pursh	5–25	n
Wild Onion, *Allium cernuum* Roth	1–5	n
Common Harebell, *Campanula rotundifolia* L.	1–5	n
Bastard Toadflax, *Comandra umbellata* (L.) Nuttall	1–5	n
Creamy Peavine, *Lathyrus ochroleucus* Hooker	1–5	n
Western Goldenrod, *Solidago lepida* de Candolle	1–5	n
Common Yarrow, *Achillea millefolium* L.	<1	n
Cut-leaved Anemone, *Anemone multifida* Poiret	<1	n
Field Chickweed, *Cerastium arvense* L.	<1	n
Richardson's Alumroot, *Heuchera richardsonii* R. Brown	<1	n
Virginia Strawberry, *Fragaria virginiana* Miller	<1	n
American Vetch, *Vicia americana* Muhlenberg ex Willdenow	<1	n
Rock Cress, *Arabis* sp.	t	n
Frog Orchid, *Coeloglossum viride* (L.) Hartman	t	n
Philadephia Fleabane, *Erigeron philadelphicus* L.	t	n
Umbellate Hawkweed, *Hieracium umbellatum* L.	t	n
Mint-leaved Bergamot, *Monarda fistulosa* var. *menthifolia* (Graham) Fernald	t	n
Silky Locoweed, *Oxytropis sericea* Nuttall	t	n
Showy Locoweed, *Oxytropis splendens* Douglas ex Hooker	t	n
Sticky Cinquefoil, *Drymocallis glandulosa* (Lindley) Rydberg var. *glandulosa*	t	n
Woolly Cinquefoil, *Potentilla hippiana* Lehmann	t	n
Prairie Cinquefoil, *Potentilla pensylvanica* L.	t	n
White-leaved Cinquefoil, *Potentilla pulcherrima* Lehmann	t	n
Strict Blue-eyed Grass, *Sisyrinchium montanum* Greene	t	n
Starry False Solomon's Seal, *Maianthemum stellatum* (L.) Link	t	n
Lindley's Aster, *Symphyotrichum ciliolatum* (Lindley) Á. Löve & D. Löve	t	n
Smooth Blue Aster, *Symphyotrichum laeve* (L.) Á. Löve & D. Löve	t	n
Veiny Meadow-rue, *Thalictrum venulosum* Trelease	t	n
Yellow Salsify, *Tragopogon dubius* Scopoli	t	e
Shrubs		
Common Bearberry, *Arctostaphylos uva-ursi* (L.) Sprengel	5–25	n
Wild Prickly Rose, *Rosa acicularis* Lindley	5–25	n
Saskatoon, *Amelanchier alnifolia* (Nuttall) Nuttall ex M. Roemer	1–5	n
Western Snowberry, *Symphoricarpos occidentalis* Hooker	1–5	n
Trembling Aspen, *Populus tremuloides* Michaux	t	n

*<1 indicates low abundance inside the plot; t (trace) indicates additional species found in the grassland area outside the plot. Species in the <1 cover class inside the plot tended to have greater frequency across the grassland than trace species that were found only outside the plot.

†n = native, e = exotic.

FIGURE 1. a. The plot used as an approximation of cover values for the grassland. b. An overview of the area with the grasslands on warm aspect slopes along the Peace River in the background. c. A patch of Mint-leaved Bergamot (*Monarda fistulosa* var. *menthifolia*) in the foreground with inflorescences of native grasses in the background. Orange markers in b are part of the gravel quarry operation. Photos: Nicholas Hamilton.

with low cover values and various levels of frequency. Low-growing shrubs occurred across the grassland, mainly Bearberry (*Arctostaphylos uva-ursi* L.) and Wild Rose (*Rosa acicularis* Lindley), with more Saskatoon (*Amelanchier alnifolia* Nutall ex M. Roemer) and Western Snowberry (*Symphoricarpos occidentalis* Hooker) near grassland-forest edges. There were several occurrences of Canada Ricegrass (*Piptatheropsis canadensis* (Poiret) Romaschenko, P.M. Peterson & Soreng); White-scaled Sedge (*Carex xerantica* L.H. Bailey) was low-cover but common. These two species are provincially red- and blue-listed, respectively (BCCDC 2022). Occasional patches of Mint-leaved Bergamot (*Monarda fistulosa* var. *menthifolia* (Graham) Fernald), which is at its BC northern limit in the Peace River valley, tended to be closer to forest edges. Near the grassland-forest boundary, there were shrubby areas, where Green Needlegrass (*Nassella viridula* (Trinius) Barworth) was more abundant than elsewhere in the grassland. The exotic grass Smooth Brome (*Bromus inermis* Leysser) was invading the grassland from the edges and was likely the most abundant grass species in shrubby forest-grassland edge areas.

Surface humus layers were absent, with substrates consisting of vegetation and grass/forb leaf litter on mineral soil. There was low cover of mosses and lichens, which were not identified to species. Soil texture above 20 cm depth was a loam with some sandy feel—indicating it is close to the boundary between classification as a loam and sandy loam. The colour of the surface mineral soil was very dark brown for the first 5 cm, indicating abundant incorporated organic matter, and dark greyish brown from 5 to 15 cm depth. Cobble content was high near the soil surface (top 5 cm), with fewer at greater (5–15 cm) depths. I did not reach the layer of gravelly deposits with higher coarse fragment content that reportedly occur beneath the loam veneer at >25 cm depth (Lord and Green 1986).

Discussion

This grassland site is an example of the biological diversity of an aspen parkland ecosystem that has been nearly extirpated in BC. Although the soils are well drained (Lord and Green 1986), the plant community reflects conditions that are less xeric than warm-aspect slopes along the river valleys. Notably, the indicators of topographically driven grasslands of the boreal climate—Northern Wheatgrass and Western Wheatgrass—are absent. Instead, the presence of numerous species indicates a strong similarity to the "Semi-open Prairies" (Raup 1934) and the "Agropyron-Stipa" plant communities Moss (1952) described for flat and gently rolling terrain in the parkland areas of the Peace regions of Alberta and BC. The diversity and abundance of native needlegrasses are similar to the higher elevation (cooler climate) grasslands of BC's Cariboo–Chilcotin region (Hamilton *et al.* 2022). However, compared with the

Cariboo–Chilcotin grasslands, the Peace grassland has more forbs, higher shrub cover, less exotic Bluegrass (*Poa pratensis* L.), and a greater abundance of Slender Wheatgrass. Also, the plant community has several species that are specific to the Great Plains (do not occur in the intermountain regions of BC), such as Spike Oat, Richardson's Alumroot (*Heuchera richardsonii* R. Brown), and Showy Locoweed (*Oxytropis splendens* Douglas ex Hooker). All the species I observed have been found by others in the Peace region (Moss 1952). The presence of cobbles near the soil surface and glaciofluvial gravels at greater depths likely contribute to limiting growth of trees on this site. However, it seems that the near-surface loam veneer has sufficient water-holding capacity to support a mesic grassland plant community. Although there is grazing tenure over the Crown land parts of the grassland, it appears that grazing has not occurred for a long time, given the absence of manure. The excessive accumulation of grass litter appears to suppress grass growth. A low-severity disturbance, such as light grazing or prescribed fire, may increase site productivity.

Grassland and parkland conditions are reported as the native vegetation for Black and Dark Gray Solod and Solonetzic Chernozem (Farstad *et al.* 1965; Lord and Green 1986)—soil types that are now entirely under cultivation and other development. Similarly in Alberta, <0.5% of upland Peace parkland grasslands remain in native condition, with losses attributed primarily to agricultural cultivation (Baker 2005). Despite the well-drained soil conditions at this level-terrain relict aspen parkland grassland, there is a strong similarity in species composition to the gentle-terrain Peace parkland grasslands described by Raup (1934), Moss (1952), and Baker (2005). Notably, Raup provides a detailed account of Peace grasslands at a time when more extensive uncultivated sites were likely still present. Raup creates two groups of grassland plant species: one more commonly occurring on steep warm-aspect slopes along river valleys, and a second occurring more commonly on mesic gentle terrain (i.e., not steep-flat or slightly sloping or gently rolling), noting there were various intermediate conditions containing plants of both groups. The relict grassland of my study contains multiple species of both groups, but is lacking indicators of the wettest and driest conditions, suggesting an edaphic condition intermediate to dry and mesic grasslands. Therefore, I suggest that instead of viewing this relict grassland as a phenomenon of well-drained soils in a predominantly forested landscape, it may be considered as representing one of the possible grassland conditions in the context of a parkland landscape that was once extensive through the Alberta and BC Peace region. A final comment on Raup's description is that some of the species and plant associations described are not present in modern accounts (e.g., Baker 2005; Willoughby *et al.* 2021), likely reflecting the loss of Peace grasslands plant communities.

Relicts are important for ecosystem management and conservation, serving as reference conditions for ecological restoration in similar areas. Remnant native grasslands are also culturally significant and can provide a source of local propagules for native plant cultivation. Peace parkland grasslands support populations of butterflies and moths that are disjunct from their main ranges in the prairie regions further south (Schmidt *et al.* 2014). According to the earliest Euro-Canadian accounts, populations of bison (likely Wood Bison [*Bison bison* var. *athabascae*]) and Elk (*Cervus canadensis*) were present along the Upper Peace River (Bowes 1963). Historically, Peace grasslands were important bison habitat and Indigenous peoples used prescribed fire to manage vegetation and bison populations (Ridington *et al.* 2013). A fur trading post, established in 1794 on a shore of the Peace River near Fort St. John, was the site of early interactions among Euro-Canadians (French and English speaking), Métis people from Central Canada and the Eastern Great Plains, and Indigenous peoples from Northern Cordillera and the Northwestern Great Plains (Burley *et al.* 1996). Initially, hunting bison along the upper Peace was an important economic activity in supplying food to fur traders, but populations were severely depleted by the early 1800s (Burley *et al.* 1996) and extirpation occurred in the late 1800s or early 1900s (Bowes 1963; South Peace Historical Society 2023).

Quarry development of this site will remove ~50 ha of grasslands, which will leave 150 ha of grassland in native condition across Crown and private land. Under climate warming scenarios and increased fire frequencies, parkland and grassy conditions are projected to expand across parts of the southern boreal forest (Hogg and Hurdle 1995; Stralberg *et al.* 2018), including southern parts of the BC Peace region (MacKenzie and Mahony 2021). Therefore, conservation of ecological relicts in the Peace region may support climate change adaptation activities, such as restoration to native non-forested and parkland vegetation conditions. Future research on Peace parklands is required to improve conservation and management efforts, especially considering the dearth of research since the work of Moss (1952).

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Frullania stylifera (Frullaniaceae), a new addition to the liverwort flora of Canada

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Abstract

Frullania stylifera (R.M. Schust.) R.M. Schust. (Frullaniaceae) is newly reported for Canada. The species grows closely appressed to the bark of trees and shrubs and was recently documented from two areas of mature forest at Buffalo Point First Nation in extreme southeastern Manitoba, Canada. These localities represent a northern range extension for the species on the continent and include two new phorophyte hosts for North America. Features used to distinguish *F. stylifera* from other known species of *Frullania* in Manitoba are provided.

Key words: Great Lakes; Jungermanniales; liverwort; Manitoba; range extension; St. Lawrence

Introduction

The liverwort family Frullaniaceae Lorch contains the single widely distributed genus *Frullania* Raddi with hundreds of accepted species worldwide (Söderström *et al.* 2016; Brinda and Atwood 2023). There are 38 *Frullania* species in North America north of Mexico including the recently described *Frullania austinii* J.J. Atwood, Vilnet, Mamontov & Konstant. (Stotler and Crandall-Stotler 2017; Mamontov *et al.* 2020, 2021). Of these, 13 species are known to occur in Canada (Stotler and Crandall-Stotler 2017; NatureServe 2023), and five are reported for the province of Manitoba: Asa Gray's Scalewort (*Frullania asagrayana* Mont.), Hairy Scalewort (*Frullania bolanderi* Austin) *sensu lato* (cf. Mamontov *et al.* 2020), New York Scalewort (*Frullania eboracensis* Lehm.), Inflated Scalewort (*Frullania inflata* Gottsche), and Oakes' Scalewort (*Frullania oakesiana* Austin; Caners 2011, 2020; NatureServe 2023).

Frullania stylifera (R.M. Schust.) R.M. Schust. was originally described as *Frullania inflata* var. *stylifera* R.M. Schust. by Schuster (1983), based on the type specimen from Whitewater State Park, Minnesota (*Schuster W14205*) and two other collections from the same area (*Schuster 14208*, *14213*; Schuster 1983). (Note: there is no common name for the species.) *Frullania inflata* var. *stylifera* was subsequently recognized as the distinct species *Frullania stylifera* by Schuster (1992) based on diagnostic morphological features, especially the very large stylus of dorsal lobes. Until recently, the species was only known from Minnesota (Schuster 1992); however, numerous new localities were reported from interior United States by Atwood (2016), mostly from Missouri, but also Arkansas, Oklahoma, and Tennessee. Subsequently, new localities were reported in New York, Illinois, and Kansas, along with additional sites in Missouri (Atwood and Brinda 2019). A Michigan specimen (*Konstantinova A4-95*) without a locality is cited in Mamontov *et al.* (2020). Atwood (2016) indicated that the diversity of habitats and woody plant phorophytes reported for *F. stylifera*, combined with the widespread distribution of many of the bryophytes associated with the species, suggests that *F. stylifera* may be much more frequent than reported. In 2020, the species was reported for the first time outside the continental United States in Eurasia (Konstantinova *et al.* 2020).

For my present study, bryophyte surveys were conducted in southeastern Manitoba to expand on the flora of the region documented by Caners (2020). The survey included collections of *Frullania* that were expected to provide new insights into the regional distribution and ecology of the genus.

Study Area

I conducted bryophyte surveys in the Great Lakes–St. Lawrence Forest Region (Rowe 1972) in southeastern Manitoba, Canada, from 12 to 17 September

2022. The forest region extends across southern Canada from the Gaspé Peninsula, Quebec, in the east to southeastern Manitoba in the west (Figure 1). It represents the northern extent of humid temperate climate in eastern North America and the transition between broad-leaved temperate forests and conifer-dominated boreal forests (Rowe 1972; Baldwin *et al.* 2020). The Great Lakes–St. Lawrence Forest Region closely matches the Eastern Cool Temperate Forest Zone in the vegetation classification system of Baldwin *et al.* (2020). I prefer Rowe's (1972) classification for my study, however, because of its more detailed division of the region into forest sections.

In Manitoba, the Great Lakes–St. Lawrence Forest Region has a restricted distribution and contains two distinct forest sections that differ in composition, terrestrial substrata, and post-glacial history (Rowe 1972; Figure 2). The Quetico Section occupies a small area on the Canadian Shield and is characterized by irregular terrain of underlying granites, sediments, and volcanic rocks (Rowe 1972). The Rainy River Section lacks rock substrates and is characterized by a mostly flat to undulating topography, extensive wetlands, and, in some areas, well-drained soils with coarse-textured glacial deposits, outwash, and old beaches and bars of glacial Lake Agassiz (Rowe 1972; Groom 2002).

The Great Lakes–St. Lawrence Forest Region has the highest total annual precipitation in Manitoba (Climate Atlas of Canada 2023) and some of the highest mean annual temperatures in the province, which are similar to those along the northern borders of adjacent Minnesota and nearby North Dakota (Climate Atlas of Canada 2023). In the Rainy River Section, the Sprague meteorological station (49°01′0″N, 95°36′0″W; 320.2 m above sea level [asl]) reports a total annual precipitation of 637.5 mm (517.0 mm as rain) and a daily average temperature of 2.7°C (1981–2010 normals; ECCC 2023a). The meteorological station closest to the Quetico Section is Pinawa (50°10′50″N, 96°03′30″W; 266.7 m asl), with a total annual precipitation of 578.3 mm (464.3 mm as rain) and daily average temperature of 2.8°C (1981–2010 normals; ECCC 2023b).

Methods

Field collections

Field collections were restricted to mixed forest

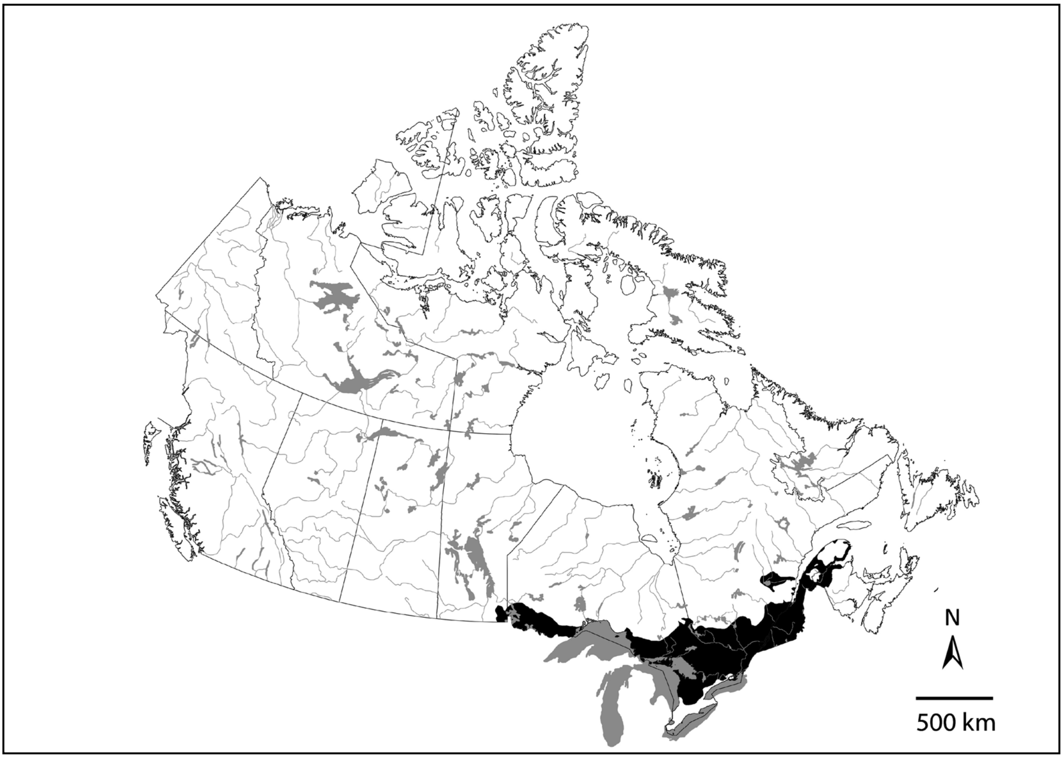

FIGURE 1. The Great Lakes–St. Lawrence Forest Region in Canada (Rowe 1972; adapted from Caners 2020), shown in black shading. Grey polygons and lines are major freshwater bodies and watercourses, respectively. The portion of the Forest Region in extreme southeastern Manitoba represents the study area in Figure 2.

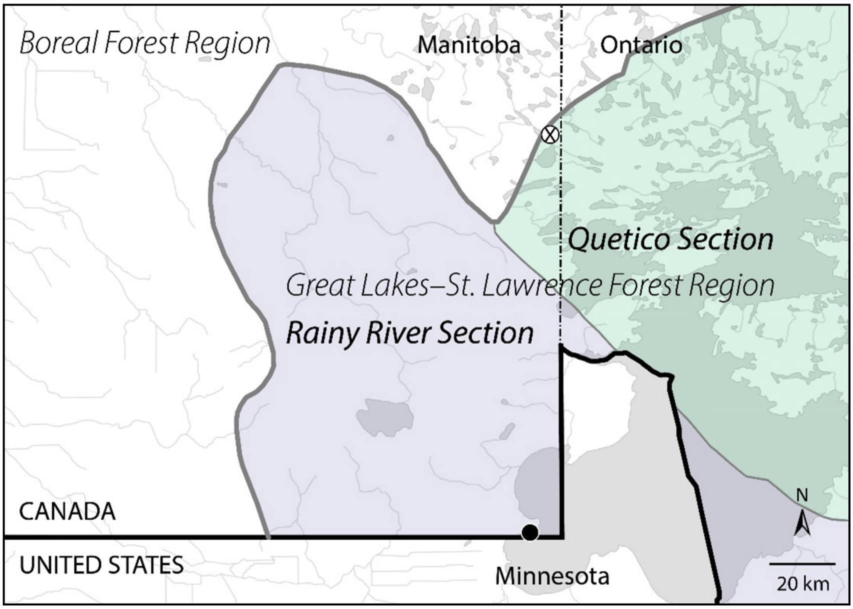

Figure 2. Study area and locality (closed circle) of *Frullania stylifera* in Buffalo Point First Nation, Manitoba, Canada. The site is situated in the Rainy River Section of the Great Lakes–St. Lawrence Forest Region. The ⊗ represents *Frullania* collection sites from my current study in Whiteshell Provincial Park in the Quetico Section that are not *F. stylifera*. *Frullania* collection sites from Caners (2020) are not depicted. The thick grey line divides the Great Lakes–St. Lawrence Forest Region and the Boreal Forest Region (Rowe 1972). The thick black line is the international border between Canada and the United States, and the dashed line is the inter-provincial border between Manitoba and Ontario. Grey polygons are water bodies and fine grey lines are watercourses. Map adapted from Caners (2020).

and treed swamp habitats and excluded marshes, shallow open water wetlands, bogs, and fens. In the Rainy River Section, surveys were limited to Buffalo Point First Nation, which is located in the extreme southeast corner of the province, on Buffalo Bay in Lake of the Woods (Figure 2). The community is the traditional land of the Anishinaabe peoples of the region and a signatory to Treaty 3. Buffalo Point First Nation contains land parcels of varying size, but for my study only the largest parcel that includes the town site was surveyed. In the Quetico Section, surveys were limited to Whiteshell Provincial Park along the Whiteshell River (Figure 2).

All specimens were deposited at the Royal Alberta Museum herbarium (PMAE). Nomenclature for liverworts follows Stotler and Crandall-Stotler (2017) except for *F. austinii,* which follows Mamontov *et al.* (2020). Nomenclature and vernacular names for vascular plants follow VASCAN (Brouillet *et al.* 2010+), except for species that are not found in Canada, which are based on NatureServe (2023).

Results and Discussion

Two specimens of *F. stylifera* were found among the samples obtained for this study. Both were from Buffalo Point First Nation, ~100 m from each other (*Caners 8783, 8790*). The species was growing in mature White Spruce (*Picea glauca* (Moench) Voss)–Paper Birch (*Betula papyrifera* Marshall)–Balsam Poplar (*Populus balsamifera* L.)–Balsam Fir (*Abies balsamea* (L.) Miller) forest that contained a large volume of dead wood. Some *Frullania* species, such as *F. stylifera*, have features that are challenging to discern in the field, requiring the collection of specimens for proper identification. I collected more than 40 *Frullania* specimens during the present study and other recent surveys of the region (Caners 2020), but no additional specimens of *F. stylifera* were detected. The collections of *F. stylifera* from Buffalo Point First Nation are the most northern for the species in North America to date, with the next closest station being the type locality in Minnesota (Schuster 1992) more than 600 km to the southeast (Figure 3).

Differentiation

Atwood (2016) reported numerous new records of *F. stylifera* from the interior United States through field collections and review of past herbarium collections that were found to be misidentified. Atwood (2016) attributed the apparent scarcity of records of *F. stylifera* to a tendency to overlook the species or to mistake it for other species, especially *F. inflata*

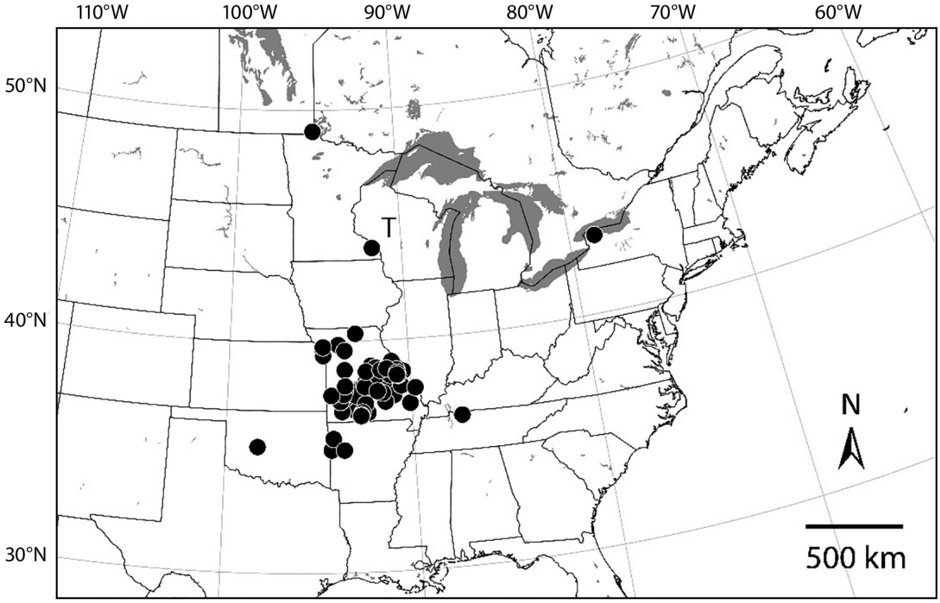

FIGURE 3. Currently known distribution of *Frullania stylifera* in North America. The closed circle in Manitoba, Canada, includes the two newly discovered collections from Buffalo Point First Nation. The other closed circles are specimen records from Atwood (2016), Atwood and Brinda (2019), and Consortium of Bryophyte Herbaria (2023). The closed circle in Minnesota, USA, marked with the letter "T", indicates the type locality from Schuster (1983). Grey polygons are major freshwater bodies. Map generated from Shorthouse (2010).

and *F. eboracensis*. The latter species are known from southeastern Manitoba, with *F. eboracensis* being much more frequent and often locally abundant (Caners 2020). Confusion with *F. inflata* may relate to the species' basionym, *Frullania inflata* var. *stylifera*. Several characters distinguish *F. stylifera* from these other species, including the size of the styli and underleaves, the shape of dorsal lobes, number of oil bodies per cell, and sexual condition (Table 1; Schuster 1992; Atwood 2017; Mamontov *et al.* 2020). *Frullania stylifera* has a very large lamellate stylus that typically measures 10–15 cells long and 4–10 cells wide (Figure 4). In comparison, the styli in *F. inflata* and *F. eboracensis* are substantially smaller, being filiform or shortly triangular and usually 3–6 cells long and 1–3 cells wide (Atwood 2017). *Frullania stylifera* has underleaves 2–3 times the width of the stem, whereas both *F. inflata* and *F. eboracensis* have underleaves usually 1.0–1.5 times the width of the stem (Atwood 2017). Dorsal lobes in *F. stylifera* are broadly reniform to ovate and with a cordate base, whereas dorsal lobes in *F. inflata* are orbicular to broadly ovate with a truncate base and in *F. eboracensis* are oval to suborbicular with a cordate base. When fresh material is available, *F. stylifera* has dorsal lobes with up to 16 oil bodies per cell (or as few as 5–8 oil bodies in scattered cells; Schuster 1992), whereas *F. inflata* and *F. eboracensis* have ~2–5 oil bodies per cell (Atwood 2017). Furthermore, *F. stylifera* and *F. inflata* are autoicous and abundantly fertile with capitate androecia, whereas *F. eboracensis* is dioicous and infrequently fertile with spicate androecia.

The remaining *Frullania* species known to occur in Manitoba (*F. asagrayana*, *F. bolanderi sensu lato*, and *F. oakesiana*) are readily distinguished from *F. stylifera* (Table 1). *Frullania asagrayana* has ocelli of the dorsal lobes; these are lacking in *F. stylifera*. These ocelli appear in *F. asagrayana* as a line of cells that runs medially from the leaf base to about halfway along the leaf length (Atwood 2017). The ocelli are usually one or occasionally two cells wide and are seen rarely as scattered cells (Atwood 2017). *Frullania asagrayana* also has a stylus that is filiform to subulate with a suborbicular appendage and is dioicous.

Frullania bolanderi has been previously considered to have a bicentric world distribution, with centres in eastern Asia and the Pacific Coast of North America and in eastern and interior North America and western Europe (Schuster 1992; Mamontov *et al.* 2020). However, morphological differences supported by molecular data in some North American and Russian populations previously included in the circumscription of *F. bolanderi* have revealed a new species, *Frullania austinii* J.J. Atwood, Vilnet, Mamontov & Konstant. (Mamontov *et al.* 2020). Both *F. bolanderi*

TABLE 1. Key features that distinguish *Frullania stylifera* from other known *Frullania* species in Manitoba.

Feature	*F. stylifera*	*F. asagrayana*	*F. austinii**	*F. eboracensis*	*F. inflata*	*F. oakesiana*
Dorsal lobe shape	Reniform-ovate, base cordate	Ovate, base auriculate	Widely ovate, base truncate	Oval to suborbicular, base cordate	Orbicular to broadly ovate, base truncate	Ovate to orbicular, base rotundate to truncate
Doral lobe size, µm	500–600 × 700–800	700 × 500	410–575 × 550–720	400–600 × 500–600	550–640 × 360–600	300–400 × 200–300
Ocelli	Absent	Present as a median line, rarely as scattered cells	Absent	Absent	Absent	Absent
Lobule size, µm	355–420 × 310–400	300 × 200	250–320 × 250–400	260–300 × 200–240	250 × 250	220–240 × 190–220
Stylus	Lamellate, 10–15 cells long, 4–10 cells wide	Filiform to subulate, with suborbicular disk like appendage with cilia and 1–2 marginal teeth	Lamellate, 6–10 cells long, 3–5 cells wide	Subulate, 3–6 cells long, 2–3 cells wide	Filiform to subulate, 4–8 cells long, (1)2–3 cells wide	Subulate, 4–5 cells long, 1–3 cells wide
Underleaf shape and size, µm	Obovate, 330–365 × 340–380	Orbicular-ovate, 400 × 400	Obovate, 160–200 × 180–250	Ovate to rhombic-ovate, 200–250 × 150–230	Orbicular to obovate, 300–320 × 240–300	Obovate, 160–180 × 130–160
Oil bodies, no./cell	8–16	2–4†	6–9	2–5	4–5	3–5
Asexual reproduction	Absent	Absent	Abundant flagelliform secondary branches with caducous leaves	Gemmae or caducous leaves	Absent	Absent
Sexual condition	Autoicous	Dioicous	Dioicous	Dioicous	Autoicous	Autoicous
Androecia	Capitate	Bracts in 3–5 pairs†	Subglobose to shortly spicate	Distinctly spicate†	Capitate	Capitate
Perianth	Abruptly contracted, one dorsal keel, two ventral keels, no accessory keels	Somewhat compressed at sides, with deep postical keel	One main keel, 2–3 smaller, accessory keels ventrally, on dorsal side often with 1–2(3) small keels	± compressed, abruptly narrowed to short, broad keel, without distinct supplementary ridges	Abruptly narrowed to beak, with one postical keel, ≥1 supplementary keels	Gradually broadened to apex, dorsiventrally flattened, one ventral, two lateral keels of equal size
Perianth beak	With inner faces weakly papillate†	Short†	Obconical, dilated at mouth, mouth sometimes occluded with papilliform cells	Short†	Short, broad, with papilloid cells on inner surface	Short, mouth fringed with projecting papillae

*Features for *F. austinii* are based on Mamontov *et al.* (2020).
†Features based on Schuster (1992).
All features not marked * or † are based on Atwood (2017).

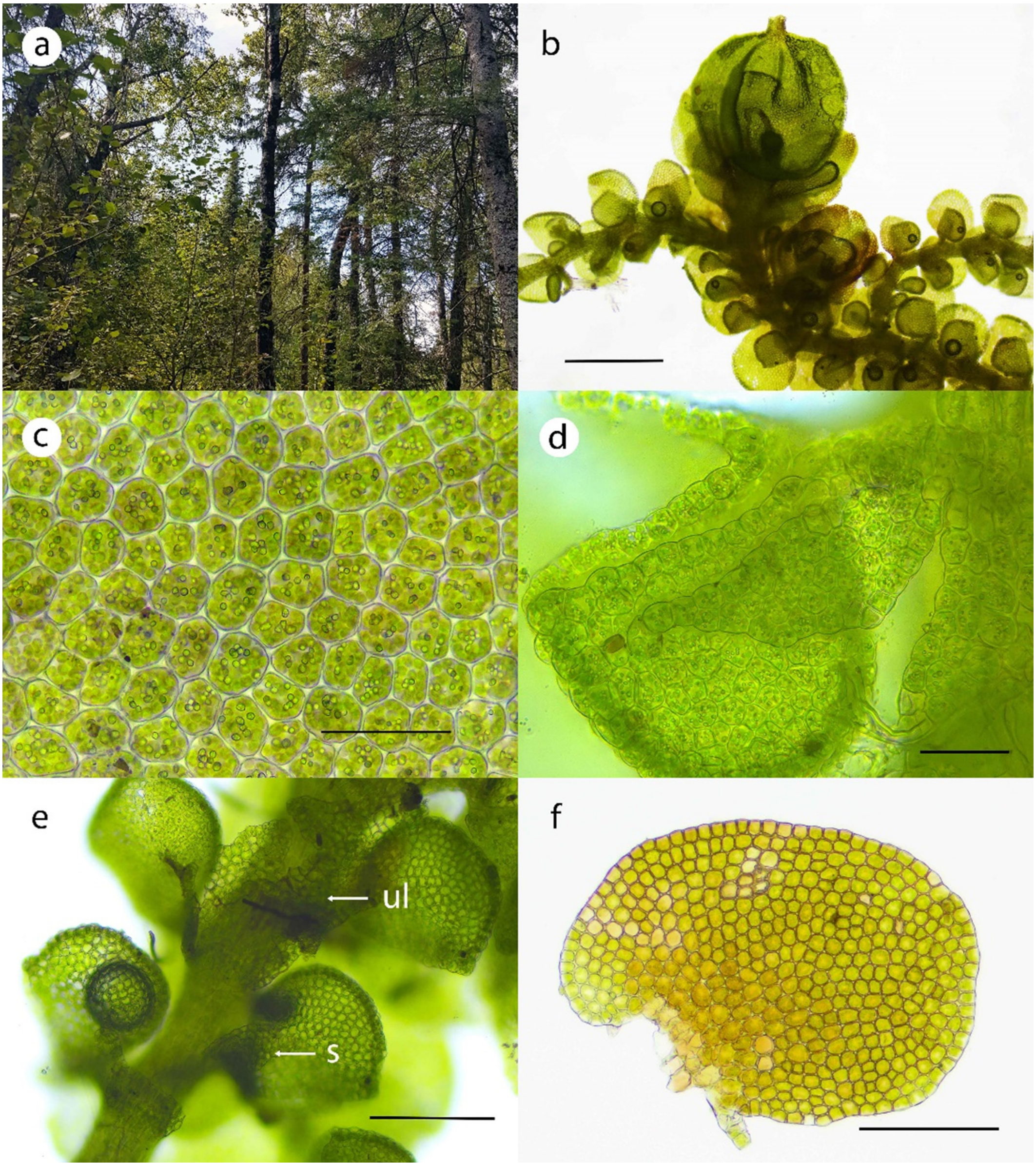

FIGURE 4. Images of *Frullania stylifera* from Buffalo Point First Nation, Manitoba, Canada. a. Forest habitat where specimens were collected (*Caners 8783, 8790*). b. Portion of a plant with capitate androecium below the perianth (scale bar = 0.5 mm; from specimen *Caners 8783*). c. Median cells of a dorsal lobe, each containing numerous oil bodies (scale bar = 50 µm; from specimen *Caners 8790*). d. Close-up of a lamellate stylus (scale bar = 50 µm; from specimen *Caners 8790*). e. Ventral view of a plant showing the stylus (s) adjacent to an underleaf that was removed, galeate lobules (typical of the genus), and an underleaf (ul) that is approximately twice the diameter of the stem (scale bar = 200 µm; from specimen *Caners 8790*). f. Dorsal lobe with cordate base (scale bar = 200 µm; from specimen *Caners 8783*). Photos: Richard Caners.

and *F. austinii* occur in North America, with the latter being widespread in the east (including the populations that were previously included within *F. bolanderi*) and the former being restricted to the west (Mamontov *et al.* 2020). The western distribution of *F. austinii* in North America has not been determined, and the presence of both species within a region is possible (Mamontov *et al.* 2020). *Frullania austinii* was recently confirmed for Manitoba, and it is likely that all material from the province named *F. bolanderi* is *F. austinii* (R.T.C. unpubl. data). *Frullania austinii* consistently has rigidly erect, flagelliform shoots with caducous leaves that are lacking in *F. stylifera*. Furthermore, *F. austinii* has slightly smaller lamellate styli that are 6–10 cells long and 3–5 cells wide, dorsal lobes with truncate bases, and dioicous sexual condition (Mamontov *et al.* 2020).

Frullania oakesiana is small relative to *F. stylifera* and other *Frullania* species in Manitoba. The species is similar to *F. stylifera* in being autoicous, but differs in having small, subulate styli that are 4–5 cells long and 1–3 cells wide at the base. The lobules of *F. oakesiana* are large relative to the size of the dorsal lobes. *Frullania oakesiana* also has dorsal lobes that are ovate to orbicular in shape and rounded or truncate at the base, with 3–5 oil bodies per cell. *Frullania stylifera* in comparison has much smaller lobules relative to the size of dorsal lobes and differs in the shape of the dorsal lobes and number of oil bodies (Table 1).

Phorophytes

Frullania stylifera has been collected from the bark of several tree and shrub host species. Schuster (1992) reported the type collection of the species from exfoliating bark of sumac (*Rhus* L.). More recently, Atwood (2016) reported new records of species from the bark of oak (*Quercus* L.), particularly Post Oak (*Quercus stellata* Wangenheim), and from hickory (*Carya* Nuttall), Black Walnut (*Juglans nigra* L.), hackberry (*Celtis* L.), maple (*Acer* L.), Persimmon (*Diospyros virginiana* L.), ash (*Fraxinus* L.), Eastern Red Cedar (*Juniperus virginiana* L.), Osage Orange (*Maclura* Nuttall), and arrow-wood (*Viburnum* L.). The specimens collected from Buffalo Point First Nation were growing on the bark of Beaked Hazelnut (*Corylus cornuta* Marshall; *Caners 8783*) and the trunk of Paper Birch (*Betula papyrifera* Marshall; *Caners 8790*). These are two new phorophyte species for *F. stylifera* in North America and globally. In Russia, the species has been collected from European Aspen (*Populus tremula* L.), Broadleaf White Birch (*Betula platyphylla* Sukaczev), European Bird Cherry (*Padus avium* Miller), and willow (*Salix* L.) (Konstantinova *et al.* 2020).

Conclusions

Frullania stylifera is currently known from temperate broadleaved forests of interior and eastern United States (Atwood 2016) and Europe (Konstantinova *et al.* 2020), as well as from the boreal zone of the mountains of south Siberia in Asian Russia where it is restricted to coniferous and mixed forests (Konstantinova *et al.* 2020). The diversity of habitats in which *F. stylifera* has been reported in North America and globally suggests that it could be found across larger areas of Canada, including the large expanse of Great Lakes forest to the east of the study area (Figure 1) and possibly into the more northerly boreal forest where *F. eboracensis* is reported, albeit infrequently (BRYOQUEL 2023; Consortium of Bryophyte Herbaria 2023). The study area where *F. stylifera* was found in Manitoba has the highest total annual precipitation and approaches the highest mean annual temperatures in the province (Climate Atlas of Canada 2023). Whether the species extends into more northerly areas of boreal forest with lower total annual precipitation and annual temperatures remains to be investigated. Several bryophytes with a temperate world distribution that are common in eastern North America seem to reach their northern and/or western distribution limits in the study area (Caners 2017, 2020) suggesting that conditions beyond these occurrences are likely unsuitable for them.

Expanded surveys for *F. stylifera* in southern Manitoba are likely to reveal additional records. The forest habitat in which the species was found at Buffalo Point First Nation is abundant in the Great Lakes–St. Lawrence Forest Region. However, the occurrence of *F. stylifera* in Manitoba is currently the most northern record for the species in North America and is presumably close to its northern range limits in the province. Inspection of past herbarium specimens, especially *F. inflata* and *F. eboracensis*, may reveal misidentified specimens of *F. stylifera*, as observed by Atwood (2016). The confirmation of new records by examining herbarium specimens could inform the potential distribution of the species in Canada and help to determine its northern limits.

Voucher specimens

CANADA, MANITOBA: c.fr. [*cum fructibus*, meaning "with sporophytes"], Buffalo Point First Nation. On the bark of a large Beaked Hazelnut (*Corylus cornuta* Marshall). 49.01°N, 95.29°W. Elevation: 330 m. *R.T. Caners 8783* (PMAE), identified by R.T. Caners and verified by John J. Atwood (Missouri Botanical Garden).

CANADA, MANITOBA: c.fr., Buffalo Point First Nation. On the bark of a large Paper Birch (*Betula papyrifera* Marshall). 49.01°N, 95.29°W. Elevation: 330 m. *R.T. Caners 8790* (PMAE), identified by R.T. Caners and verified by John J. Atwood.

Specimens examined

The following specimens of *F. stylifera* from Missouri Botanical Garden (MO) were examined:

USA, MISSOURI: **Montgomery County**. Grand Bluffs Conservation Area, Grand Bluffs Natural Area, forested bluff top ~0.8 mile [1.3 km] NE of Bluffton, persimmon grove with 3–4″ [7.6–10 cm] dbh (diameter at breast height) trees on SW slope, on tree trunks with *Frullania eboracensis*, 38.7069°N, 91.60897°W, 850–900 feet [262–274 m], 24 July 2018, *John J. Atwood 3672* (MO-6898570), determined by J. Atwood (2018). **Camden County**. Open field with exposed limestone along county road H, ca. 2 miles [3.2 km] west of Richland, Sec. 14, R14W, T36N, 37.85°N, 92.4288°W, 23 September 1960, *Paul L. Redfearn, Jr. 7516* (MO-3957657), determined by J.J. Atwood (2015). **Cedar County**. Bark of oak, ~1 mile [1.6 km] SW of Bear Creek, Sec. 21, T34N, R25W, 37.6852°N, 93.676°W, 22 July 1960, *Paul L. Redfearn, Jr. 6859A* (MO-3956669), determined by J.J. Atwood (2015).

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Retrospective comparison of the distribution and abundance of breeding Prairie Warbler (*Setophaga discolor*) along eastern Georgian Bay, Ontario, Canada

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Abstract

Species inhabiting rare habitats or unique geographic regions may be underrepresented in standard surveys. More intensive, periodic surveys may be required to improve data quality, especially for species of conservation concern. Prairie Warbler (*Setophaga discolor*) has experienced range-wide declines of >50% in recent decades and is a species of conservation concern in Canada. The largest continually occupied breeding population of this species in Canada occurs along the shoreline of eastern Georgian Bay, Ontario, where annual Breeding Bird Survey and eBird coverage is generally poor. In 2015, we replicated a spatially intensive 1997 survey of this species along the eastern shore of Georgian Bay, visiting the same sites and using comparable methods. We detected more male birds at the survey sites in 2015 (estimated >350 breeding pairs) than in 1997 (estimated 265 breeding pairs). We also surveyed sites farther north than those covered in 1997, but the breeding range appears not to have moved substantially northward. We also conducted additional surveys and canoe transects in the core range in southern Georgian Bay to ensure that breeding birds were not being missed. Combining data from all our surveys in 2015, we estimated a total of 427 singing males in eastern Georgian Bay. Although overall numbers here appear to have increased in recent decades, localized declines in some areas warrant further investigation. The population appears to be stable or increasing in this region, but we recommend intensively re-surveying this population on at least a 20-year basis.

Key words: Warbler; songbird; Neotropical migrant; survey; conservation; management

Introduction

Monitoring bird species over time and space is critical for documenting population changes and informing management efforts (Ralph *et al.* 1995). When the goal is to infer changes in population distribution or abundance, species occupying rare or more remote habitats may be missed by existing large-scale monitoring efforts (Tulloch *et al.* 2013). This is especially true if high reliability of inference is needed to guide actions, such as assessing a species status (Francis *et al.* 2009) or deciding on management for species of conservation concern (Regan *et al.* 2008). Therefore, habitats or regions that are underrepresented by existing surveys may require periodic targetted surveys to improve data quality and coverage (Tulloch *et al.* 2013).

The breeding range of Prairie Warbler (*Setophaga discolor*) includes much of the eastern United States and a few known locations in southern Ontario, Canada (Lambert and Smith 1984; Sullivan *et al.* 2009; Nolan *et al.* 2020). The widespread, nominate subspecies, *Setophaga discolor discolor*, typically occupies shrubby, early-successional habitats maintained by fire or human disturbance across the breeding range (Askins *et al.* 2012; Akresh *et al.* 2015; Can *et al.* 2019). In Ontario, breeding habitat generally consists of sparsely vegetated rock barrens maintained by periodic fire or harsh climatic conditions, and occasionally sparse, shrubby sand dunes (Lambert and Smith 1984; Sutherland and Harris 2007). Typical breeding sites on vegetated rock barrens include Common Juniper (*Juniperus communis* L.) and a sparse overstorey of Eastern White Pine (*Pinus strobus* L.), White Oak (*Quercus alba* L.), and Red Oak (*Quercus rubra* L.; Harris 1998). The largest continually occupied breeding population of Prairie Warbler in Ontario occurs along the shoreline and numerous nearshore islands in southeastern Georgian

Bay. Other small and intermittently occupied breeding populations occur at a few scattered inland sites on the southern edge of the Precambrian Shield in southern Ontario (Sutherland and Harris 2007; Hannah *et al.* 2021). Given that most Prairie Warbler breeding sites in Ontario are associated with areas of exposed granitic rock and shoreline, road densities in these areas are low and access is logistically challenging. Because most breeding sites remain remote and isolated, routine surveys to assess population status and distribution for this species preclude routine inferences about population status, distribution, and trends. We did not find any nests in our coarse evaluation of habitat so cannot expand on these general descriptions.

Based on estimated range-wide population declines of approximately 53% (−1.72%/year) and ongoing habitat loss on both breeding and wintering grounds, conservation concern for this species is high (Environment Canada 2014; Rosenberg *et al.* 2016). In recent decades, several small, isolated breeding populations have disappeared in southern Ontario (Sutherland and Harris 2007), suggesting the species might be declining in the province. Previous estimates suggest that the population in Ontario consisted of ~320 breeding pairs, with 270 of them occurring in southeastern Georgian Bay (Harris 1998; Sutherland and Harris 2007). In recent decades, increased human activity along eastern Georgian Bay, including residential and cottage developments (Sivarajah *et al.* 2018; Neumann *et al.* 2021), may be negatively affecting breeding habitat for this species at the core of its breeding range in Ontario.

In 1997, Harris (1998) conducted the largest and most systematic survey of Prairie Warbler in eastern Georgian Bay to date, visiting 420 sites with suitable habitat. In 2015, we repeated and expanded the spatial extent of this original survey. We hypothesized that the population may have declined in recent decades, based on increased human development in eastern Georgian Bay, combined with increased threats during the non-breeding season (Rosenberg *et al.* 2016). We also hypothesized that, because of these human developments and the possible succession of habitat into more closed-canopy forests through climate change (Hitch and Leberg 2007), the breeding population of this species may have expanded northward. Because very few breeding season records exist for this species along the northern half of the eastern shore of Georgian Bay (Sullivan *et al.* 2009), we were uncertain whether the current breeding range was a result of lack of survey coverage, a habitat or climate limitation, or both. To determine if the species occurs north of the previously described range, we also selected and surveyed random sites north of those visited by Harris (1998). Finally, we summarize the results from all of our surveys and incidental detections in eastern Georgian Bay in 2015 to estimate the total number of Prairie Warbler in our study area.

Methods

Study area

Georgian Bay is the eastern arm of Lake Huron and has a surface area of 15 000 km^2 (Campbell 2017). The shoreline of eastern Georgian Bay is rugged, consisting of granite outcrops and numerous offshore islands (Harris 1998). Vegetation is characterized by mature, but stunted, forest (e.g., ~3–6 m canopy), consisting mainly of mature White Pine, Red Oak, White Oak, and Common Juniper (Lambert and Smith 1984). The area also contains small, localized agricultural and urban developments (~6% of the area; Neumann *et al.* 2021).

Survey designs

Harris 1997—Harris (1998) restricted surveys (Figure 1) to sections of the eastern Georgian Bay shoreline with suitable habitat or sites where Prairie Warbler was recently sighted. Habitat was judged visually for suitability based on the presence of open rock outcrops with mature trees (pine and oak) and shrubby vegetation (juniper and oak). A total of 420 locations were visited across the survey area, stretching from Midland in the south, to just west of Parry Sound in the north. Attempts were made to maintain a minimum distance of 400–500 m between adjacent survey points because bird song seemed to travel extensively over water, but because of the convoluted nature of the shoreline this was not always possible. Sites were visited systematically to reduce the potential for duplicating counts of singing birds. Given the low density of roads in this area and the high suitability of shoreline habitat for this species, most surveys, with few exceptions, were conducted by motorized boat. All survey sites were recorded on a 1:10 000 base map of the region.

Harris re-survey 2015—Survey sites visited by Harris in 1997 were georeferenced so that 2015 revisits were as close to the original sampling sites as possible. Similar to the 1997 surveys, we used motorized boats and visited sites systematically to reduce potential for double-counting individual birds (Harris 1998).

Northern Georgian Bay—To sample areas north of the original Harris survey area from 1997, we used a grid consisting of 1-ha (~50-m radius) hexagons along the shoreline of Georgian Bay as our sampling frame. The general sampling area extended from Parry Sound in the south to French River Provincial Park in the north (Figure 1). To include birds on numerous large nearshore islands, we extended the sampling grid out to 2 km from the mainland. Hexagons with centroids located in water were eliminated

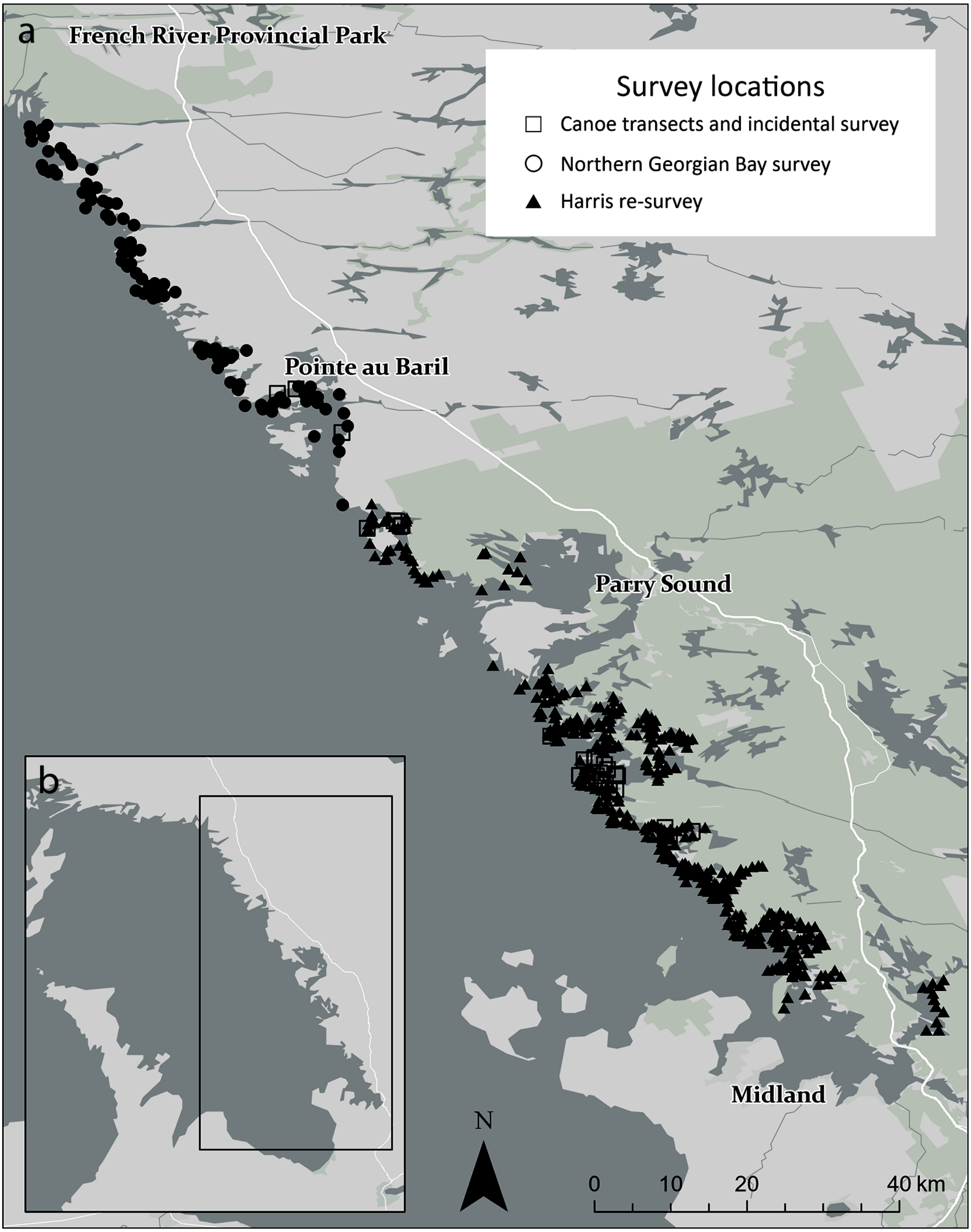

FIGURE 1. a. Prairie Warbler (*Setophaga discolor*) survey locations in eastern Georgian Bay, Ontario in 2015, by survey type. Inset map b. provides the location of the study area in eastern Georgian Bay.

unless 25–75% of the total area within the hexagon was land. Given that male Prairie Warblers appear to prefer shoreline habitat in this area, this range was chosen to avoid selecting sites with little or no shoreline. We randomly selected 350 centroids as our survey sample.

Canoe transects—In extensive areas of shoreline in both northern Georgian Bay and the core of the Prairie Warbler's breeding range, we were unable to conduct surveys using motorboats. We supplemented counts from motorboats with constant-effort shoreline surveys conducted by canoe (Figure 1). This method enabled us to sample many of the shallow bays and small inlets that motorboats were unable to access. The starting points for transect survey routes were selected based on existing spatial coverage gaps, but we defined specific survey routes and sampling duration by daily logistics and weather. Canoes were occupied by a team of two observers and transect routes were typically within hearing distance (≤100 m) of the shoreline.

Field methods

Point count surveys—At each survey point for both the Harris 1997 re-survey and the Northern Georgian Bay survey, we conducted a standard 5-min, unlimited radius point count. Surveys were conducted from 26 May to 20 June 2015, starting around local sunrise and typically ending by late morning. On days when weather permitted, we extended surveys into the afternoon to cover more points. Male Prairie Warblers continue vocalizing well into the afternoon and evening, although often at reduced rates (Harris 1998; Hannah *et al.* 2021). To account for reduced singing rates, we broadcast a 1-min playback of the primary song of Prairie Warbler immediately following the 5-min passive point count during every survey. Harris (1998) mentions including call playback during surveys as well, but the duration and success of this approach were not described. We added an additional 1-min passive listening period following playback to record any birds not detected during the first 5 min. We conducted point counts on days with favourable weather (calm winds) and little precipitation.

Canoe transect surveys—Tracklogs were recorded on handheld global positioning units and a locational waypoint was recorded whenever a singing Prairie Warbler was detected. We used a compass to estimate distance and bearing for each singing bird from a marked waypoint to estimate its location more accurately. We mapped these waypoints and compared them with the locations of our other survey points (i.e., historical and northern Georgian Bay point counts). To avoid double-counting individuals, we removed any detections of singing birds from canoe surveys that were ≤400 m from an existing survey location. Similar to point counts, surveys often extended into the afternoon, so we used shorter 3-min call-playback surveys (1 min passive listening, 30 s call playback, 90 s passive listening) at sites with apparently suitable habitat, but outside the typical morning bird survey period, to encourage male singing. Transect surveys were also conducted during favourable weather conditions.

Incidental detections—We marked waypoints and estimated the distance and direction of all incidental detections of singing birds heard ≥400 m from an existing survey location. We also conducted targetted searches along extensive stretches of shoreline in areas of suitable habitat not covered by existing point counts. Our survey technique involved slowly cruising the shoreline in the motorboat listening for singing birds, noting their location if present and periodically conducting short-duration (3 min) call-playback surveys if spontaneous singing was not detected. We focussed our incidental survey efforts in the core areas of the breeding range in southeastern Georgian Bay.

Population estimate

To estimate the population size in the areas we surveyed in eastern Georgian Bay, we counted all individual singing male Prairie Warblers. This estimate includes a total count of unique males from the Harris 2015 re-survey, the northern Georgian Bay survey, the canoe transect surveys, and any additional incidental detections.

Results

Compared with Harris's 1997 survey (Harris 1998), we detected more birds (321 versus 241) in 2015 at the same sites and more of the 416 accessible sites were occupied (233 versus 170; Table 1). To

TABLE 1. Detection of Prairie Warbler (Setophaga discolor) in a 1997 survey and in our 2015 re-survey.

	1997 sites*		2015 sites
	All	Accessible in 2015†	
No. sites surveyed	420	416	416
No. occupied sites (%)	174 (41.4)	170 (40.9)	223 (53.6)
Total no. individuals observed	245	241	321
Mean no. birds per site (SD)	0.582 (0.843)	0.579 (0.838)	0.772 (0.872)
Estimated no. breeding pairs (+10%)	270	265	353

*Harris 1998.

†Four sites visited in 1997 were not accessible in 2015 because of slightly lower water levels and use of a larger motorboat.

determine any potential northward shifts in the core Prairie Warbler breeding range, we surveyed 97 randomly selected sites in northern Georgian Bay from 1 to 7 June and detected only three singing males at two sites. Given that sites occupied by males were at the southern limit of our northern survey and we detected no additional males farther north, we discontinued this survey to focus our efforts elsewhere.

We detected 36 male Prairie Warbler on the 12 canoe transects (2–11 June) which covered 211.58 km of shoreline (average 17.63 km ± 5.6 km SD). We recorded an additional 28 males incidentally in eastern Georgian Bay, while travelling in motorboats from 2 to 20 June 2015. Although the detection of several males was purely incidental (e.g., hearing spontaneous singing while anchored near shore), we detected several birds while slowly cruising the shoreline or circumventing several large, previously unsurveyed islands that were outside the Harris (1998) survey area.

In total, we detected 388 individual singing male Prairie Warbler from the Midland area in the south, north to Pointe au Baril Channel (Figure 2) during point count surveys, canoe transect surveys, and incidental observations in eastern Georgian Bay.

Discussion

In our various surveys in eastern Georgian Bay in 2015, we detected 388 male Prairie Warbler. Although this is a considerable increase over the previous estimate of 270 breeding birds in 1997, we surveyed areas that were previously missed (Harris 1998; Sutherland and Harris 2007). Even though Harris (1998) compensated for missing birds on his 1997 surveys by adding an additional 10% to the total count (as we did: see Table 1), this is still likely an underestimate. As Harris (1998) made no reference to incidental observations (i.e., birds detected at non-survey locations), it is assumed there were none. In contrast in 2015, we spent considerable time conducting additional surveys in areas of suitable habitat that were not surveyed in 1997 and documenting all incidental observations. Given the >4500 km of shoreline in eastern Georgian Bay (Midwood *et al.* 2012), portions of which remain relatively inaccessible, the number of male Prairie Warbler we detected likely still represents an underestimate. Adding an additional 10% to our 388 total—a conservative number— results in a total estimate of 427 males in our survey area.

In contrast to our first hypothesis that numbers of birds have declined because of various threats, we detected more Prairie Warbler overall and a greater average number of birds per survey site in 2015 (Table 1) compared with 1997 (Harris 1998). In addition to detecting more individuals and more occupied sites in the 2015 surveys, we also detected 64 additional males during canoe transects and incidentally, methods not used and data not collected by Harris (1998). Our more spatially extensive systematic survey in the core range of Prairie Warbler in Canada included many areas of suitable habitat that had not been previously surveyed. Most areas with suitable habitat appeared to be occupied by singing males, detected as a result of our increased sampling efforts.

Disregarding these additional detections, our repeat point counts could suggest a population increase since 1997. Harris (1998) thought it unlikely that he had overlooked significant sections of the Georgian Bay shoreline and immediately adjacent mainland, based on the 420 sites surveyed. It seems unlikely that a substantial amount of additional suitable habitat would have been created in the decades since the original survey. Because both surveys were conducted in a single year and bird density can vary between years (e.g., Sillett *et al.* 2000; Rodenhouse *et al.* 2003), it is possible that one or both survey years may not have been representative of the typical population. However, surveying this population more frequently is both logistically challenging and costly, although subsampling smaller areas in the core breeding range might be a feasible compromise.

We did not find evidence of a substantial northward expansion of the breeding range of Prairie Warbler in eastern Georgian Bay caused by habitat changes and human development, our second hypothesis. Harris (1998) detected six individuals at five sites in the two most northerly survey areas near Parry Sound. Our 2015 count in these areas was only slightly higher at nine individuals at eight sites. Despite the lack of any obvious visual changes in the habitat structure or tree species composition along the eastern shore of Georgian Bay, we only detected a small number of birds north of the known breeding range. Others have suggested that the breeding range of Prairie Warbler, a neotropical migrant, has shifted slightly north in recent decades as a result of global climate change (e.g., 1967–1971 versus 1998–2002 in Hitch and Leberg 2007; Rushing *et al.* 2020). Although we detected male Prairie Warbler in the Pointe au Baril area, ~30 km north of the most northerly occupied sites in the Parry Sound area in 1997, this area was not surveyed by Harris. Therefore, it is possible that breeding Prairie Warbler may have been this far north in Georgian Bay, but were not detected previously. The cooler temperatures of the bay could moderate the climate of the eastern Georgian Bay shoreline Prairie Warbler habitat; reduced insect prey abundance or availability may therefore limit the bird's distribution in this region. Continued monitoring of suitable habitats north of the known breeding range may be important

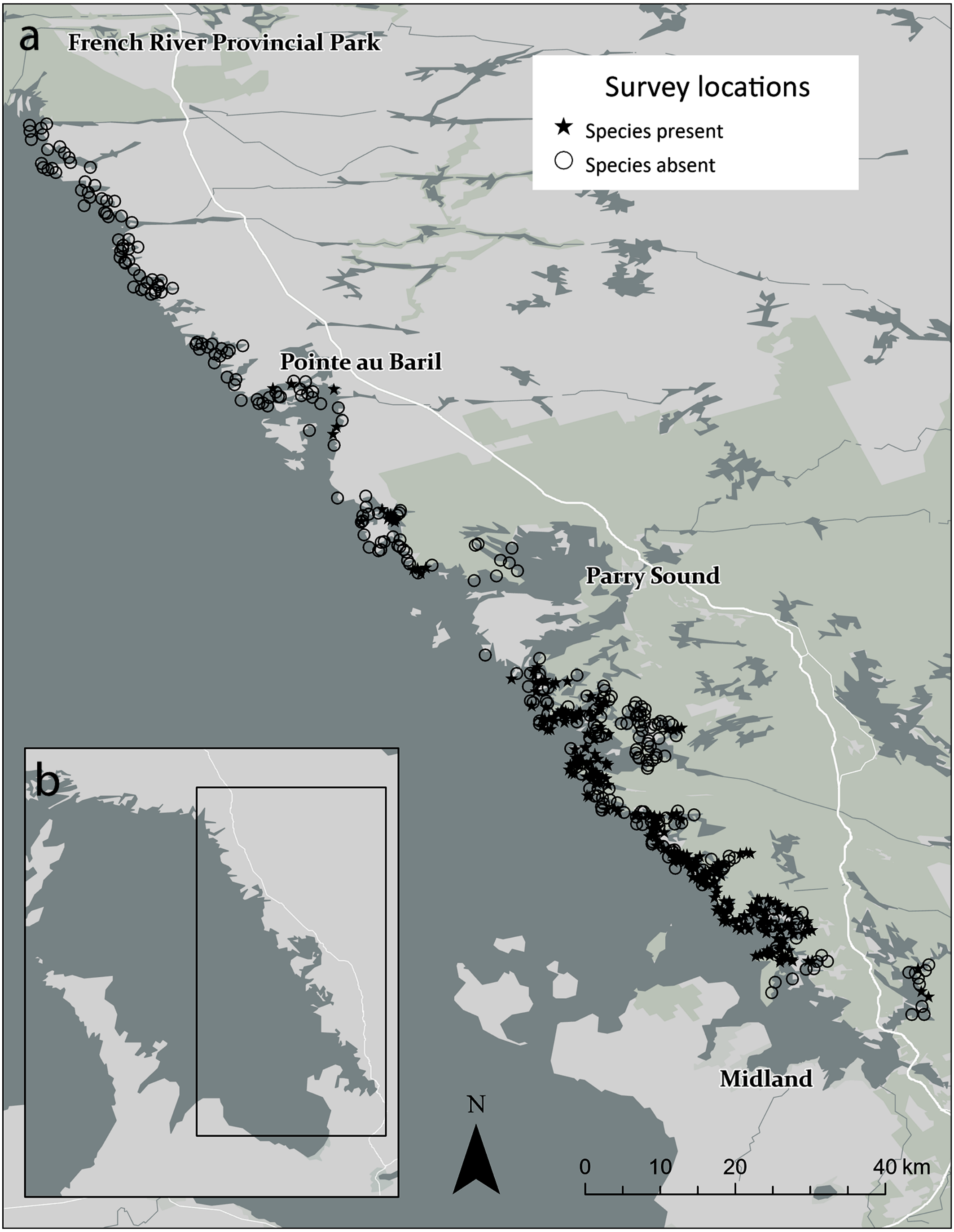

FIGURE 2. a. Survey locations in eastern Georgian Bay, Ontario, where Prairie Warbler (*Setophaga discolor*) was present or absent in 2015. Inset map b. provides the location of the study area in eastern Georgian Bay.

in understanding if range shifts are occurring. Similarly, it would be valuable to develop species distribution models in eastern Georgian Bay to understand which habitat variables are important for this species and their distribution in this region.

Clearly, despite the perceived habitat changes resulting from increased housing and cottage development in this region in recent decades (Sivarajah *et al.* 2018; Neumann *et al.* 2021), there was no decline in the detectable Prairie Warbler population. Our surveys suggest that Prairie Warblers are largely unaffected by the presence of lakeside cottages, as many birds detected in 2015 were close (<100 m) to dwellings. The limited presence of human activity during the June nesting period may be one reason why the birds seem undisturbed by the presence of cottages, many of which were not in active use during the 2015 survey period. Perhaps too, because the vast majority of cottage owners have left their properties in a natural state (i.e., native vegetation, such as Common Juniper, not replaced with manicured lawn), the openings around the dwellings still provided good breeding habitat for Prairie Warblers. The southeast portion of the study area was an exception to this pattern of cottage activity and native landscaping; housing density along the shoreline often approached urban levels. Many cottages in this area were used year-round, in part because of ease of road access, and many were surrounded by manicured grounds. It may not be coincidental that few Prairie Warblers were found in that area in 2015.

Despite recent concerns for this breeding population of Prairie Warbler in eastern Georgian Bay, our survey results clearly suggest that this population has not declined overall in recent decades and may, in fact, have increased. Given the remoteness of much of this region and the lack of coverage by most bird monitoring programs, we recommend that this survey be repeated on a 20-year basis. In addition, as in our 2015 survey, efforts should be made to survey suitable habitat between established point count locations and in shallow bays. Finally, future surveys should also be considered north of Pointe au Baril to determine if the range of this breeding population is moving northward.

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Note

Branching Burreed (*Sparganium androcladum* (Engelmann) Morong; Typhaceae) rediscovered in Ontario, but conservation status unclear

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Abstract

We report three new records of Branching Burreed (*Sparganium androcladum*), which has not been seen in Ontario in several decades. This species is understudied and has been confused with other taxa, primarily American Burreed (*Sparganium americanum*). It is not known when it was last collected in the province, and its conservation status is unclear. Specimens identified as Branching Burreed are few and do not fully clarify the situation; of the 14 putative *S. androcladum* specimens we examined, five are too immature to verify confidently, and at least seven are misidentified. Previous specimen-based maps are probably not accurate representations of Branching Burreed's provincial distribution, but it is likely more widespread than records indicate. We provide a description of our new records and notes on identification to provide a basis for additional study of this plant.

Key words: Rubanier rameux; Branched Burreed; *Sparganium androcladum*; rediscovery; Canada; Ottawa River

We found three new locations of *Sparganium androcladum* (Engelmann) Morong (Branching Burreed, Rubanier rameux) in eastern Ontario in 2022 and 2023. Two are along the Ottawa River in the City of Ottawa (François Dupont Park and Petrie Island) and one is in a bay of the Rideau River at Murphys Point Provincial Park. Both Ottawa River locations are in emergent riverine marshes (Figure 1) dominated by mostly vegetative *Sparganium* spp., often with *Pontederia cordata* L. (Pickerelweed, Pontédérie cordée), *Sagittaria latifolia* Willdenow (Broad-leaved Arrowhead, Sagittaire à larges feuilles), *Hydrocharis morsus-ranae* L. (European Frog-bit, Hydrocharide grenouillette), and *Nymphaea odorata* Aiton (Fragrant Water-lily, Nymphéa odorant). The *Sparganium* marshes consisted mostly of plants without fruiting stems. Aside from local patches of *Sparganium eurycarpum* Engelmann (Broad-fruited Burreed, Rubanier à gros fruits), almost all vegetative plants were consistent in size with the fruiting plants we confirmed as Branching Burreed. We estimate this could amount to thousands to tens of thousands of Branching Burreed plants. Detailed collection notes were not made for the Murphys Point location.

Branching Burreed is a native species that is noteworthy for being uncommon over a discontinuous range from the Great Lakes, east across southern Quebec and Maine, and south to Oklahoma and Tennessee (Kaul 2000). This North American endemic is of conservation concern in almost all provinces and states within this distribution (NatureServe 2022). Before our discoveries, it had not been reported from Ontario for several decades (Argus *et al.* 1987). However, as we discuss below, it has likely been overlooked because of its morphological similarity to the common and widespread *Sparganium americanum* Nuttall (American Burreed, Rubanier d'Amérique). It may be a legitimately rare plant for reasons not yet understood; its true conservation status in Ontario, and likely elsewhere, remains incompletely known. This is reflected in the current provincial conservation status rank, which has been updated to SU (Unrankable; NHIC 2024) following our discoveries.

Previously, Argus *et al.* (1987) reported Branching

FIGURE 1. Branching Burreed (*Sparganium androcladum*) habitat. a. François Dupont Park, Ottawa, Ontario, *Chapman-Lam & Sokoloff 5748.* b. Petrie Island, Ottawa, Ontario, *Chapman-Lam & Sokoloff 5749*. Photos: P.C. Sokoloff.

Burreed as a rare species in Ontario, mapping only nine widespread records in the province, roughly from Casselman, eastern Ontario, southwest to the Niagara Peninsula and the London area. They noted that only three of these localities are represented by collections made since 1935. There have been no other new confirmed Ontario reports since the Argus *et al.* (1987) synopsis, although Étienne Léveillé-Bourret (pers. comm. 2023) has verified several 2021 specimens from the Parc national de Plaisance, on the Quebec side of the Ottawa River, roughly 27 km east of Petrie Island (reported in Garon-Labrecque *et al.* 2022).

We reviewed all Ontario specimens of putative *S. androcladum* and *S. americanum* that are in the major herbaria in Ottawa, the National Herbarium of Canada (CAN) and the National Collection of Vascular Plants (DAO), as well as the Gray Herbarium, Harvard University (GH), the Royal Botanical Gardens Herbarium, Hamilton (HAM), and the University of Guelph Herbarium (OAC). Will Van Hemessen (pers. comm. 2023) examined the American Burreed specimens at the Dr. Laurie L. Consaul Herbarium, University of Western Ontario (UWO). Of the 14 putative Branching Burreed specimens, we found that five were too immature to determine with complete certainty and suspected that at least seven were misidentified. Branching Burreed is typically distinguished by its larger, shiny fruit; however, definitive measurements can only be made when they are mature (Sulman and Smith 2019). We could be confident that the original identifications were correct for only three of the 14 specimens. The most recent of these was collected from Chippewa Creek Conservation Area, Niagara Region, in 1973 (*Putman 123*), 49 years before our 2022 collections.

Reports of Branching Burreed are often based on misidentifications (J. Sulman pers. comm. January 2023), most likely because of its morphological similarity to American Burreed. Scoggan (1978: 193) considered Branching Burreed “scarcely separable” from American Burreed and Fernald and Eames (1907) included the former within the latter. Recent works have treated Branching Burreed as a species (e.g., Crow and Hellquist 2000; Haines 2011; Voss and Reznicek 2012; Sulman and Smith 2019). This similarity has probably also led to Branching Burreed being overlooked. For example, Albert Dugal conducted a botanical inventory of Petrie Island in 1977, reporting only two burreeds: American Burreed and Broad-fruited Burreed (Hanrahan 2003). Unfortunately, we could find no corresponding specimens. We scoured nearly all accessible marshes on Petrie Island (over 4 km) in 2022 and found only Branching Burreed and Broad-fruited Burreed. This suggests that Dugal likely overlooked Branching Burreed on Petrie Island and, perhaps, confused Branching Burreed with American Burreed.

With so few confirmed records and considerable identification issues, it is difficult to reliably assess Branching Burreed’s conservation status in Ontario. It seems that existing specimen-based distribution maps (e.g., Hébert 1973; Argus *et al.* 1987) are probably not accurate representations of its provincial distribution. As an overlooked species, it is likely more widespread than current records indicate; however, it is difficult to estimate how common it may be as its presence in suitable habitat is generally sporadic and unpredictable (J. Sulman pers. comm. January 2023). Its river and lakeshore habitat appears relatively abundant, but we cannot predict how much of this habitat it occupies without further search effort. We encourage targetted searches for Branching Burreed along the Ottawa River, at historical sites, elsewhere in Ontario, and beyond.

To support search efforts, we compiled key characters from the literature that distinguish Branching Burreed from American Burreed. We recorded measurements during our specimen review and summarize the characters and our results in Table 1. The characters are also illustrated in Figure 2. Our three Ontario specimens with mature fruit generally fall within the dimensions reported for Branching Burreed (see Table 1). We found that stigma length could be highly variable within a single pistillate head, but examination of many achenes yielded several with stigmas that exceeded the range reported for American Burreed. Hébert (1973) and É. Léveillé-Bourret (pers. comm. 2023) note that Branching Burreed has red flecks at the base of its achenes, which we also observed on mature Ontario specimens (Figure 3). We have not seen this character reported elsewhere, although Voss and Reznicek (2012) have noted basal red flecks on *Sparganium emersum* Rehmann (Green-fruited Burreed, Rubanier à fruits verts). Even immature

TABLE 1. Morphological characters distinguishing Branching Burreed (*Sparganium androcladum*) from American Burreed (*Sparganium americanum*)*.

Morphological feature	*Sparganium androcladum*	*Sparganium americanum*
Mature fruit	Glossy apically; dull, pitted, and with red flecks basally	Dull throughout
Head diameter	2.5–3.5 cm (2.4–2.6 cm)†	1.5–2.5 cm (2.0–2.5 cm)
Beak length	4.0–7.0 mm (5.0+ mm)	1.5–5.0 mm (3.0–5.0 mm)
Stigma length	2.0–3.2 mm (2.2–2.8 mm)	0.8–1.5 mm (0.7–1.5 mm)
Anther length	1.1–1.4 mm (1.1–1.3 mm)	0.6–1.1 mm (0.8–1.2 mm)
Inflorescence branches	Staminate heads only (rarely with a pistillate head)	Usually 1–3 pistillate heads each

*Sources: Compiled from Sulman and Smith (2019), Haines (2011), Hébert (1973), and Kaul (2000).

†Note: Measurements in parentheses are from mature Ontario specimens (three *S. androcladum* and nine *S. americanum*).

FIGURE 2. Branching Burreed (*Sparganium androcladum*) a. habitat at Petrie Island, Ottawa, Ontario, *Chapman-Lam & Sokoloff 5749*; b. staminate heads; and c. fruiting pistillate heads, François Dupont Park, Ottawa, Ontario, *Chapman-Lam & Sokoloff 5748*. Photos: P.C. Sokoloff.

Green-fruited Burreed material is typically readily distinguished from Branching Burreed by its supra-axillary pistillate heads. However, Voss and Reznicek (2012) note that rarely, Green-fruited Burreed may have entirely axillary pistillate heads. These should be distinguishable from Branching Burreed by their unbranched inflorescences and typically smaller fruit (see references in Table 1 for measurements).

Specimens Examined

Sparganium americanum Nuttall—CANADA, Ontario. Note all Ontario specimens in CAN, DAO, HAM, and OAC were examined. The following is a list of specimens from which measurements were taken: **Frontenac Co.**, 7258 m (4.5 miles) in Arab Lake Loop, very abundant around beaver pond, 26 July 1977, *S. Wiesenberg s.n.* (DAO); Frontenac

FIGURE 3. Mature achenes of Branching Burreed (*Sparganium androcladum*: a. *Chapman-Lam & Sokoloff 5748,* b. *Macoun 28051*, and c. *Gillett 14657*) and d. American Burreed (*Sparganium americanum*, *Brunton 2677*). Scale bars are 1 mm for a–c and 750 µm for d. Photos: P.C. Sokoloff.

Park, S shore of Salmon Lake, floating bog margin, 5 August 1968, *Hainault & MacDonald 4607* (DAO); **Haliburton Co.**, Wren Lake, at Highway 35, sheltered (from waves) on sand, 13 August 1975, *H.M. Dale s.n.* (OAC); **Hastings Co.**, Westemakoon Lake Road, Bancroft area, 13 August 1979, *E. Woodley & L. Alex s.n.* (OAC); **Middlesex Co.**, 10 miles [16 km] SW of London, shallow water, few–scarce, 21 June 1952, *L.E. James 1571* (DAO); **Muskoka District Municipality**, Sparrow Lake, muck, water depth 1–2 m, 16 September 1978, *B.S. Bullock s.n.* (OAC); **Peterborough Co.**, Lake Kasshabog east edge half way along lake, pond near shoreline, 9 July 1978, *Wildeman s.n.* (OAC); **Renfrew Co.**, Barrys Bay. Concession I, Chippawa Lodge. Barrys Bay, juncture of Highways 60 and 62, 4.3 miles [6.9 km] SE on 62, Chippawa Road, 2 miles [3.2 km] SW, marina SE corner of property, small population in shallow water with pickerel weed, 4 August 1977, *J. Vermeer 132* (OAC); Petawawa Forest Experiment Station, Chalk River, in Young's Creek at Racehorse Road, 9 September 1960, *T.C. Brayshaw s.n.* (CAN).

Sparganium androcladum (Engelmann) Morong—CANADA, Ontario. **Lanark Co.**, Murphys Point Provincial Park, mucky edge of bay, in mono-specific stands, 12 September 2023, *C.J. Chapman-Lam 5897* (CAN); **Regional Municipality of Niagara**, Chippewa Creek Conservation Area, shallow water, 11 September 1973, *W.L. Putman 123* (DAO); **City of Ottawa**, François Dupont Park, organic marsh dominated by *Sparganium* spp., with *P. cordata*, *S. latifolia*, and *H. morsus-ranae*, 45.491246°N, 75.52087317°W, ±10 m, 11 September 2022, *C.J. Chapman-Lam and P.C. Sokoloff 5747* (CAN); same location, 45.491253°N, 75.520797°W, ±10 m, 11 September 2022, *C.J. Chapman-Lam and P.C. Sokoloff 5748* (CAN); Petrie Island, *Sparganium* marsh, with *S. latifolia* and *N. odorata*, 45.49978183°N, 75.4843805°W, ±10 m, 11 September 2022, *C.J. Chapman-Lam and P.C. Sokoloff 5749* (CAN); Billings Bridge, Rideau River, 9 August 1894, *Macoun 7369* (CAN); **Prescott & Russell Co.**, Nation River at Casselman, wet places, 21 August 1884, *Macoun 28.051* (CAN).

Additional S. androcladum*, not verifiable or misidentified*—CANADA, Ontario. **Bruce Co**., Spring Creek, shallow water, 14 August 1934, *P.V. Krotkov 8622* (GH); **Grey Co.**, Eugenia, Artemisia Township Conc. IX. Lot 34, 2 miles [3.2 km] E of Eugenia, up to "21 m" (unclear if this is the depth) water over peat of marshy bay, 22 July 1976, *R.S.W. Bobbette 4791* (CAN); **Haliburton Co.**, Wilberforce, stream edge – water 4" [10 cm], *D.A. Smith s.n.* (DAO); **Muskoka District Municipality**, Morrison Lake, bogs, mud, 12 August 1940, *D.W. Kirk 445* (CAN); **City of Ottawa**, Britannia Village, dried marsh, part of deciduous woods, 4 July 1953, *E. Truman 1121* (DAO); **Renfrew Co.**, Petawawa, Forks Island, in mouth of River Petawawa into Lac du Bois Dur, abundant in swamp, 11 October 1961, *T.C. Brayshaw s.n.* (CAN); Petawawa, Lagoon along the Ottawa River, 20 July 1948, *A.J. Breitung 6854* (DAO); **Thunder Bay District**, mouth of Shadow Creek at Orient Bay, 4 miles [6.4 km] S of MacDiarmid, in shallow water up to 80 cm deep at creek mouth rooted in mud, 29 July 1960, *C.E. Garton 7893* (DAO); logging road to Postagoni Lake, 2 miles [3.2 km] E of Highway 11, mucky shore of beaver pond in water up to 30 cm deep, 27 July 1960, *C.E. Garton 7874* (DAO).

Author Contributions

Writing — Original Draft: C.J.C.-L.; Writing — Review & Editing: C.J.C.-L. and P.C.S.; Conceptualization: C.J.C.-L.; Investigation: C.J.C.-L. and P.C.S.; Funding Acquisition: C.J.C.-L. and P.C.S.

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Declining population of Harlequin Duck (*Histrionicus histrionicus*) on the Bow River, Alberta, Canada: 25 years of monitoring

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Abstract

Harlequin Duck (*Histrionicus histrionicus*) is a small sea duck that winters in coastal waters and breeds on fast-moving mountain streams in western North America. Because of its dependency on streams and coastal near-shore habitat with healthy macroinvertebrate populations, population trends of this species can be used as an indication of healthy freshwater and marine ecosystems. From 1995 to 2020 we conducted roadside surveys for Harlequin Ducks on the Bow River in Banff National Park, Alberta. We calculated the population's trend by modelling maximum annual count, which showed a population decline over the 25 years of 3.3% per year. The trajectory varied over time: a relatively stable population from 1995 to 2005, a steep decline until 2011, then stabilising at a much lower level with a slight rebound in recent years. The predicted number of ducks from our state-space model closely tracked the maximum number of ducks observed in annual counts. During stable or slightly increasing population estimates the male:female (M:F) ratio fluctuated considerably but stayed high (1.4:1 and 1.3:1, respectively), and during the period of steep population decline the M:F ratio was at its lowest (1.1:1). This declining population trend is concerning because it is occurring in a protected area, but it is similar to data from other studies in the Rocky Mountains and at the coastal wintering area, suggesting that causes may not be solely due to issues on the breeding streams.

Key words: Harlequin Duck; *Histrionicus histrionicus*; Bow River; population trend; state-space model; sex ratio

Introduction

Harlequin Duck (*Histrionicus histrionicus*) is a small sea duck that winters in coastal waters and breeds along fast-moving mountain streams (Robertson and Goudie 2020). Harlequin Ducks exhibit delayed sexual maturity, low annual productivity, high annual adult survival (Goudie *et al.* 1994), and exhibit strong site fidelity to breeding (Smith *et al.* 2000) and wintering (Robertson *et al.* 2000) areas. Harlequin Ducks do not defend a stretch of river however males do guard their mates from other males, particularly on the breeding stream (Lazarus *et al.* 2004).

The welfare of Harlequin Ducks appears to be intimately related to the availability of fast-flowing, non-polluted water (Soulliere and Thomas 2009; Robertson and Goudie 2020), and because of their tendency to locate their nests close to water, they also need streams where they can breed and nest away from human disturbance (Wiggins 2005; ASRD 2010). Because of the Harlequin Duck's dependency on streams and coastal near-shore habitat with healthy macroinvertebrate populations, population trends of this species can be used as an indication of healthy freshwater and marine ecosystems (Vaughan *et al.* 2007).

Understanding wildlife population trends is essential for effective species management and conservation (Mills 2013). Data on population size are important when setting limits on recreational activities such as sport harvest or commercial recreation or when considering impacts of industrial activities such as mining or logging. Accurate population data are also important when monitoring effectiveness of conservation actions such as habitat recovery or protection.

Sex ratios also have long been used as demographic tools for waterfowl management (e.g., Bellrose *et al.*

1961). Males are often hunted in higher numbers than females due to their attractiveness as trophy mounts, while the inexperience of juveniles of either sex leads to higher mortality of that age class for many species. While sex ratio at hatching is usually equal (Bellrose *et al.* 1961), subsequent male-biased ratios have been generally attributed to differential survival of male and female ducklings to recruitment (Lehikoinen *et al.* 2008) and to differential mortality between the sexes resulting from increased predation of females during incubation and brood rearing (reviewed in Donald 2007). While a male-biased sex ratio should not influence population trends, because females are not limited by male availability, more males may negatively affect female reproduction through energy loss and reduced foraging because of increased number of pursuit flights and attempted extra-pair copulations (Pöysä *et al.* 2019).

The eastern population of Harlequin Duck (*Histrionicus histrionicus pacificus*) in Canada is legally listed as a species of Special Concern under the federal *Species at Risk Act* (SARA; SARA Registry 2023). The Government of Alberta (2024) considers Harlequin Duck a Species of Special Concern due to specific breeding habitat requirements; threats to habitat integrity from logging, mining, grazing, and recreational activities; relatively small breeding population size; and sensitivity to disturbance during breeding. There is currently no reliable index of population size or trend for Harlequin Ducks in western North America.

Our 25 years of data, from 1995 to 2020, on the Bow River in Banff National Park, Alberta is one of the longest monitoring studies for a breeding population of Harlequin Ducks. Our objectives were to (1) calculate population indices and (2) document sex ratio in this population.

Methods

Study area

We observed Harlequin Ducks on the Bow River in Banff National Park, Alberta, Canada, during May and June, 1995–2020. The section of interest was a 25-km stretch of river starting ~4.5 km downstream of Lake Louise (51.4028°N, 116.1611°W) to Castle Junction (51.2633°N, 115.9219°W; Figure 1), along which the river decreases in elevation from 1545 m to 1440 m. The study area falls within the Lower Subalpine Ecoregion, predominantly forested with Lodgepole Pine (*Pinus contorta* Douglas ex Loudon) and Buffalo Berry (*Shepherdia canadensis* (L.) Nuttall; Holland and Coen 1983). The 30-year average (1991–2017) spring precipitation and temperature varied from 157.9 mm and 3.5°C near Lake Louise, to 152.4 mm and 4.0°C near Castle Junction (Clark and Kienzle 2022). The Bow River normal flow ranges from 2 to 4 m^3/s (lower quartile) on 1 May to 14 to 28 m^3/s (upper quartile) on 1 June, with a level of 1 to 1.45 m in height during the same period (Government of Alberta 2022).

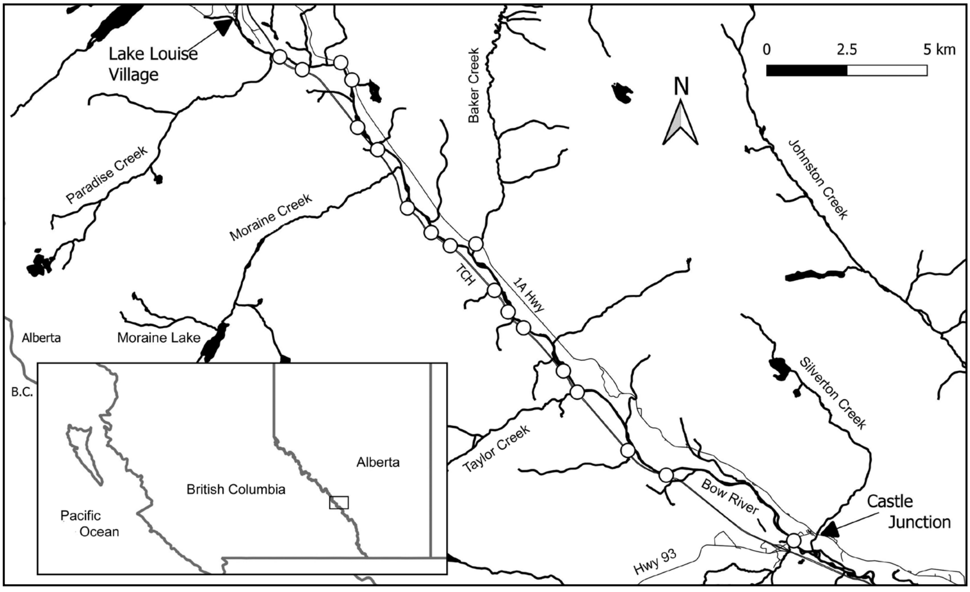

FIGURE 1. The 18 roadside survey stops (circles) for Harlequin Duck (*Histrionicus histrionicus*) covered 14 km of the 25 km along this section of the Bow River in Banff National Park, Alberta. Circles represent highway stopping locations and do not correlate with length of river observed at each stop.

Field surveys

We established a repeatable survey route along the Bow River in 1995, using 18 road-accessible locations along the Trans-Canada Highway (TCH; Highway #1) and Bow Valley Parkway (Highway #1A), between Castle Junction (the junction of the TCH and Highway #93 South) and the TCH bridge downstream of Lake Louise (a distance of 25 km; Figure 1). From the survey stops 14 km (56%) of the river could be observed. Most locations were within view of the road, but a few required walking a short distance through intervening tree cover. Not all segments of the river are equal, as there are local differences in ecologically relevant factors such as prey availability, and stream depth and velocity (Heath *et al.* 2006).

Confirmation that our chosen roadside survey stops adequately sampled the local Harlequin Duck population was provided by conducting boat surveys along the entire 25-km stretch of river described above, from 1996 to 2002, using expert canoeists who were also experienced wildlife observers. Ninety-one percent of the observations (CI 87–98%; range 71–100%) during 16 boat surveys (median 2/year, range 1–3) were at the same location as roadside survey stops.

The purposes of the roadside surveys were to: (1) obtain counts of ducks for population indices and (2) obtain sex ratios. Sex ratio data are presented as raw data and have not been statistically analysed but are included to better understand what may be driving population trends over time. At each survey stop we counted the total number of ducks and recorded the number of each sex. We do not report number of pairs because it can be difficult to distinguish pairs in a large group of birds and the time it would take to observe definitive pair behaviour would impact our ability to complete the survey in a practical length of time. While each survey was conducted in a single day, the amount of time we spent at each survey stop varied (minimum 5 min), depending on whether or not, and how many, ducks were present. Three to nine surveys (average six) were conducted each year. Surveys were spread out during the prescribed period as equally as possible depending on suitable weather conditions (no or little precipitation to ensure good visibility) and staff availability.

The colourful plumage of Harlequin Duck males increases their observability. Female Harlequin Ducks are more camouflaged, but at the time of year of our surveys, females are almost always accompanied by males, either their mate or single males. Observers are trained to scan the shorelines methodically with the spotting scope, which reduces the likelihood of missing loafing birds. Ducks in flight are easy to see as they fly very low to the water, following the river channel closely. There is a possibility of double counting individuals if birds fly or swim into another segment, as the survey can take several hours to complete. Because of the use of binoculars and spotting scopes, observers do not need to get particularly close to the birds, which reduces disturbance. While surveyors varied among years, new surveyors were always trained by an experienced surveyor.

Single males are the first to arrive on the river (median date 21 April), followed by pairs (median date 3 May; Smith 2000). We conducted surveys between 1 May (median start date 10 May) and 15 June; however, we truncated the early survey data before 7 May to eliminate surveys that may have had a higher proportion of early-arriving single males. We also truncated data after 2 June after plotting the ratio of male to female ducks during the full survey period. The mean male:female ratio (M:F) was significantly higher after 2 June than before 2 June (2.0:1.0 versus 1.3:1.0, respectively; $Z = -3.75$, $P < 0.001$), which suggested that the females were starting to leave the main river for smaller streams to lay eggs and then to incubate and would be less likely to be observed on the river. Smith (2000) estimated that the median date to initiate egg laying was 1 June for 11 female Harlequin Ducks that were radio tracked, and the median date for initiating incubation was 15 June. Including data after 2 June would bias the sex ratio towards males.

Analysis methods

Negative binomial generalized additive model (GAM)—To assess the effect of year and survey date, duck counts were modelled using generalized additive models (GAMs) using "mgcv" version 1.8.40 (Wood 2011). Negative binomial regression is a standard alternative to Poisson regression when modelling overdispersed count data (dispersion parameter = 1.9; Zuur *et al.* 2009). We used the maximum count of Harlequin Ducks for each year as an unadjusted number. The maximum count included all males and females observed, regardless of whether they were paired or not. Covariates were survey date (converted to ordinal date) and year. Data exploration was carried out following the protocol in Zuur *et al.* (2010). Visual inspection suggested non-linear relationships between counts and covariates, so we included linear and smoothed terms for day of survey and year in model selection. We applied a stepwise backward regression method to select the best model using AIC.

Generalized linear model (GLM)—To estimate a linear trend in the maximum count of Harlequin Ducks each year, we modelled the maximum count of ducks as a function of the covariates using a negative binomial GLM with a log link function using the "mass" package version 1.8.40 (Venables and

Ripley 2002) in R (R Core Team 2020). The GLM estimate of the trend was used because it provides a useful metric for understanding population status. We checked the model fit using standard residual plots and explained deviance. We checked the assumptions of the negative binomial GAM using gam.check in 'mgcv' and inspected the scatterplots of residuals plotted against fitted values and the explanatory variable and no obvious patterns were detected.

State-space exponential growth model (SSM)—Notably, some of the changes in maximum counts between years would be due to a change in the actual number of Harlequin Ducks, and some may have been due to differences in detectability or observer error. To address this, we used an additional method to detect trends in maximum counts. This method, called the 'state-space' exponential growth model (known hereafter as the state-space model or SSM) is a linear mixed model that treats the Observation Error Model and the Process Variation Model as special cases with corresponding variance parameters equalling zero, and uses maximum likelihood (and restricted maximum likelihood) to solve for the optimum parameter estimates. The SSM has been used to analyse ungulate population trends where population estimates are lacking (Flesch *et al.* 2016) and can also incorporate missing data in the time series (Humbert *et al.* 2009). The parameter of interest produced by the SSM is μ, which is the natural logarithm of lambda, or the expected change in numbers over time. The state-space modelling was conducted in the R programming language (version 3.24.3.2; R Core Team 2020), using a model from Humbert *et al.* (2009). We used Markov chain Monte Carlo modelling within package "nimble" (de Valpine *et al.* 2023) to fit parameters and credible intervals for the SSM population predictions. Convergence was assessed with the Gelman-Rubin test, and goodness of fit was assessed using Bayesian *P*-values (Royle *et al.* 2013) and Freeman–Tukey residuals. For each iteration, we simulated response data then summed observed and simulated Freeman–Tukey residuals. We calculated the percentage of iterations, where observed sums were larger than simulated sums. Values less than 0.05 or greater than 0.95 indicated poor fit. Five chains were run with 200 000 iterations with a 20 000 burn in. Package "ggplot2" (Wickham 2016) was used for graphing.

SSMs can operate at two levels (observation and process) by assuming that the process level is autocorrelated; i.e., a large population at time t will probably lead to a large population size at time t+1 (Auger-Méthé *et al.* 2016). There are two components to an SSM: process variation and observation error. The process variation model assumes that between time intervals there can be perturbations to the growth rate (due to environmental variation), and that these perturbations are random, distributed normally, and exhibit no serial autocorrelation (Humbert *et al.* 2009). So, the process is autocorrelated, but the perturbations should not be autocorrelated. It is difficult to know if this is precisely true for any population, however it is reasonable to think that a negative perturbation in one year (e.g., high water causing poor reproductive success) could be offset by a positive perturbation in another (e.g., high prey abundance causing increased survival). The observation error model assumes that the error term is normally distributed with a mean of zero, i.e., sampling error is independent across sampling periods. This is, we believe, a reasonable assumption for our population—poor detectability in one year (for example due to poor weather) would not necessarily be followed by poor detectability in the following year.

Results

An average of six roadside surveys (range 3–9) were conducted annually (1995–2020, except 2000) between 7 May and 2 June. The highest maximum annual count of Harlequin Ducks was in 1997 ($n = 64$) and the lowest count was in 2011 ($n = 17$). The M:F ratio (Figure 2), based on the roadside survey annual high count day, averaged 1.3:1.0 (range 0.9–1.9).

The optimal GAM predicting maximum annual counts (Table 1) included year as a smoothed term and survey date as a linear effect indicating early stability followed by a decade of declining counts, to recent stability at a lower level (Table 2, Figure 3a). Annual maximum counts were higher when they were recorded earlier in the season (Figure 3b). We plotted the relationship between the number of surveys conducted in a year and the maximum count, but there was no relationship. The model explains 76.9% of the null deviance.

We observed an annual decline of 3.3% in the maximum count of Harlequin Ducks from 1995 to 2020 on the Bow River (Table 3, Figure 4a,b). Validation plots of the negative binomial GLM, which included the linear effect of year indicated a non-linear pattern in duck counts over years which supported the use of a GAM to assess the effects of year and survey date. Explained null deviance was 57.5%.

The SSM, which accounts for observer error, mirrored maximum values of the other methods (Figure 5). The model appeared to converge based on a visual examination of the trace plots and because the Gelman-Rubin test statistics were <1.03 for all parameters. Fit was also good (proportion of observed greater than predicted Freeman–Tukey residuals was 0.60). The SSM trend was −0.0243, with a credible interval of −0.0748 to 0.0300. The observation variance

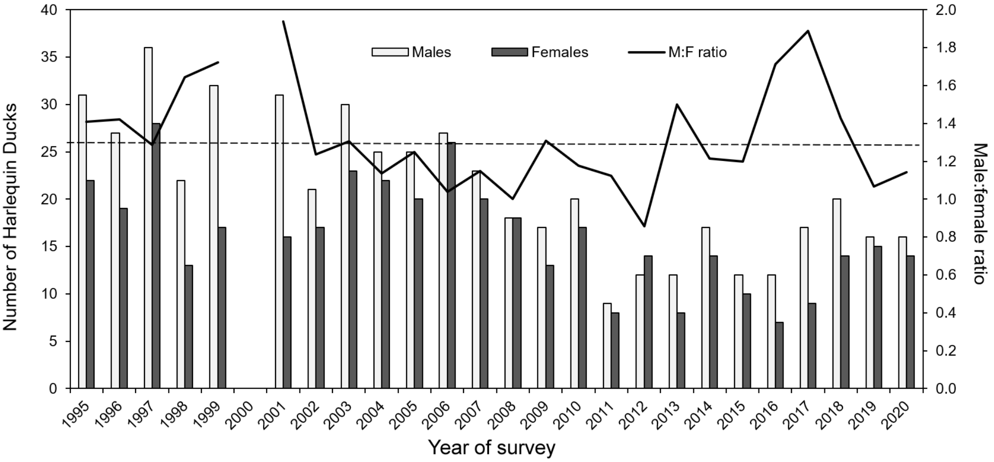

FIGURE 2. Number of male and female Harlequin Duck (*Histrionicus histrionicus*) and male:female ratios (M:F), observed from maximum annual counts during roadside surveys along the Bow River, Banff National Park, Alberta, 1995–2020. The horizontal dashed line is the median M:F ratio (1.3:1.0) during the 25 years.

TABLE 1. Akaike Information Criterion (AIC) table comparing generalized additive model fits for annual counts of Harlequin Duck (*Histrionicus histrionicus*) from roadside surveys, Banff National Park, Alberta, 1995–2020.

Model	df	AIC	ΔAIC
Survey date + s(Year)	7.9830	175.2133	0.0000
s(Survey date) + s(Year)	7.9838	175.2149	0.0020
s(Year)	6.9409	176.0891	0.8758
s(Survey date) + Year	4.0001	181.9957	6.7824

TABLE 2. Our negative binomial generalized additive model explaining maximum annual counts of Harlequin Duck (*Histrionicus histrionicus*) on roadside surveys, Banff National Park, Alberta, 1995–2020, and year and survey date. Edf = effective degrees of freedom; DE = deviance explained.

Predictors	Estimates	SE	*P*	DE (%)
(Intercept)	4.8052	0.8093	<0.0001	76.9
Survey date	−0.0087	0.0058	0.1300	
Smooth predictors	Edf	χ^2	*P*	
Year	4.084	58.07	<0.0001	

was 0.0706 and the process variance was 0.0339. Importantly, there was stability in the population until 2006, when the population declined sharply and then appears to have stabilized, but at a lower level.

Discussion

Our maximum annual count and the SSM both indicate a relatively stable population of Harlequin Ducks on the Bow River from 1995 to 2005, then a steep decline until 2011, with the population thereafter stabilising at a much lower level, and showing a slight rebound in the most recent years, although it may be too early to tell. A similar pattern has shown up on another breeding stream in Alberta, and one in Idaho. Maximum annual counts on the McLeod River in Alberta showed a slightly declining population from 1996 to 2005, then a steep decline to 2011, where it has since stabilised (B. MacCallum pers. comm. 16 November 2020). In Idaho, pair counts on the Lochsa River steeply declined from 30 in 1995 to four in 2011, then stabilised around the lower level (J. Sauder pers. comm. 20 April 2020). Our 1995–2020 trend of −3.3% is also similar to the overall trends observed for 1999–2019 at British Columbia wintering areas, where Harlequin Ducks aggregate from many breeding areas, including the Bow River (Smith and Smith 2003); trends varied from −0.70% per year (CI −1.98–0.70) in the Salish Sea (Strait of Georgia)

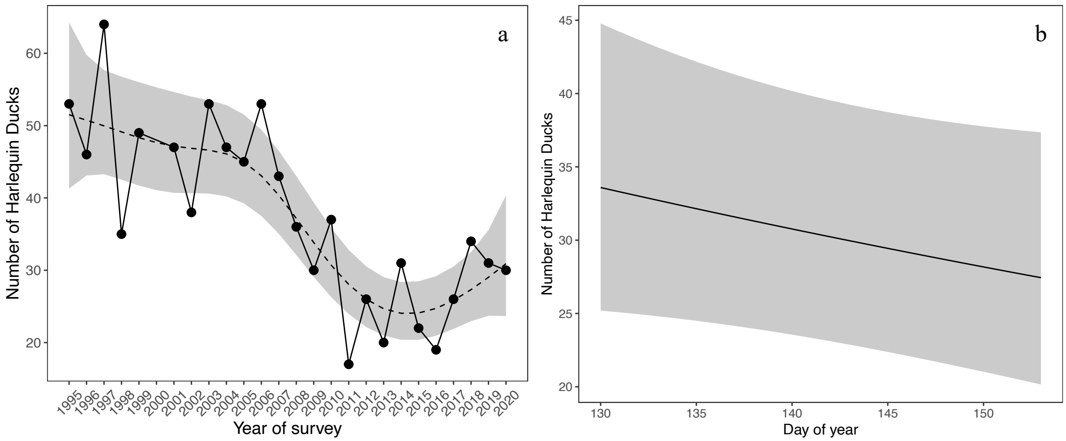

FIGURE 3. Fitted values (dotted line) and 95% confidence bands for the optimal negative binomial generalized additive model applied on the Harlequin Duck (*Histrionicus histrionicus*) count data, Banff National Park, 1995–2020. Plots were constructed using the range of values for year (a) and survey date (b) while holding the remaining predictor variable at the mean value. Black circles are the observed maximum counts.

TABLE 3. Our negative binomial generalized linear model explaining the linear relationship between the maximum annual counts of Harlequin Duck (*Histrionicus histrionicus*) on roadside surveys, Banff National Park, Alberta, 1995–2020, and year and survey date. DE = deviance explained.

Effects	Coefficient	SE	*P*	DE (%)
Intercept	71.8781	11.4499	<0.0001	57.51
Survey date	−0.0079	0.0063	0.2110	
Year	−0.0335	0.0057	<0.0001	

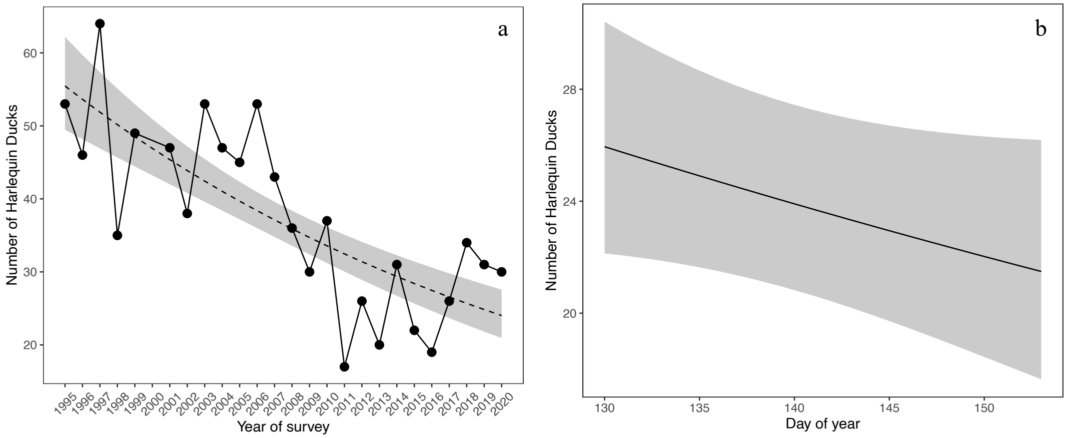

FIGURE 4. Fitted values (dotted line) and 95% confidence bands for the optimal negative binomial generalized linear model applied on the Harlequin Duck (*Histrionicus histrionicus*) count data on the Bow River, Banff National Park, 1995–2020. Plots were constructed using the range of values for year (a) and survey date (b) while holding the remaining predictor variable at the mean value. Black circles are the observed maximum counts.

to −4.97% per year (CI −11.4–2.22) on the outer Pacific Coast (Ethier *et al.* 2020).

Sex ratio averaged 1.3:1.0 (M:F) in the 25 years of our study, which is the same as that found in the Strait of Georgia, British Columbia wintering area (Rodway *et al.* 2015). Rodway *et al.* (2015) suggested that changes in sex ratios can function as early warning signals of population decline; an increasing

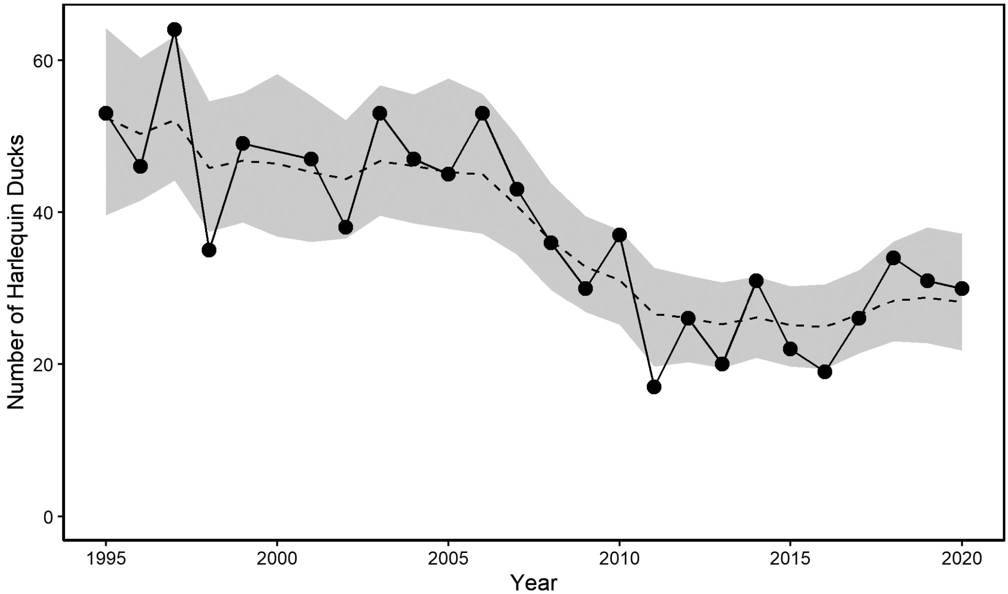

FIGURE 5. The predicted number of Harlequin Duck (*Histrionicus histrionicus*; dashed line) using a state-space model closely tracked the maximum number of ducks observed per year (black dots with black line), on the Bow River, Banff National Park, Alberta,1995–2020. The gray area represents 95% CI.

M:F ratio could signal declining female survival that would impact productivity and recruitment. In our study the lowest M:F ratio was during the period of steepest population decline, but it is difficult to determine if that was correlation with no obvious causation. A period of increased predation on males at the wintering area, because they are more colourful and perhaps easier to target, could reduce the number of males in the population. The recovery of some coastal Bald Eagle (*Haliaeetus leucocephalus*) populations in recent decades have influenced the distribution and abundance of sea birds and sea ducks (Middleton *et al.* 2018).

The similar trajectory of declining trends for Harlequin Ducks among various breeding and wintering populations suggest that the causes of the Bow River decline could be multifactoral, including threats outside the protected area. Harlequin Ducks may be impacted by numerous interacting threats: environmental pollution (Souillier and Thomas 2009), climate change affecting stream flows (Hansen *et al.* 2019) and invertebrate food sources (Souillier and Thomas 2009), habitat loss and alteration (MacCallum 2001; Souillier and Thomas 2009), increasing recreational activities (MacCallum 2001), increased numbers of predators in breeding and/or wintering habitat (Heath *et al.* 2006), and hunting mortality (Smith and Goudie 2021). More in-depth research into causes of the decline is warranted.

Our study proved that our roadside survey approach was effective and efficient for monitoring a Harlequin Duck population that is of Special Concern, and that this technique may be suitable for other species with similarly accessible breeding habitat.

Author Contributions

Writing — Original Draft: C.M.S.; Writing — Review & Editing: B.S., M.B., and S.H.; Conceptualization: C.M.S.; Investigation: C.M.S. and S.H.; Methodology: C.M.S.; Formal Analysis: B.S., and M.B.; Funding Acquisition: C.M.S. and S.H.

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Duck counts on the Lochsa River. Jesse Whittington helped with the MCMC analyses and provided valuable insight on interpretation of Bayesian results. Research was conducted under Parks Canada Agency Research and Collection Permits for Banff National Park, including Parks Canada Animal Care Committee Protocol Reviews. All applicable ethical guidelines for the use of birds in research have been followed, including those presented in the Ornithological Council's "Guidelines to the Use of Wild Birds in Research" (Fair *et al.* 2010) and the Canadian Council on Animal Care (2003). We thank two anonymous reviewers for their helpful comments on previous drafts of this manuscript.

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Evolutionary isolation of Canadian terrestrial vertebrate species

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Abstract

Conservation prioritization has become increasingly important as a practical response to ongoing biodiversity loss and limited resources. One tool, evolutionary distinctiveness (ED) is based on a measure of evolutionary isolation and has merit for identifying taxa with few close relatives. Here we present the first ever national-level ED scores for any jurisdiction, applying the measures to all Canadian tetrapods. We updated and pruned global dated phylogenies of all terrestrial vertebrates (amphibians, squamates, turtles, mammals, and birds) down to native Canadian species and calculated Canadian ED scores and rankings for each and compared them to their global ED ranks. Canada's terrestrial ectotherm vertebrates (amphibians and reptiles) include most of Canada's most evolutionarily isolated species and many score and rank higher nationally than globally in their ED scores. These taxa are also the most imperilled in Canada and so species with populations assessed as at-risk by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) represent, on average, more than expected national evolutionary history. Interestingly, several exotic species also have very high national ED scores. To the extent that evolutionary isolation captures aspects of local and national biodiversity worth preserving, our lists may provide useful input to conservation agencies engaging in conservation prioritization exercises.

Key words: Canadian vertebrates; phylogeny; evolutionary distinctiveness; species age; pendant edge; conservation; prioritization

Introduction

In the face of current pressures on biodiversity, various prioritization methods have been developed for allocating the limited resources available for conservation (Myers *et al.* 2000; Marsh *et al.* 2007; Olsen and Dinerstein 2008; Gerber *et al.* 2018). Prioritization methods include consideration of the ecological role (Grainger *et al.* 2013), conservation status (Carter *et al.* 2000; zeroextinction.org), aesthetic and cultural value (Rodríguez *et al.* 2004), and the potential for and cost of recovery (Marsh *et al.* 2007) of individual species. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) prioritizes status assessments for full taxonomic species followed by discrete and evolutionary significant units of biodiversity (= Designatable Units [DU]) below the species level that are most prone to becoming Extinct or Extirpated (COSEWIC 2020) as mandated by the *Species at Risk Act* (SARA 2002).

One intriguing prioritization metric considers evolutionary isolation, or how distantly related a species is to others (Atkinson 1989). Isolated species, whose evolutionary history is not shared with others, contribute more to the Tree of Life (Steel *et al.* 2018). Evolutionary history may have inherent value (Soulé 1985), and evolutionarily isolated species often express nonredundant (even unique) biological features (Faith 1992; Forest *et al.* 2007; Tucker *et al.* 2019; Gumbs *et al.* 2020). A broad variety of biological features is thought to offer benefits to humans both in the short-term, through augmenting ecosystem services or offering aesthetic uses, and in the long-term, by providing a variety of options for future unknown uses (e.g., Faith 1992; Forest *et al.* 2007; Tucker *et al.* 2019). A recent example documenting a positive relationship between global evolutionary isolation and currently useful features to humans can be found in Molina-Venegas (2021), and the arguments for preserving isolated species as a means to preserve the Tree of Life and to preserve future options are made explicitly by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES; Díaz *et al.* 2020).

One popular measure of evolutionary isolation is evolutionary distinctiveness (ED; Redding 2003; Isaac *et al.* 2007), promulgated through, for example, the Zoological Society of London's Edge of

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Existence program (www.edgeofexistence.org). Evolutionary distinctiveness apportions an entire phylogenetic tree among its constituent species fairly (Figure 1), such that species isolated on longer branches and that have fewer close relatives, i.e., that share their evolutionary history with fewer other species, are given higher scores (Isaac *et al.* 2007). The metric has a clear theoretical interpretation as a Shapley value or the expected amount of unique evolutionary history contributed by a species to unknown future subsets of species (Fuchs and Jin 2015; Wicke *et al.* 2020). Evolutionary distinctiveness can be a useful tool to aid in decisions involved with, for example, choosing species-at-risk for conservation investment. The metric has been applied globally to mammals (Collen *et al.* 2011), birds (Jetz *et al.* 2014), amphibians (Isaac *et al.* 2012), corals (Curnick *et al.* 2015), squamates (Tonini *et al.* 2016), sharks (Stein *et al.* 2018), and conifers (Forest *et al.* 2018). However, many values of biodiversity accrue nationally rather than globally. For example, Canada's SARA does not consider a species' global threat status (although COSEWIC's prioritization of species for which status reports will be commissioned does include global conservation ranking; COSEWIC 2021a), but rather whether Canada is at risk of losing the species and so depleting Canada's biodiversity. The same logic could be applied to Canada's Tree of Life: some species are more evolutionarily isolated in Canada than others, such that their loss would prune Canada's Tree of Life more. In addition, and as a complement to national at-risk status i.e., the status assessment by COSEWIC that could lead to formal listing under SARA, national isolation scores for Canadian

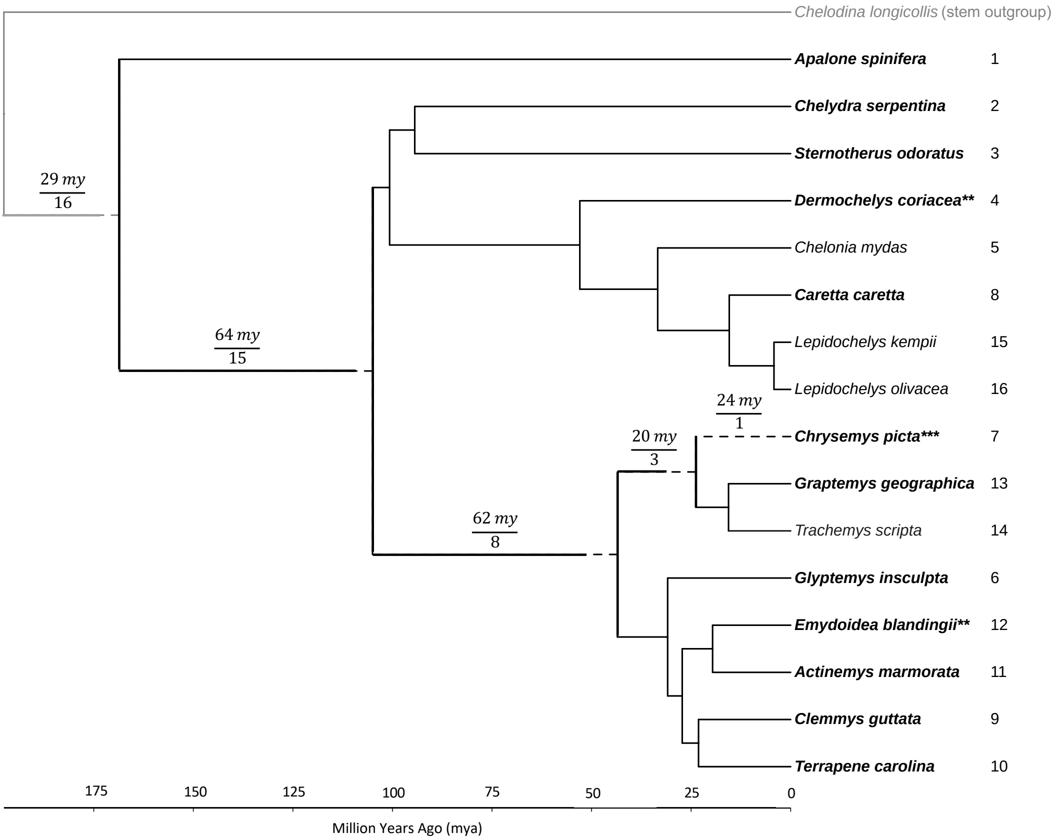

FIGURE 1. Canadian phylogeny of turtles. Species representing multiple designatable units (DUs) in Canada are indicated by *, with the number of symbols corresponding to the number of DUs represented. At-risk species, defined as a species with at least one DU assessed as at-risk by COSEWIC, are represented in bold. The outgroup *Chelonia longicolis* (Eastern Long-necked Turtle) is native to Australia. *Trachemys scripta* (Pond Slider) is native to the United States but is an exotic in Canada (NGSWG 2020). Measuring evolutionary distinctiveness (ED) on a phylogenetic tree is illustrated by the dashed lines. Here, ED for *Chrysemys picta* is the sum of the apportioned dashed branch lengths, with each branch length (numerator) inversely weighted by the number of living species descended from it (denominator). Species' ED rankings are listed next to their species' name.

terrestrial vertebrate species may be of use to conservation and funding organizations as they engage in conservation prioritization exercises.

Here we present and discuss the first lists of Canadian ED scores for Canada's terrestrial vertebrate species. Because of the differing legal considerations for native and exotic species, we first consider all recognized native Canadian species, ranked by their isolation on the Tree of Life in relation to other Canadian species within their taxonomic group (birds, mammals, squamates, turtles, and amphibians). We then discuss how these ED scores change when we include exotic, non-native species, species not usually considered for conservation attention nor currently eligible for listing or protection under SARA.

Methods

Canadian vertebrate taxonomy

To calculate ED scores for Canadian vertebrates, we used the taxonomy of all Canadian vertebrates from Wild Species Canada (NGSWG 2020). This list recognizes 222 mammal, 674 bird, 48 amphibian, and 49 reptile species extant within Canada, but not subspecies or COSEWIC DUs. As taxonomies often vary due to changing nomenclature, and due to revisions to species names at genus and species levels (Cooke *et al.* 2020), we updated the Canadian species lists to meet all current revisions. We made two revisions to the Canadian mammal and bird species lists: (i) Domestic Dog (*Canis lupus familiaris*) was removed as it is now considered a subspecies of Gray Wolf (*Canis lupus*; Wang and Tedford 2008); (ii) Eurasian Wren (*Troglodytes troglodytes*) is no longer considered to be conspecific with Winter Wren (*Troglodytes hiemalis*) and Pacific Wren (*Troglodytes pacificus*) and was therefore removed as its range is outside of Canada (Chesser *et al.* 2010). We also created two lists: one of all recorded species and one "native" list that excludes the 10 bird, 11 mammal, and two reptile species classified as "exotic" by Wild Species Canada (CESCC 2016). We contrast the scores of these two lists.

Measuring evolutionary isolation

We calculated two measures of evolutionary isolation: (i) a very simple measure of isolation, the pendant edge (PE) length, or the length of the branch that joins the focal species to the rest of the tree (on a complete tree, this is sometimes referred to as the species "age"; Redding *et al.* 2008); and (ii) evolutionary distinctiveness (ED), also known as fair proportion (FP), which is the sum of branch lengths from a species tip to the root of the tree, each branch length inversely weighted by the number of living species descended from it (Redding 2003; Redding *et al.* 2008; Isaac *et al.* 2007; also see Biega *et al.* 2019; Gumbs *et al.* 2023). Evolutionary distinctiveness is composed of the PE score plus input from deeper in the tree, and is our focus.

To calculate global ED, we obtained a random sample of 500 dated global phylogenetic trees from a distribution of "birth-death node-dated set of 10k completed trees" mammal (Upham *et al.* 2019), "Stage 2 MayrAll Hackett" bird (Jetz *et al.* 2014), and "Posterior All Species' trees" squamate and amphibian (Tonini *et al.* 2016; Jetz and Pyron 2018) phylogenies. For turtles, we used a single fully resolved dated phylogeny from Pereira *et al.* (2017). We then produced phylogenies for Canadian ED scoring by pruning each set of global trees to match their respective Canadian species list (using package "ape" in R version 1.2.5033; Paradis and Schliep 2018; R Core Team 2020; Appendix S1). For both the global and Canadian trees, we generated ED and PE scores using the "picante", "ape", "geiger", and "phytools" packages in R (Kembel *et al.* 2010; Paradis and Schliep 2018; Pennell *et al.* 2014; Revell 2012, respectively). The global and Canadian species ED and PE scores reported were generated by taking the median ED and PE values (in millions of years, to the nearest 100 thousand years) from the set (of size 500) of global and Canadian trees, respectively. Evolutionary distinctiveness and PE scores and rankings for global mammals have yet to be published and so we include them in Appendix S2. We generated two Canadian sets of isolation scores, either including or excluding the exotic species.

All phylogenetic datasets were matched to the nomenclature and taxonomy of our Canadian species lists (NGSWG 2020) to ensure all recognized Canadian species were included in our calculations. Two mammal and 12 bird species listed by Wild Species Canada were not recognized by Upham *et al.* (2019) and Jetz *et al.* (2014). We added these species to the respective trees prior to calculating our isolation scores (see Appendix S3 for details).

The stem age for each Canadian clade (e.g., the portion of the evolutionary history of turtles shared by all Canadian turtles) was also extracted from the global trees to make ED scores among taxa comparable. To determine stem age, we calculated the maximum depths of each pruned Canadian phylogeny and the depth of the encompassing global tree. Within-taxon stem ages were calculated by taking the difference between these maximum tree depths. This stem age was divided by the number of species present in their respective Canadian clade, and this constant was added to the ED score of each species (Figure 1).

Evolutionary distinctiveness rankings

Species were given both a global and Canadian ED rank based on their global and Canadian ED scores, respectively. Species within each taxonomic group were ranked highest to lowest, with the most evolutionarily isolated species with the highest ED score ranked as 1.

Conservation status

To compare ED scores with conservation status, we collected global and Canadian conservation status data for each species on our Canadian species lists. We obtained global conservation statuses from the IUCN Redlist (IUCN 2020). Both COSEWIC assessments (COSEWIC 2019) and SARA listings (SARA 2020) were used for Canadian status. Because COSEWIC assessments and SARA listings sometimes differ, we followed COSEWIC assessments when discussing species' Canadian status. If any population or DU was assessed as Extirpated, Endangered, Threatened, or Special Concern by COSEWIC, we scored the encompassing full species as "at risk". Species were scored "not at risk" if no DUs within a species were assessed as at-risk by COSEWIC (including species that were "not assessed" and species that were assessed as "Not at Risk").

Statistical analyses

To examine the relative amount of evolutionary history represented by species at risk in Canada, we first tested Canadian ED scores for normality using a Shapiro-Wilk Normality test. Scores were not normally distributed ($W = 0.98$, $P < 0.05$) and could not be transformed using log, square root, or inverse transformations. Therefore, we ran a Mann-Whitney test to compare the difference in average Canadian ED scores held by species at-risk and those not at risk.

Results and Discussion

Our primary goal is to offer conservation biologists in Canada a new perspective and a new resource for prioritization activity. Below we first highlight and discuss ED score ranges, average scores, and top scoring species for each taxonomic group separately, then move to considering patterns across the major groups, and end with a discussion of the influence of exotic species and overall conclusions. The lists we present for each taxon include the taxonomy, Canadian and global ED ranking, and the Canadian and global conservation status for each species (see Appendices S4–S8 for lists without exotics and S9–12 for lists including exotic species). ED scores within lists are broadly comparable across taxa, although we note there is no complete global vertebrate phylogeny linking the major taxa and so we are unable to account for stem ages linking them, resulting in some small amount of unaccounted for evolutionary history. Because ED distributes shared evolution among all species, the additions to some groups due to these missing stem ages are likely to be small, and, importantly, will accentuate any cross-taxon comparisons we report below. Importantly, species ED rankings within groups will be unaffected as these missing stem ages are taxon-specific constants. We note that both PE and ED scores are very strongly right skewed (see, e.g., Bocharov *et al.* 2022 for a discussion) and so we report medians throughout, in contrast to Pie and Carron (2023), who report mean PE scores.

Turtles

Canadian turtles have a national median PE score of 23.8 million years (compared to a median global PE score of 5.4 million years). National ED scores for Canada's 15 turtle species ranged from 45.2 to 178.4 million years, with a median score of 56.6 million years (Table 1, Appendix S4). Together, Canada's 15 species represent 1.1 billion years of independent Canadian evolutionary history. Canada's most evolutionarily isolated turtle is Spiny Softshell Turtle (*Apalone spinifera*; national ED rank of 1), representing 178.4 million years of independent evolutionary history in Canada. Canada's second and fourth most isolated species, Snapping Turtle (*Chelydra serpentina*; ED score: 112.5 million years) and Leatherback Sea Turtle (*Dermochelys coriacea*; 77.5 million years) are also the 12th and 15th most isolated species worldwide, respectively.

Twelve Canadian turtle species are considered at some level of risk in Canada, and the other three have not been assessed, but are considered at-risk globally. Ten turtle species are considered at-risk globally on the IUCN Red List (Table 1). One globally listed species, Green Sea Turtle (*Chelonia mydas*), has not been assessed by COSEWIC and is one of Canada's, and the world's, most isolated species. While not at-risk globally, Spiny Softshell Turtle and Snapping Turtle, Canada's top two isolated turtles, are assessed as Endangered and Special Concern in Canada, respectively. Two additional species, Eastern Box Turtle (*Terrapene carolina*; ED ranked 10th in Canada), and Northwestern Pond Turtle (*Actinemys marmorata*; 12th) are assessed as Extirpated from Canada. Together, these two extirpated species represent a loss of 101.8 million years of evolutionary history (as measured by the sum of ED).

Amphibians

Canadian amphibians have a national median PE score of 17.8 million years (compared to a median global PE score of 6.8 million years). National ED scores for Canada's 48 amphibian species ranged from 30.9 to 158.9 million years, with a median score of 49.7 million years (Table 2, Appendix S5). Collectively, Canadian amphibians represent 3.0 billion years of independent Canadian evolutionary history. Overall, Canadian toads (Bufonidae) were the lowest ED ranking amphibian family, with four

TABLE 1. Canadian turtle species ranked in descending order of their Canadian evolutionary distinctiveness (ED) score. Canadian ranking is accompanied with the species' taxonomy and global ED ranking, Canadian status assessed by COSEWIC (NA = Not at Risk or not assessed in Canada, SC = Special Concern, T = Threatened, E = Endangered, XT = Extirpated), and global status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

Canadian (global) ED rank	Family	Scientific name	Common name	Canadian (global) ED	Canadian status	Global status
1 (72)	Trionychidae	*Apalone spinifera*	Spiny Softshell Turtle	178.4 (36.7)	E	LC
2 (12)	Chelydridae	*Chelydra serpentina*	Snapping Turtle	112.5 (61.2)	SC	LC
3 (213)	Kinosternidae	*Sternotherus odoratus*	Eastern Musk Turtle	112.5 (18.7)	SC	LC
4 (15)	Dermochelyidae	*Dermochelys coriacea*	Leatherback Sea Turtle	77.5 (60.4)	E	VU
5 (60)	Cheloniidae	*Chelonia mydas*	Green Sea Turtle	62.8 (38.2)	NA	EN
6 (209)	Emydidae	*Chrysemys picta*	Painted Turtle	56.8 (19.1)	E	LC
7 (257)	Emydidae	*Graptemys geographica*	Northern Map Turtle	56.8 (10.5)	SC	LC
8 (165)	Emydidae	*Glyptemys insculpta*	Wood Turtle	56.6 (24.8)	T	EN
9 (138)	Emydidae	*Clemmys guttata*	Spotted Turtle	51.8 (27.1)	E	EN
10 (218)	Emydidae	*Terrapene carolina*	Eastern Box Turtle	51.8 (18.2)	XT	VU
11 (104)	Cheloniidae	*Caretta caretta*	Loggerhead Sea Turtle	50.8 (31.0)	EN	VU
12 (168)	Emydidae	*Actinemys marmorata*	Western Pond Turtle	50.0 (24.6)	XT	VU
13 (181)	Emydidae	*Emydoidea blandingii*	Blanding's Turtle	50.0 (23.0)	E	EN
14 (155)	Cheloniidae	*Lepidochelys kempii*	Kemp's Ridley Sea Turtle	45.2 (25.4)	NA	CR
15 (156)	Cheloniidae	*Lepidochelys olivacea*	Olive Ridley Sea Turtle	45.2 (25.4)	NA	VU

of the six species in the bottom four rankings (45th–48th) in Canada. All 10 Canadian species of the largest salamander family, lungless salamanders (Plethodontidae), fall within the top 20 most isolated Canadian amphibians. Canada's only completely aquatic amphibian, Mudpuppy (*Necturus maculosus*; Seburn and Seburn 2000), is Canada's most isolated amphibian, with an ED score of 158.9 million years.

Three top ED ranked amphibian species in Canada are also some of the most evolutionarily isolated species worldwide (Table 2). Canada's second and third ED ranked amphibian, Rocky Mountain Tailed Frog (*Ascaphus montanus*) and Coastal Tailed Frog (*Ascaphus truei*), are the sole members of an ancestral lineage of tailed frogs, Ascaphidae (Nielson *et al.* 2001; COSEWIC 2011), each representing 120.4 million years of evolutionary history in Canada. Globally, they each represent 96.4 million years of independent evolutionary history, making them the sixth and seventh most isolated amphibians worldwide. Canada's ninth ED ranked amphibian, Four-toed Salamander (*Hemidactylium scutatum*) is the sole member of its genus within the old lineage of lungless salamanders, Plethodontidae (Neill 1963), and is ranked 15th worldwide with a Canadian and global ED score of 92.1 and 77.8 million years, respectively.

Half of Canada's 20 most isolated amphibians (Table 2) are assessed as at-risk by COSEWIC and listed on Schedule 1 of SARA. Of note, Rocky Mountain Tailed Frog and Coastal Tailed Frog are assessed and listed as Threatened and Special Concern, respectively. Three species, Blanchard's Cricket Frog (*Acris blanchardi*; ED ranked 17th in Canada), and two DUs of Allegheny Mountain Dusky Salamander (*Desmognathus ochrophaeus*; 19th), and Northern Dusky Salamander (*Desmognathus fuscus*; 20th) are all assessed and listed as Endangered.

Squamates

Canadian squamates have a national median PE score of 8.8 million years (compared to a median global PE score of 5.1 million years). Canada's 32 native squamate species had national ED scores ranging from 15.5 to 159.0 million years, with a median score of 29.0 million years (Table 3, Appendix S6). Together, Canada's squamate species represent 1.3 billion years of independent evolutionary history in Canada. Overall, Canadian lizard species ranked higher than snake species, except for Northern Rubber Boa (*Charina bottae*), which ranked second in Canada with an ED score of 90.0 million years.

The two most evolutionarily isolated squamates in Canada are each the only members of their family in Canada (Table 3). The top ranked squamate is Canada's only Anguidae (a group that includes legless slowworms and glass lizards), Northern Alligator Lizard (*Elgaria coerulea*; ED ranked first), which represents 159.0 million years of independent evolutionary history. The second and third ED ranked squamates include Canada's only boa (Boidae), Northern Rubber

TABLE 2. Top 20 evolutionarily isolated amphibian species in Canada, ranked in descending order of their Canadian evolutionary distinctiveness (ED) score. Canadian ranking is accompanied with the species' taxonomy, and global ED ranking, Canadian status assessed by COSEWIC (NA = Not at Risk or not assessed in Canada, SC = Special Concern, T = Threatened, E = Endangered, XT = Extirpated) and global status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

Canadian (global) ED rank	Family	*Scientific name*	Common name	Canadian (global) ED	Canadian status	Global status
1 (266)	Proteidae	*Necturus maculosus*	Mudpuppy	158.9 (39.4)	NA	LC
2 (6)	Ascaphidae	*Ascaphus montanus*	Rocky Mountain Tailed Frog	120.4 (96.4)	T	LC
3 (7)	Ascaphidae	*Ascaphus truei*	Coastal Tailed Frog	120.4 (96.4)	SC	LC
4 (410)	Dicamptondontidae	*Dicamptodon tenebrosus*	Coastal Giant Salamander	112.9 (34.1)	T	LC
5 (372)	Pelobatidae	*Spea bombifrons*	Plains Spadefoot	107.1 (35.0)	NA	LC
6 (373)	Pelobatidae	*Spea intermontana*	Great Basin Spadefoot	107.1 (35.0)	T	LC
7 (1851)	Salamandridae	*Taricha granulosa*	Rough-skinned Newt	102.1 (19.9)	NA	LC
8 (1175)	Salamandridae	*Notophthalmus viridescens*	Eastern Newt	102.1 (23.6)	NA	LC
9 (15)	Plethodontidae	*Hemidactylium scutatum*	Four-toed Salamander	92.1 (77.8)	NA	
10 (54)	Plethodontidae	*Ensatina eschscholtzii*	Ensatina	78.9 (63.7)	NA	LC
11 (1314)	Plethodontidae	*Aneides vagrans*	Wandering Salamander	76.1 (22.7)	SC	NT
12 (3978)	Plethodontidae	*Plethodon cinereus*	Eastern Red-backed Salamander	73.2 (14.4)	NA	LC
13 (4444)	Plethodontidae	*Eurycea bislineata*	Northern Two-lined Salamander	72.1 (13.6)	NA	LC
14 (5424)	Plethodontidae	*Gyrinophilus porphyriticus*	Spring Salamander	72.1 (12.1)	T	LC
15 (507)	Plethodontidae	*Plethodon vehiculum*	Western Red-backed Salamander	67.5 (31.6)	NA	LC
16 (1046)	Plethodontidae	*Plethodon idahoensis*	Coeur d'Alene Salamander	67.5 (24.7)	SC	LC
17 (1267)	Hylidae	*Acris blanchardi*	Blanchard's Cricket Frog	63.6 (23.1)	E	LC
18 (343)	Ranidae	*Rana sylvatica*	Wood Frog	56.3 (36.2)	NA	LC
19 (3816)	Plethodontidae	*Desmognathus ochrophaeus*	Allegheny Mountain Dusky Salamander	56.1 (14.7)	E	LC
20 (2937)	Plethodontidae	*Desmognathus fuscus*	Northern Dusky Salamander	56.1 (16.6)	E	LC

Boa, and Greater Short-horned Lizard (*Phrynosoma hernandesi*; ED score: 85.5 million years), the only member of the spiny lizard (Phrynosomatidae) family not extirpated from Canada.

Seventeen of the top 20 most evolutionarily isolated squamate species in Canada are considered at-risk by COSEWIC (Table 3). Of these, all species of the viper (Viperidae; $n = 2$ species), spiny lizard (Phrynosomatidae; $n = 2$), skink (Scinicidae; $n = 3$), and boa (Boidae; $n = 1$) families fall within these at-risk species. Of note, Ontario's only lizard and viper species, Common Five-lined Skink (*Plestiodon fasciatus*; ED ranked sixth in Canada) and Massasauga (*Sistrurus catenatus*; 11th) have DUs assessed as Endangered (COSEWIC 2012a, 2021b), and Canada's only boa is assessed as Special Concern. Two of three squamate species extirpated from Canada, Pygmy Short-horned Lizard (*Phrynosoma douglasii*) and Timber Rattlesnake (*Crotalus horridus*) fall within the top 20 most isolated species and together represent a loss of 117.8 million years of evolutionary history.

Mammals

Canadian mammals have a national median PE score of 4.0 million years (compared to a median global PE score of 1.6 million years). Canada's 210 native Canadian mammal species have ED scores that range from 4.3 to 158.8 million years and together represent 2.9 billion years of independent Canadian evolutionary history (Table 4, Appendix S7). Canadian mammal species had a median ED score of 10.2 million years, much less than half the average for the ectotherms considered above. Canada's most isolated mammal, Virginia Opossum (*Didelphis virginiana*) has a particularly high ED score (158.8 million years) compared to all Canadian mammals, representing more than twice the evolutionary history held by Canada's second ranked species, North American Porcupine (*Erethizon dorsatum*; 63.8 million years), and

TABLE 3. Top 20 evolutionarily isolated squamate species in Canada, ranked in descending order of their Canadian evolutionary distinctiveness (ED) score. Canadian ranking is accompanied with the species' taxonomy, and global ED ranking, Canadian status assessed by COSEWIC (NA = Not at Risk or not assessed in Canada, SC = Special Concern, T = Threatened, E = Endangered, XT = Extirpated), and global status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

Canadian (global) ED rank	Family	Scientific name	Common name	Canadian (global) ED	Canadian status	Global status
1 (3234)	Anguidae	*Elgaria coerulea*	Northern Alligator Lizard	159.0 (13.8)	NA	LC
2 (1286)	Boidae	*Charina bottae*	Northern Rubber Boa	90.0 (19.6)	SC	LC
3 (4778)	Phrynosomatidae	*Phrynosoma hernandesi*	Greater Short-horned Lizard	85.5 (11.34)	SC	LC
4 (4394)	Phrynosomatidae	*Phrynosoma douglasii*	Pygmy Short-horned Lizard	85.5 (11.9)	XT	LC
5 (5617)	Scincidae	*Plestiodon skiltonianus*	Western Skink	71.7 (10.2)	SC	LC
6 (6459)	Scincidae	*Plestiodon fasciatus*	Common Five-lined Skink	64.4 (8.7)	E	LC
7 (6439)	Scincidae	*Plestiodon septentrionalis*	Prairie Skink	64.4 (8.7)	SC	LC
8 (7533)	Colubridae	*Hypsiglena chlorophaea*	Desert Nightsnake	43.2 (6.7)	E	LC
9 (3279)	Colubridae	*Contia tenuis*	Common Sharp-tailed Snake	37.0 (13.8)	E	LC
10 (764)	Colubridae	*Diadophis punctatus*	Ring-necked Snake	37.0 (23.0)	NA	LC
11 (2724)	Viperidae	*Sistrurus catenatus*	Massasauga	34.7 (14.9)	E	LC
12 (5300)	Viperidae	*Crotalus horridus*	Timber Rattlesnake	32.4 (10.6)	XT	LC
13 (5254)	Colubridae	*Opheodrys vernalis*	Smooth Greensnake	31.4 (10.7)	NA	LC
14 (7245)	Colubridae	*Coluber constrictor*	North American Racer	31.4 (7.3)	E	LC
15 (3981)	Colubridae	*Heterodon platirhinos*	Eastern Hog-nosed Snake	30.1 (12.6)	T	LC
16 (5900)	Colubridae	*Heterodon nasicus*	Plains Hog-nosed Snake	30.1 (9.8)	SC	LC
17 (8417)	Viperidae	*Crotalus oreganus*	Western Rattlesnake	27.8 (5.3)	T	LC
18 (7963)	Viperidae	*Crotalus viridis*	Prairie Rattlesnake	27.8 (6.1)	SC	LC
19 (8848)	Colubridae	*Lampropeltis triangulum*	Milksnake	24.9 (4.4)	SC	LC
20 (8248)	Colubridae	*Nerodia sipedon*	Common Watersnake	23.2 (5.7)	SC	LC

more than 15× the isolation of the average Canadian mammal. This high ED score is unsurprising, because Virginia Opossum is the only marsupial in Canada (Gardner 1982), a group that diverged from all placental mammals 120–150 million years ago (Foster and Graves 1994).

Alongside Virginia Opossum, four other of Canada's top 20 isolated mammals are the only member of their family in Canada and fall within the top 10 rankings (Table 4). Big Free-tailed Bat (*Nyctinmops mactrois*; ED ranked fourth in Canada) is not an actual resident of Canada, but an occasional migrant that has only been sighted in Canada a few times (BC Conservation Data Centre 2015). One native species that is endemic to North America, Mountain Beaver (*Aplodontia rufa*; sixth), is a semi-fossorial rodent and the only living member of the most primitive rodent family, Aplodontidae (Arjo 2007). This species possesses some of the most primitive morphological, physiological, and anatomical characteristics of any living rodent worldwide, including a primitive renal anatomy which is unable to concentrate urine, and a relatively low reproductive potential compared to other rodents (Arjo 2007; COSEWIC 2012b; British Columbia Ministry of Environment 2013). Mountain Beaver represents 37.2 million years of unique evolutionary history in Canada as well as 35.3 million years globally, making it the 21st most isolated mammal species worldwide (Table 4). Only four of the top nationally ED ranked mammals have been assessed as at-risk by COSEWIC (Table 4).

Birds

Canadian birds have a national median PE score of 5.2 million years (compared to a median global PE score of 2.9 million years). Canada's 664 native bird species have national ED scores ranging from 1.8 to 64.0 million years, with a median score of 10.9 million years (Table 5, Appendix S8). Together, Canada's bird species represent 9.4 billion years of independent evolutionary history in Canada. Belted Kingfisher (*Megaceryle* a*lcyon*) has the highest national ED score in Canada, 64.0 million years. Two top ranked species in Canada, Osprey (*Pandion haliaetus*; ED ranked fifth) and Red-throated Loon (*Gavia stellata*;

TABLE 4. Top 20 evolutionarily isolated mammal species in Canada, ranked in descending order of their Canadian evolutionary distinctiveness (ED) score. Canadian ranking is accompanied with the species' taxonomy, and global ED ranking, Canadian status assessed by COSEWIC (NA = Not at Risk or not assessed in Canada, SC = Special Concern, T = Threatened, E = Endangered, XT = Extirpated), and global status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

Canadian (global) ED rank	Family	Scientific name	Common name	Canadian (global) ED	Canadian status	Global status
1(1323)	Didelphidae	*Didelphis virginiana*	Virginia Opossum	158.8 (7.5)	NA	LC
2 (750)	Erethizontidae	*Erethizon dorsatum*	North American Porcupine	63.8 (9.7)	NA	LC
3 (51)	Castoridae	*Castor canadensis*	American Beaver	52.5 (26.9)	NA	LC
4 (1638)	Molossidae	*Nyctinomops macrotis*	Big Free-tailed Bat	41.9 (6.6)	NA	LC
5 (73)	Talpidae	*Neurotrichus gibbsii*	American Shrew Mole	38.0 (23.2)	NA	LC
6 (21)	Aplodontiidae	*Aplodontia rufa*	Mountain Beaver	37.2 (35.3)	SC	LC
7 (47)	Talpidae	*Condylura cristata*	Star-nosed Mole	36.5 (27.0)	NA	LC
8 (1733)	Heteromyidae	*Dipodomys ordii*	Ord's Kangaroo Rat	33.7 (6.4)	E	LC
9 (1405)	Ochotonidae	*Ochotona collaris*	Collared Pika	31.0 (7.3)	SC	LC
10 (1407)	Ochotonidae	*Ochotona princeps*	American Pika	31.0 (7.3)	NA	LC
11 (1205)	Cricetidae	*Neotoma cinerea*	Bushy-tailed Woodrat	29.3 (7.9)	NA	LC
12 (859)	Vespertilionidae	*Nycticeius humeralis*	Evening Bat	27.5 (9.1)	NA	LC
13 (146)	Talpidae	*Parascalops breweri*	Hairy-tailed Mole	26.7 (18.6)	NA	LC
14 (3741)	Geomyidae	*Geomys bursarius*	Plains Pocket Gopher	25.9 (3.9)	NA	LC
15 (1643)	Geomyidae	*Thomomys talpoides*	Northern Pocket Gopher	25.9 (6.6)	NA	LC
16 (454)	Heteromyidae	*Perognathus fasciatus*	Olive-backed Pocket Mouse	25.5 (11.8)	NA	LC
17 (1678)	Heteromyidae	*Perognathus parvus*	Columbia Plateau Pocket Mouse	25.5 (6.5)	NA	LC
18 (2236)	Soricidae	*Blarina brevicauda*	Northern Short-tailed Shrew	24.5 (5.5)	NA	LC
19 (2439)	Soricidae	*Cryptotis parva*	Least Shrew	24.5 (5.2)	NA	LC
20 (874)	Vespertilionidae	*Antrozous pallidus*	Pallid Bat	24.2 (9.1)	T	LC

12th) rank high globally, being seventh and 16th, respectively (Table 5). Both these species belong to small families, with Osprey being the sole member of its family, Pandionidae (Bierregaard *et al.* 2020; Rizzolo *et al.* 2020).

Half of Canada's top 20 most evolutionarily isolated bird species are not residents or have no breeding populations in Canada (Table 5; Roy 2001; Burrell *et al.* 2017; Riley *et al.* 2019; Buckley *et al.* 2022). Only two of the top 20 have been assessed as at-risk by COSEWIC (Table 5). Many of these species are accidental migrants with only a few confirmed sightings in Canada, so would not be eligible for status assessment. Among them is Canada's second and fourth ranked bird species, Wood Stork (*Mycteria americana*; ED score: 62.7 million years; Roy 2001), and Magnificent Frigatebird (*Fregata magnificens*; ED score: 57.10 million years; Burrell *et al.* 2017).

All Canadian taxa

Canadian terrestrial vertebrates have a national median PE score of 5.2 million years (compared to a median global PE score of 4.2 million years). Overall, amphibians and reptiles contain Canada's highest-ranked ED species. These groups contain the fewest species and are all members of old clades worldwide. Canada's smallest group, the turtles, holds some of the most evolutionarily isolated species overall including the most evolutionarily isolated species in Canada, Spiny Softshell Turtle. Canadian birds and mammals rank much lower than Canadian amphibians and reptiles. One mammal, however, Virginia Opossum, has an ED score comparable to Canada's top reptile and amphibian species, making it another one of Canada's most isolated vertebrate species overall.

Reptiles and amphibians are not just evolutionarily isolated, they have the highest proportion of at-risk species in Canada (ECCC 2018), meaning many millions of years of independent evolutionary history is under threat in Canada. Fifty-eight percent of amphibians and reptiles in Canada have populations assessed as at-risk by COSEWIC, and these species make up 30% of Canada's at-risk tetrapods. For instance, the most evolutionarily isolated species in Canada, Spiny Softshell Turtle, is at risk in Canada.

TABLE 5. Top 20 evolutionarily isolated bird species in Canada, ranked in descending order of their Canadian evolutionary distinctiveness (ED) score. Canadian ranking is accompanied with the species' taxonomy, and global ED ranking, Canadian status assessed by COSEWIC (NA = Not at Risk or not assessed in Canada, SC = Special Concern, T = Threatened, E = Endangered, XT = Extirpated), and global status (LC = Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered).

Canadian (global) ED Rank	Family	Scientific name	Common name	Canadian (global) ED	Canadian status	Global status
1 (1686)	Alcedinidae	*Megaceryle alcyon*	Belted Kingfisher	64.0 (11.1)	NA	LC
2 (671)	Ciconiidae	*Mycteria americana*	Wood Stork	62.7 (16.8)	NA	LC
3 (960)	Tytonidae	*Tyto alba*	Barn Owl	61.1 (14.2)	E	LC
4 (492)	Fregatidae	*Fregata magnificens*	Magnificent Frigatebird	57.1 (19.4)	NA	LC
5 (7)	Pandionidae	*Pandion haliaetus*	Osprey	55.9 (56.1)	NA	LC
6 (596)	Phoenicopteridae	*Phoenicopterus ruber*	American Flamingo	53.6 (17.9)	NA	LC
7 (690)	Threskiornithidae	*Eudocimus albus*	White Ibis	52.3 (16.6)	NA	LC
8 (116)	Cathartidae	*Cathartes aura*	Turkey Vulture	51.9 (28.8)	NA	LC
9 (67)	Cathartidae	*Coragyps atratus*	Black Vulture	51.9 (33.4)	NA	LC
10 (736)	Accipitridae	*Elanus leucurus*	White-tailed Kite	51.9 (16.1)	NA	LC
11 (6256)	Cuculidae	*Cuculus canorus*	Common Cuckoo	50.8 (5.2)	NA	LC
12 (16)	Gaviidae	*Gavia stellata*	Red-throated Loon	49.6 (49.5)	NA	LC
13 (152)	Threskiornithidae	*Platalea ajaja*	Roseate Spoonbill	47.3 (27.5)	NA	LC
14 (46)	Podicipedidae	*Podilymbus podiceps*	Pied-billed Grebe	44.1 (36.0)	NA	LC
15 (211)	Hydrobatidae	*Pelagodroma marina*	White-faced Storm-Petrel	40.3 (25.3)	NA	LC
16 (609)	Hydrobatidae	*Oceanites oceanicus*	Wilson's Storm-Petrel	40.3 (17.8)	NA	LC
17 (148)	Accipitridae	*Elanoides forficatus*	Swallow-tailed Kite	40.2 (27.7)	NA	LC
18 (65)	Hydrobatidae	*Oceanodroma castro*	Band-rumped Storm-Petrel	39.9 (33.6)	NA	LC
19 (1412)	Apodidae	*Cypseloides niger*	Black Swift	38.5 (11.9)	E	VU
20 (348)	Apodidae	*Streptoprocne zonaris*	White-Collared Swift	38.5 (21.4)	NA	LC

Overall, at-risk vertebrate species (as we have defined them) have, on average, higher national ED scores than all other Canadian vertebrates ($W = 93282$, $P < 0.001$), a pattern driven by turtles where 12/15 species are assessed as at risk under our criteria. This pattern was not found within any of the major taxa (birds $W = 26576$, $P = 0.06$; amphibians: $W = 297.5$, $P = 0.78$; squamates: $W = 142$, $P = 0.11$; turtles: $W = 28$, $P = 0.17$; mammals: $W = 3681$, $P = 0.57$) and is consistent with global patterns (Verde Arragoitia *et al.* 2013; Tonini *et al.* 2016; Jetz *et al.* 2018). For this analysis we conservatively considered species not assessed by COSEWIC as Not at Risk; some proportion of the unassessed species may indeed have populations at risk in Canada.

Exotic species

Exotic species are those that have been introduced to Canada as a result of human activity. They are currently not considered suitable targets for conservation (CESCC 2016) nor are they eligible for assessment by COSEWIC and can even be considered a threat to native Canadian species (COSEWIC 2019). These species, however, are still a part of Canadian biodiversity, both collectively and as part of local ecosystems. Interestingly, many of these exotic species are the only members of their family in Canada, making them evolutionarily isolated. Indeed, when we use the phylogenies of all Canadian species, seven exotic species fall within the top 20 rankings for their respective taxonomic groups (Table 6: note, the inclusion of exotic species can change ED scores for related native species). Among these is Common Wall Lizard (*Podacris muralis*; national ED score: 166.81 million years), a species introduced to Vancouver Island, British Columbia in 1970 (Allan *et al.* 2006) that currently coexists and competes with Canada's most isolated squamate, Northern Alligator Lizard (Engelstoft *et al.* 2020). Another isolated exotic species, Feral Horse (*Equus ferus*; national ED score: 62.0 million years), is a culturally valued and iconic species of the Sable Island (Nova Scotia) and Chilcotin highlands (British Columbia) landscapes, despite its negative impact on native flora (Freedman *et al.* 2011; Parks Canada 2019). Wild Boar (*Sus scrofa*) is another isolated exotic Canadian species (national ED score: 54.4 million years) that has met with a

TABLE 6. Canadian ranking of exotic tetrapods introduced to Canada had they been included in our calculations. Ranks based on species' evolutionary distinctiveness (ED) score placement within their respective class. Ranking is accompanied with the species' taxonomy and range, and global status (NA = Not Assessed, LC= Least Concern, EN = Endangered).

ED rank in respective class	Class	Family	Scientific name	Common name	Canadian ED (million years)	Global status
14	Turtles	Emydidae	*Trachemys scripta*	Pond Slider	47.4	LC
1	Squamates	Lacertidae	*Podacris muralis*	Common Wall Lizard	166.8	LC
2	Mammals	Equidae	*Equus caballus*	Feral Horse	62.0	NA
3	Mammals	Suidae	*Sus scrofa*	Wild Boar	54.4	LC
6	Mammals	Myocastoridae	*Myocastor coypus*	Nutria	49.1	LC
11	Mammals	Muridae	*Mus musculus*	House Mouse	35.3	LC
20	Mammals	Muridae	*Rattus rattus*	Black Rat	25.5	LC
32	Mammals	Muridae	*Rattus norvegicus*	Brown Rat	25.5	LC
36	Mammals	Leporidae	*Oryctolagus cuniculus*	European Rabbit	21.2	EN
57	Mammals	Felidae	*Felis catus*	Domestic Cat	15.2	NA
58	Mammals	Leporidae	*Lepus europaeus*	European Hare	15.0	LC
92	Mammals	Cervidae	*Dama dama*	Fallow Deer	11.8	LC
113	Mammals	Cricetidae	*Myodes glareolus*	Bank Vole	10.0	LC
84	Birds	Columbidae	*Columba livia*	Rock Pigeon	25.4	LC
90	Birds	Alaudidae	*Alauda arvensis*	Eurasian Skylark	24.2	LC
113	Birds	Sturnidae	*Sturnus vulgaris*	European Starling	22.5	LC
114	Birds	Phasianidae	*Alectoris chukar*	Chukar	22.4	LC
124	Birds	Columbidae	*Streptopelia decaocta*	Eurasian Collared-dove	21.5	LC
154	Birds	Odontophoridae	*Callipepla californica*	California Quail	19.2	LC
168	Birds	Passeridae	*Passer domesticus*	House Sparrow	18.2	LC
180	Birds	Phasianidae	*Perdix perdix*	Gray Partridge	17.6	LC
181	Birds	Phasianidae	*Phasianus colchicus*	Ring-necked Pheasant	17.6	LC
407	Birds	Anatidae	*Cygnus olor*	Mute Swan	9.3	LC

decidedly more mixed reception (Barrios-Garcia and Ballari 2012; NCC 2020). We highlight these species and their place in the current Canadian Tree of Life mindful of the pace of global change and the blurring lines between what is native and what is not (Thomas 2017). We predict that an analysis of Canadian flora would produce similar patterns.

Prioritization

Conservation organizations contributing to the recovery of species-at-risk work with limited resources and may welcome ways to help prioritize efforts. Metrics like ED to distinguish among species for on-the-ground intervention or for education and outreach may be helpful. For instance, the ED metric may be used alongside conservation status to prioritize between species or populations of equal threat status. ED has also been previously used to identify ambassador mammal species for conservation marketing (Macdonald *et al.* 2017). Such applications may benefit outreach campaigns to increase awareness and contribute to recovery actions for Canadian biodiversity.

For our analyses, we chose to measure ED at the species level. While we acknowledge that infra-specific entities are recognized in law and by COSEWIC as integral to Canada's biodiversity, measuring species' ED scores provides a more stable ranking list: infra-specific designations (e.g., the identification of DUs) are prone to change upon species reassessment and increasing data availability (see Appendix S13 for details). Importantly, Canada's glaciation history means much of it is still being recolonized from refugia, such that its current biodiversity complement is not at equilibrium. Given that the rate of terrestrial vertebrate speciation is higher at higher latitudes (reviewed in Schluter and Pennell 2017), it is also unclear if Canada's set of DUs comprise many incipient species, or many ephemerata, and how they should be treated in the context of evolutionary isolation. This is fertile territory for future work.

Conclusion

The national ED scores for Canadian tetrapods highlight Canada's most evolutionarily isolated species, many of which hold a great deal more evolutionary history in Canada relative to their global ranking. This is expected for any pruned phylogeny (because close relatives are found elsewhere) but highlights how local faunas sampled from the more inclusive clade can contain few representatives of many disparate taxa, making each one more distinctive at the local and national scale. There is a strong link between evolutionary isolation and the contribution of non-redundant evolutionary features (Faith 1992; Tucker *et al.* 2019). If the conservation of such features is a goal of conservation work in Canada, then these rankings may provide a useful metric for ongoing prioritization and conservation action by agencies tasked with conserving Canadian biodiversity.

Author Contributions

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SUPPLEMENTARY MATERIALS:

APPENDIX S1. Consensus trees of each Canadian clade as nexus files.

APPENDIX S2. List of global evolutionary distinctiveness and pendant edge scores and rankings for global mammal species.

APPENDIX S3. Augmenting the global trees for newly recognized Canadian species.

APPENDIX S4. List of Canadian evolutionary distinctiveness scores and rankings for Canadian turtle species.

APPENDIX S5. List of Canadian evolutionary distinctiveness scores and rankings for Canadian amphibian species.

APPENDIX S6. List of Canadian evolutionary distinctiveness scores and rankings for Canadian squamate species.

APPENDIX S7. List of Canadian evolutionary distinctiveness scores and rankings for Canadian mammal species.

APPENDIX S8. List of Canadian evolutionary distinctiveness scores and rankings for Canadian bird species.

APPENDIX S9. List of Canadian evolutionary distinctiveness scores and rankings for Canadian turtle species, including exotic species.

APPENDIX S10. List of Canadian evolutionary distinctiveness scores and rankings for Canadian squamate species, including exotic species.

APPENDIX S11. List of Canadian evolutionary distinctiveness scores and rankings for Canadian mammal species, including exotic species.

APPENDIX S12. List of Canadian evolutionary distinctiveness scores and rankings for Canadian bird species, including exotic species.

APPENDIX S13. Calculating national evolutionary distinctiveness scores and rankings at the species level.

The Canadian Field-Naturalist

Book Reviews

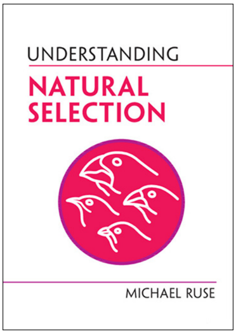
Book Review Editor's Note: *The Canadian Field-Naturalist* is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those on any species (native or non-native) that inhabits Canada, as well as books covering topics of global relevance, including climate change, biodiversity, species extinction, habitat loss, evolution, and field research experiences.

Currency Codes: CAD Canadian Dollars, USD United States Dollars, EUR Euros, AUD Australian Dollars, GBP British Pounds.

BIOLOGY

Understanding Natural Selection

By Michael Ruse. 2023. Understanding Life Series. Cambridge University Press. 188 pages, 56.95 CAD, Hardcover, 22.95 CAD, Paper.



Canadian philosopher of science Michael Ruse believes that the process of natural selection "strikes right to the heart of our being" (p. 149). His book, *Understanding Natural Selection*, while not always light reading, is a useful short outline of the theories, historical contexts, and disagreements within the field of evolutionary biology. It is opinionated and peppered with the occasional polemic and many entertaining quips. For instance, on the calculation of kin selection benefits for survival, Ruse reminds his readers of geneticist J.B.S. Haldane's comment that "I would lay down my life for two brothers or eight cousins" (p. 98).

Charles Darwin's centrality lies in his theory of evolution—laid out in *On the Origin of Species* (John Murray, First Edition 1859)—which today is accepted in biology as near fact. When Darwin first formed his theory, he borrowed from the social sciences, including economist Adam Smith's ideas about the division of labour (p. 8). This perspective, Ruse suggests, was incorporated into Darwin's theory that species will adapt to fill a variety of ecological niches and then spread (speciate) into a Tree of Life. Darwin "was ever a Lamarckian" (p. 4) and, although he found that approach an insufficient explanation for diversity with modification among species, he did believe acquired characteristics could be inherited and passed on. He was also inspired by Thomas Malthus's observations about exploding human population growth outpacing slower production of consumable resources. Darwin "incorporated this argument in its entirety into his theory" of the struggle for existence (p. 6).

In his studies of pigeons, and later barnacles, Darwin came to ask whether over "the course of thousands of generations" individuals having an "advantage, however slight, over others, would have the best chance of surviving and of procreating their kind?" (p. 7). Then his moment of clarity: "This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection" (p. 7).

Ruse reminds us that Darwin, absent a gene-based Mendelian explanation (more on Mendel below), faced many obstacles proving his theory, such as trying to explain how sterile family members (certain insects, for example) could contribute to a community's survival. More problematic was the "extreme imperfection of the geological record" (p. 14)—a problem that persists today. But, as for transitional forms, Darwin's view was that if what was available in nature was good enough to afford an evolutionary advantage even if "not necessarily the best possible [structure] under all possible conditions" (Darwin 1872: 101) then it held explanatory power. He thought transitional forms were rare to begin with, and therefore hard to find. Yet, even this low expectation of the fossil record was unsatisfactory to him: "To the question why we do not find rich fossiliferous deposits belonging to these assumed earliest periods prior to the Cambrian system, I can give no satisfactory answer" (Darwin 1872: 197).

This conundrum would continue to generate explanatory models from other theorists. One prominent proposal, punctuated equilibrium, was offered by Niles Eldredge and Stephen Jay Gould in 1972. They argued that the fossil record should be taken at face value. Fossil evidence of transitional forms is rare or absent because speciation often happens relatively suddenly, not gradually. "Speciation is a rare and difficult event that punctuates a system in homeostatic equilibrium" (Eldredge and Gould 1972: 115). Ruse writes that their theory "doesn't necessarily deny Darwinian forces" (wrongly implying, it seems to me, that this was the authors' intention; p. 92). In their view, rather, it was "extremely improbable that we shall be able to trace the gradual splitting of a lineage merely by following a certain species up through a local rock column" (Eldredge and Gould 1972: 94).

As he sailed on *The Beagle* around the globe, Darwin read Charles Lyell's recently published *Principles of Geology* (John Murray, 1830–1833), and it led him towards a more deistic (non-interventionist) explanation for species diversity (p. 30). (Darwin had studied theology at the University of Cambridge, but under the influence of biologist Thomas Huxley, he would turn towards agnostic views later in life.) Darwin had begun to pursue a "naturalistic solution to the origins question" (p. 30), and Lyell provided a uniformitarian (a continuous and unvarying process) approach to geological change. A significant inspiration also came from observing finches on the Galápagos Islands, where he noticed birds that were similar in appearance but also slightly different from each other. "Darwin did not know what causes variations, how frequent they are, what different kinds they are, and crucially what happens to variations during reproduction" (p. 37).

Mendelian factors—which we now call genes—were the significant breakthrough in the mid-1860s that later revealed the primary source of species variation. (While friar Gregor Mendel knew of Darwin, the reverse wasn't true.) Mendel saw that species traits were not necessarily found blended in offspring, but dominant or recessive attributes offered by both parents could be retained and passed on even if not visibly expressed (p. 57). Population geneticists would come to the fore in the 1930s and begin the synthesis of Darwinian natural selection and Mendelian genetics (pp. 60–61). While mutations are the building blocks of evolutionary change, in Ruse's determined view the course of evolution is still directed by "natural selection or nothing" (p. 61).

Harder to follow is Ruse's outline of neo-Darwinian genetic drift, which doesn't rely on adaptive advantage but dynamic equilibrium whereby there is primarily group and not individual selection. He finds wanting the idea that random genetic drift (rather than selective factors such as heat and humidity) could be a primary causal evolutionary mechanism, where "some form of group selection pass[es] the successful genes through the whole population" (p. 112).

Theodosius Dobzhansky's (1937) book *Genetics and the Origin of Species* is acknowledged by Ruse as "arguably the most important—certainly the most influential—book on evolutionary theory in the twentieth century" (pp. 70–72). Dobzhansky, through his work on fruit flies, showed how seasonal ecological conditions, such as food scarcity, forced genetic fluctuations and significantly influenced the life cycles of small, isolated populations.

A most interesting chapter in Ruse's book is devoted to whether Darwinian natural selection is the primary driver of evolution. Ruse explores whether that mechanism can lead to speciation (macroevolution) and not only variation within a species (microevolution). Darwin dismissed the term "species" (even in the sixth edition of *Origin*) as something "given, for the sake of convenience, to a set of individuals closely resembling each other, and that it does not essentially differ from the [similarly arbitrary] term variety which is given to less distinct and more fluctuating forms" (Darwin 1872: 37). Today, however, Maize (*Zea mays*), fruit fly, and Greenish Warbler (*Phylloscopus trochiloides*) examples provide more evidence of how new (reproductively isolated) species develop. Similarly, the rate of evolution can be sped up through species seclusion on remote islands (pp. 93–94). This is still a difficult thing to directly observe, except for in viruses, and much of the solid evidence is found fossilized in layers of rock or in gene sequence analysis. For Darwin, if a hypothesis "explains many phenomena it comes in time to be admitted as real" (p. 86). Ruse argues that newer studies of Galápagos finches, sticklebacks, mosquitoes, and the fruit fly species Apple Maggot (*Rhagoletis pomonella*) have provided further proof that "in short pieces of time, you can get changes that any reasonable person" will acknowledge to be speciation (p. 95).

Major Debate—The Spandrels Paper

While Ruse's own prominence rose during the anti-creationist battles in public schools in the 1980s, he only peripherally mentions this fight in the context of evolutionary biologists putting aside their disagreements to form a united front against evolution deniers. Then, about two-thirds into the book, Ruse enters the divisive debate over adaptationism. This is an important subject area because it illuminates how we interpret intermediary forms and functions in evolution. Ruse refers to the very influential "Spandrels Paper" (Gould and Lewontin 1979). Its authors, Gould and Richard Lewontin, argued that some biological features are incidental by-products (like the ceiling spaces called spandrels formed by happenstance in domed cathedrals), which should not be confused with other functions that provide actual evolutionary adaptive advantages. They were appealing to evolutionists to provide more rigorous explanations for visible features and to avoid *ad hoc* 'just-so stories'. (A well-known illustration of this is that the human nose did not evolve to hold eyeglasses, despite appearances, but for smell.)

Ruse is dismissive of Gould and Lewontin (1979). He sees their argument as a "general critique of Darwinism" and evidence that they were arguing against natural selection being primary in evolution (pp.108–109). Michael Rose and George Lauder were more generous (in 1996), describing the maligned Spandrels Paper as an important critique of the kind of adaptationist thinking that had become prevalent in biology:

> All features of organisms are viewed *a priori* as optimal features produced by natural selection specifically for current function. Instead, Gould and Lewontin advocated for a more pluralistic view of evolutionary investigation, recognizing that traits *may arise* [my emphasis] by other means than natural selection. (Rose and Lauder 1996: 1)

This was also related to the "5% of a wing" problem. The adaptive advantage of wings (for flying) is obvious, but what about the intermediate stages of pre-wings—how do they provide adaptive advantage? This had been a challenge for Darwin, too, and he responded to critics in updated editions of *On the Origin of Species*. He said that there were intermediary functions for proto-wings other than flight. Redundancy provides both a capacity for each appendage or organ to work in more than one way (for example, the air sac of fish) and for functions to be performed by more than one functional element (Darwin 1872: 125).

While the Spandrels Paper has had supporters and detractors, Ruse's dismissive critiques of Gould and Lewontin continues relentlessly throughout the book, right to the bitter end (pp. 105–109, 116, 135–138, and 152). On the last page he writes that, in the Spandrels Paper, Gould and Lewontin "notoriously" reduce natural selection "to a mere clean-up role. This is simply not true" (p. 152). A more conciliatory approach is that adaptation is not the sole determinant of evolution and does allow for structural restrictions. Pluralists (such as Gould and Lewontin) are also right to argue that "the correct evolutionary explanation may not even include natural selection for the trait" (Stanford 2010). Similarly, Rasmus Nielsen wrote that while the Spandrels Paper "did not spell the end to adaptationist storytelling" much was learned (Nielsen 2009: 2487). Evolutionary biologists are "more reluctant to invent adaptive stories without direct evidence for natural selection acting on the traits in question" (Nielsen 2009: 2487). The last words go to Gould, who published in the final year of his life that Darwinian selection has been "overwhelmingly validated, both empirically and theoretically as a dominant mechanism of evolutionary change in populations at generational timescales" (Gould 2002: 1322).

The Idea of Progress

Seeing evolution as a linear progression from slug through chimp, with humans at the apex, is no longer in vogue. Although, as Ruse writes, denying any hierarchy is "taking animal rights activist Peter Singer too seriously" (p. 117). But, it is still presumptuous in biological terms to anoint humans as "superior to every possible virus that might strike" us (a reflection derived from our COVID-19 era; p. 117). Darwin had a mixed view about this subject, too. At one point he dismissed any "absolute tendency to progression" but did not deny that there were "higher animals", nor specialization that led (for example) to advancement of the brain where "natural selection clearly leads towards highness" (pp. 117–118).

Ruse closes with an interesting discussion. Evolutionist Alfred Russel Wallace wrote to Darwin to recommend that he address the problem of the phrase "natural selection" being misinterpreted as meaning a kind of mastermind or higher intelligence that was in charge. Herbert Spencer's term was proposed (and accepted) as an alternative, but "survival of the fittest" would forever face the charge of being a tautology. And besides, as Ruse notes, it is actually "*reproduction* that matters, not survival, and it is *fitter* that counts, not fittest" [my emphasis] (p. 130). Philosopher Karl Popper pointed out that the same goes for the word "adaptation", another tautological suspect: to be adapted for is simply to not be eliminated in the survival Olympics (pp. 129–131). Another approach is to see natural selection not as a causal agent at all, but just the statistical way we see species living on or dying out. "Natural selection is simply keeping score" (p. 133). But causes aren't real things either, Ruse muses. They only provide conceptualization that helps us explain the world to ourselves, which is why the phrase "natural selection" does so well in describing how evolution works.

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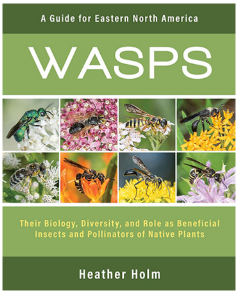
ENTOMOLOGY

Wasps: a Guide for Eastern North America: their Biology, Diversity, and Role as Beneficial Insects and Pollinators of Native Plants

By Heather Holm. 2022. Pollination Press LLC. 416 pages, 39.95 USD, Paper.



From the author of other related works, including *Pollinators of Native Plants* (Pollination Press LLC, 2014) and *Bees: an Identification and Native Plant Forage Guide* (Pollination Press LLC, 2017), *Wasps* is a worthy addition to your library. This is a substantial book—416 pages, 27.5 cm × 22.5 cm, and 1.8 kg—best suited as a desk copy or reference book versus a field guide. Of excellent quality, the many photos and diagrams are high resolution and well captioned. The book consists of 18 chapters plus a well-designed Glossary, Bibliography, and Index, which includes a three-page photographic guide to wasp genera (pp. 412–414).

Following a short general introduction, the first five chapters of *Wasps* cover ecological basics, including classification, sociality, nesting behaviour, life cycles, anatomy, diet, and the ecosystem services provided by wasps. Totalling 64 pages, these sections provide fascinating information and vivid photography. The diet and ecosystem services sections are particularly interesting, giving wasps well-deserved recognition as pollinators and actors in invasive species and pest insect control. The next 12 chapters (Chapter 6 to Chapter 17) are each dedicated to a wasp family and are further organized by subfamily, then genus. Each genus is represented by one species, and each two-page species entry provides details such as seasonality, appearance, nesting biology, prey, range, and native nectar plants for that species. Many species entries also include one or two interesting facts or quotes from wasp reference works from the 1900s.

The final chapter (Chapter 18) contains a planting guide for eastern North America divided into geographic areas, e.g., Mid-Atlantic, Great Lakes, and Atlantic Maritime. It includes a two-page wasp–plant interaction guide that indicates which wasp genera visit which genera of plants. This was developed from "thousands of citizen scientist wasp-plant interaction observations in eastern North America" (p. 385). Each geographic region has a full-page planting guide listing the scientific and common names of native wasp-friendly perennial plants, vines, and shrubs suitable for that region.

This book is not intended as an exhaustive identification guide to wasp species—there are no dichotomous keys, and most of the parasitic wasps are not included. Wasp diversity is staggering; the 70 genera and 150 species profiles selected for inclusion in this book are those wasps that regularly visit flowers and are relatively easy to recognize. Holm's goal is

> to provide the natural history and biology of flower-visiting wasps that a keen observer, pollinator enthusiast, biology, or conservation professional may find in their garden, nearby park, natural area, or nature preserve. (p. 12)

I had been looking forward to this book and was not disappointed. It is both informative and beautiful, with large, high-quality photos that provide notations for key identifying features. This would make a great coffee-table book for the wasp-curious. For those with an established interest in these under-loved insects, it is a treasure.

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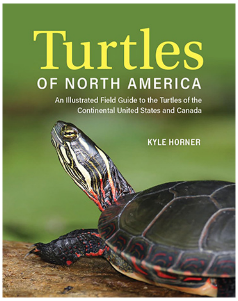
HERPETOLOGY

Turtles of North America: an Illustrated Field Guide to the Turtles of the Continental United States and Canada

By Kyle Horner. 2024. Firefly Books. 208 pages and 264 colour photos and illustrations, 29.95 CAD, Paper.



Turtles stir excitement and curiosity in us all. They can become vehicles in young minds to think about our planet and the conservation of our wild friends. Author Kyle Horner has produced an exquisite book on the turtles of North America, which is certain to become a classic reference to these fascinating reptiles.

I was probably around six years old when I encountered my first turtle. My uncle stopped by with this strange creature in hand; he said he had been driving down the street and saw a black lump crossing the road. He stopped and soon discovered it was a turtle. I remember it being black with yellow markings with its head partially hidden inside the shell. Thinking back on this memory it was probably a Common Box Turtle (*Terrapene carolina*), like those featured on pages 162–165 of Horner's book. I think about that turtle often, wondering where it came from—was it an escaped pet (box turtles are not native where I grew up)? I don't recall what my uncle did with it, but I assume he gave it a better home.

This book has everything—it covers all 64 species of turtles that "inhabit Canada, the continental United States, and the ocean waters that surround them" (p. 9). The introductory section is a must read to gain a better understanding of turtle biology and ecology. Topics include turtle evolution, taxonomy, anatomy, behaviour, and conservation. Each of these topics are broken down into various subtopics, covering all aspects of turtle and tortoise ecology (all tortoises are turtles, but not all turtles are tortoises). I learned a lot reading these sections—for example, I did not realize that turtles have two ways of protecting their heads. One neck retraction strategy involves the turtle bending its neck sideways and tucking it under the front edge of its shell. Approximately 80 species of turtles protect their necks this way; they make up the suborder Pleurodira and are commonly called "side-necked turtles". These species occur in the Southern Hemisphere in places like Africa, South America, and Australia (pp. 13–14). The species covered in this book belong to the suborder Cryptodira, also called the "hidden-necked turtles", that bend their necks into an 'S' shape and draw them back into their shells between their front legs.

The species accounts are the highlight and represent the bulk of the book. Each account is rather brief, however, and is not as comprehensive as accounts in some other turtle guides. To cover 64 species—and, I assume, keep publication costs down—the author uses short paragraphs to present information. The accounts cover a variety of topics but are succinct in their delivery; key facts are listed under bolded headings including Identification, Similar Species, Range, Habitat, Diet, Reproduction, and Conservation. The accounts feature colour photos of each species and range maps. The photos alone make up for the brief written accounts and are a visual treat. Most photos take up a half page and were likely selected for their appeal and clarity to help with identification in the field. Each range map is colour coded and, depending on the species, provides subspecies ranges, introduced populations, intergrade zones, and other information. Scattered throughout the accounts are callout boxes exploring additional topics that may be of interest to the reader. For example, page 115 features a callout on Pond Slider (*Trachemys scripta*) about how this species has been introduced into local ponds and wetlands by pet owners. (Pond Sliders are popular pets, but they generally become unmanageable when they reach adulthood. Pet owners then release them into nearby waterways.) The range map of Pond Slider illustrates these purposeful introductions well.

The sea turtle accounts are especially great reads. Most of these species are major focusses of conservation. Some are listed as Endangered under the United States' *Endangered Species Act* and also have a global conservation status of Critically Endangered or Vulnerable. Their diets are fascinating (e.g., jellyfish for some species), and the accounts alert us to the impacts that egg harvesting on beaches and fishing nets in the oceans are having on these wonderful creatures (pp. 189–203). The end of the book includes a Glossary, Photo Credit Section, and Index.

Overall, Horner's *Turtles of North America* is a fascinating journey into the colourful and exciting worlds of these often-misunderstood reptiles. I recommend this guide to anyone interested in North American turtles, especially the upcoming generation that wants to learn more about the animals with which we share the world. Horner's book is a vehicle to communicate the much-needed conservation efforts required to save what global biodiversity is left.

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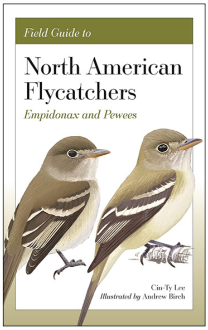
EDITOR'S COMMENT: The statuses of Canadian turtles are listed in the following article in this issue:

Kominek, E., O. Cornies, H. McCurdy-Adams, and A.Ø. Mooers. 2023. Evolutionary isolation of Canadian terrestrial vertebrate species. Canadian Field-Naturalist 137(4): 367–380. https://doi.org/10.22621/cfn.v137i4.2673

ORNITHOLOGY

Field Guide to North American Flycatchers: Empidonax and Pewees

By Cin-Ty Lee. Illustrations by Andrew Birch. 2023. Princeton University Press. 168 pages, 55 pages of colour and black and white illustrations, and 19 pages of maps, 24.99 CAD, Paper, 19.99 CAD, E-book.



Many birders talk about "confusing fall warblers" because at that time of year the birds no longer have their colourful spring breeding plumages. I find flycatchers in the fall to be even more confusing. (At least in the spring you might hear a song to help you with identification!) This new *Field Guide to North American Flycatchers* should help anyone who shares the same angst.

Lee's stated goal in producing this guidebook is to create "a more holistic approach: not just focusing on plumage features but also looking at overall structure, shape, size, and impression" or "gestalt" (p. 1). Using words and painted illustrations, Lee and Birch contrast the shapes and proportions of different species, along with their voices, habitats, behaviours, and seasonal statuses.

Over 20 pages at the beginning of the book are dedicated to the main field marks that the authors suggest one should study: crown shape, forehead angle, bill length, lower mandible colour, tail length and width, primary projection (relative to tertials), wingbar contrast (relative to upperparts), wing panel contrast, upper/underpart contrast, eye-ring, and overall colouration. Each of these field mark sections has an explanation on the left-hand page and multiple colour illustrations on the right-hand page, some of which are accompanied by line drawings that show the differences among, for example, the various crown shapes (i.e., round, flattish, peaked, or crested). Birders often struggle to understand subjective field guide descriptions—such as short, medium, and long—but this guide does the best job I've seen in clarifying and illustrating these subtle differences. Beside each field mark illustration is a list of species that generally show that characteristic. But Lee and Birch don't stop there. They have compiled a one-page Field Mark Matrix (scan it for a handy cheat sheet) and two comparison plates, one for western birds and one for eastern birds. Another interesting feature is a Visual Similarity Map where species are arranged according to how similar they appear to each other. Those that are nearly identical overlap, such as Willow (*Empidonax traillii*) and Alder (*Empidonax alnorum*) Flycatchers.

Each species account has sections on size, general identification, habitat, similar species, voice, one or more spectrograms with mnemonics or other notes, multiple illustrations showing salient field marks, side-by-side comparisons of similar species (often both in colour and pen-and-ink), and two range maps.

The range maps are unique. Each starts with a standard colour map showing breeding, migration, wintering, and year-round ranges. However, one map is overlaid with arrows showing spring migration directions and approximate routes, and the second map depicts fall migration patterns. Contour lines on each map show the approximate arrival months (solid line) and arrival weeks (dotted line) of each species on a continental scale. Each map is accompanied by a series of simple horizontal graphs showing the relative seasonal abundance at various localities throughout the calendar year. For example, Olive-sided

Flycatcher (*Contopus cooperi*) spring migration graphs are for Yukon, Newfoundland, southern British Columbia, Ohio, the Upper Texas Coast, and southeastern Arizona; the fall migration graphs are for southern California, southern Mexico, and Colombia. At first glance these maps seem confusing, but with a little effort to understand them they are very useful.

The detail provided can be overwhelming at first, but a methodical study of this book will be invaluable to any birder, regardless of skill level. Sometimes unique features in a book are just window dressing, but in this case they contribute to the authors' goal to "make *Empidonax* identification a possibility for everyone" (p. 1). While I have had this small book for many months, I feel that I have barely scratched the surface in what I can learn from it. This is the first field guide that Princeton published on this difficult family group; the second, *Field Guide to North American Flycatchers*: *Kingbirds and Myiarchus*, also by Lee and Birch, was published in April 2024. You can also watch a webinar that Lee and Birch gave to the Santa Clara Valley Audubon Society, which is available online at https://www.youtube.com/watch?v=3t6CA2Akbwc.

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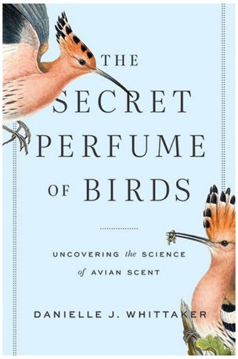
The Secret Perfume of Birds: Uncovering the Science of Avian Scent

By Danielle J. Whittaker. 2022. Johns Hopkins University Press. 296 pages, 11 black and white photos, and 14 black and white illustrations, 36.95 CAD, Hardcover. Also available as an E-book.



When Whittaker was a postdoctoral researcher, she was annoyed by the conventional wisdom that said birds did not possess a sense of smell. There were acknowledged exceptions—such as vultures that can smell carrion—but it didn't make sense to her that a whole class of animals would lack this ability. She felt that researchers "were asking the wrong questions, muddling the answers, and coming to unsupported conclusions" (p. 8). Her scientific pursuit of this question, and the convoluted route she took to do so, is the basis of *The Secret Perfume of Birds*.

Olfaction is the ability to smell, named for the olfactory bulb, which is the part of the brain that receives information from receptors in the nose. (Throughout the book, specialized words are in italics; a definition is given either within the text or in a footnote and then explained in more detail in the nine-page Glossary.) When she began her research, Whittaker was particularly interested in how birds use odours in social and reproductive behaviour. Her study subjects were Dark-eyed Juncos (*Junco hyemalis*) because they are common and, as ground feeders and nesters, are also easy to observe and catch. She felt that her research conclusions might apply to other birds with similar biologies, too. Juncos also do well in captivity, which allowed Whittaker and her colleagues to design experiments in a laboratory setting and test various hypotheses. She started with two basic questions: Did Dark-eyed Juncos detect the smell of other juncos of the same species or unrelated species? If so, what role did these chemical odours play in social and reproductive behaviour?

The uropygial gland, also known as the preen gland, is unique to birds and is located on the dorsal base of the tail. It has long been known that birds spread the gland's secretions (called preen oil) on their feathers to protect them from the elements and ectoparasites, and to maintain their appearance for attracting mates. Preen oil is also the source of body odours in birds. Each species has a specific blend of volatile and semi-volatile chemical compounds in its preen oil, and each individual has different quantities of these compounds, resulting in a unique olfactory signature. Whittaker wanted to know what information these compounds convey about an individual, such as overall health and readiness to breed. She found that scent is helpful to avoid mating with close relatives and preen oil-based odours can predict which individuals have higher numbers and better survival rates of offspring.

The complexity of the research grew when Whittaker and her colleagues discovered that it is a diverse array of symbiotic bacteria living in the uropygial gland that produces the odours important for reproductive behaviour. Social and sexual behaviour then spreads these bacteria quickly between individuals. Whittaker, who studied primates in Indonesia for her Ph.D. in anthropology, linked this research back to her earlier interest in the genetic basis of mate choice through the major histocompatibility complex (MHC). The MHC is a large family of genes that are part of a vertebrate's self-recognition system: proteins coded by MHC genes allow the animal's immune system to detect both itself and any foreign substances that shouldn't be there. A diverse MHC will result in a less diverse microbiome because the immune system can identify and kill more species of bacteria. Thus, an individual should choose a mate that has more dissimilar MHC genes to ensure more diverse bacteria are identified and killed. It is also possible that mates who have more similar MHC genes seek out extra-pair copulations to ensure their offspring will have more dissimilar MHC.

Whittaker's research on avian scent and odours has also broken away from the gender bias in ornithology, where male birds are typically studied more frequently than females. Males may have the brighter plumage, but when it comes to producing scent females are the champions. In conducting a meta-analysis of studies of avian odours, Whittaker and her colleague Julie Hagelin discovered that females have larger uropygial glands (which produce higher concentrations of chemical compounds), greater diversity of volatile compounds in their preen oil, and more varied bacteria. Both sexes rely on chemical signals for stimulating reproduction, mate attraction (in competition with others of the same sex), and parental care. Whittaker wonders

> if one of the reasons that the existence of chemical communications in birds has been overlooked for so long is that many of the lead people researching it, especially early on, have been women. (p. 220)

This book is a good example of the scientific method, whereby a researcher forms a hypothesis and tests it, and if the data don't support their original hypothesis, they investigate why they don't and revise their hypothesis. In Whittaker's book, the phrase "it didn't quite turn out as expected" (p. 168) is a common refrain, one not admitted by enough scientists. Whittaker is obviously enthusiastic about her research and the natural world, with a buoyant and at times humorous writing style, poking fun at herself and the situations she found herself in during her research. In this book she has made a complex topic very accessible.

The only error I noticed is on page 2, where Whittaker states that there are nearly 20 000 species of birds—perhaps this total included subspecies? The latest estimate from the International Ornithological Congress is around 11 000 species (IOC 2023). In case the level of detail in this book isn't sufficient for some readers, the 21-page References section, organized by chapter (in smaller font, so there are lots of them), should enable anyone to access more information.

Literature Cited

International Ornithological Congress (IOC). 2023. IOC world bird list version 14.1, updates. Accessed 20 March 2024. https://www.worldbirdnames.org/new/updates/.

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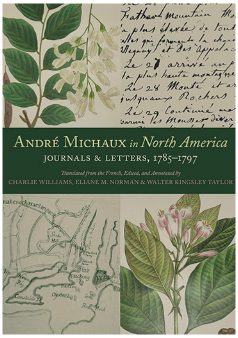
OTHER

André Michaux in North America: Journals & Letters, 1785–1797

Edited by Charlie Williams, Eliane M. Norman, and Walter Kingsley Taylor. Translated by Eliane M. Norman. Foreword by James E. McClellan. 2020. University of Alabama Press. Distributed in Canada by UBC Press. 608 pages, 124 colour figures, 18 black and white figures, and 16 maps, 68.95 CAD, Hardcover.



This weighty tome (literally, it weighs almost 2.3 kg!) provides a day-to-day account of the North American travels and discoveries of iconic 18th century French naturalist André Michaux (1746–1802). Those discoveries were essential in his preparation of *Flora Boreali-Americana* (Parisiis et Argentorati [i.e., Paris et Strasbourg, France], Apud fratres Levrault, 1803). When posthumously published in 1803, it represented the first flora for eastern North America.

André Michaux in North America does more than just translate his original journals from French. The editors of this attractive and physically well-produced book copiously annotate and expand upon Michaux's raw entries. They fill in many of the frequent gaps in the record with information gleaned from his miscellaneous papers and from correspondence by him and/or his associates.

And what a time he had! Venturing out from Charleston, South Carolina, where he maintained a large garden property, Michaux scoured the wild areas of what is now the eastern United States on foot and by horseback in search of plants of economic, medicinal, or scientific significance. The prize finds were sent back to his royal (and later republican) sponsors in France. Such an undertaking would have been incredibly challenging—even life-threatening—for anyone in the late 18th century. This was a period of immense political and social upheaval both in North America and back in Europe. The American Revolution had just ended; the French Revolution exploded in the midst of his American period. Working under such conditions would have to have been even more difficult for Michaux, someone raised in the Versailles gardens of Louis XV but now reporting from afar to republican administrations not noted for recent kindness to royalists! However, one of the many insights offered by the supplementary materials gathered by the editors is strong evidence that Michaux was a republican at heart and did not mourn the passing of the French monarchy.

Oddly, the botanical information contained in his field journals is relatively slim. These were essentially daily diaries, highlighting travel and logistical facts but rarely going into great detail on the plants he saw, let alone the particular specimens he collected. While some entries list a dozen or so of the species he encountered in a day, others provide only descriptive statements or generic determinations, and some list no plants at all. That is frustrating, especially for Canadian botanists interested in details of Michaux's monumental canoe trip into northern Quebec. Some Quebec entries, like that for 22 August 1792 on the Mistassini River north of Lac Saint-Jean (p. 185), offer fulsome landscape descriptions but virtually nothing on the plant species he saw. The editors provide valuable supplementary information in this case, however, obtained from a list found elsewhere amongst Michaux's papers. Thankfully, they do this in many other places in the book, too. Of particular value are the footnotes, which untangle the often-fragmentary descriptions and archaic nomenclature employed by Michaux and express likely meanings in contemporary terms (e.g., suggesting that "*Cerasus racemosa* petioles glandular" [p. 186] may indicate these Mistassini River plants were Choke Cherry [*Prunus virginiana* L.] [p. 472]). Yet many of the journal entries record little more than logistical issues and a notation of the distance travelled that day.

I had hoped to see some mention of the Mistassini Primrose (*Primula mistassinica*) that Michaux famously discovered at Lac Mistassini between 4 and 7 September 1792, and which he described as new to science in *Flora Boreali-Americana*. Its absence from the journal entries seems odd, as Michaux would undoubtedly have immediately recognized this distinctive plant to be something unusual, if not unique.

Providing such an abundance of information unavoidably makes for a lengthy volume. Significant reductions in the book's length (and cost) could have been realized with no significant loss of understanding by a judicious editing of certain sections. The Foreword goes on for nine pages where one (or two) would have done the trick. Omitting an 18-page, full-colour Appendix (pp. 355–372) comprised of pleasant but only marginally useful photos of some of the taxa mentioned would surely have reduced publication costs. And was there really a need for six pages of names in the Acknowledgements?

On the other hand, the Table of Described Plants (pp. 373–414) that identifies and then cites page numbers for every Michaux journal observation is pure gold. Indeed, this and the superb biographical sketch of Michaux's life and scientific contributions (pp. 1–24) will probably be of greatest interest to most readers. Those of us more deeply interested in the details of Michaux's peregrinations will greatly appreciate the numerous and informative footnotes populating most pages.

I found the placement of the text for the footnotes in stand-alone listings at the back of the book, their numbering restarting with each chapter, to be unnecessarily cumbersome. Having footnote numbers running continuously throughout the volume would have been simpler. It would also significantly reduce the annoying degree to which flipping back and forth is required to keep up with the valuable commentaries provided by the editors.

Those commentaries are particularly rich in detail about the people and places Michaux encountered, especially in the southern United States. Details in the footnotes underscore what a high-powered socio-political world Michaux operated in when he was not slogging through swamps, climbing the Appalachian Mountains, or sailing along the Spanish-held islands off the Florida coast. He routinely associated with members of the elite of the time, including such famous intellectual and political American personalities as Thomas Jefferson and George Washington.

André Michaux in North America is more a scholarly reference book than it is a can't-put-it-down adventure tale. However, the information and insights the editors provide (and I've not even mentioned their commentaries of Michaux's political intrigues against the Spanish on behalf of France and the United States during this time) could very well support the telling of such a tale. In detailing all this for a contemporary audience, the editors have served the history of North American botanical exploration very well. Still, I can't wait for the movie!

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NEW TITLES

Prepared by Jessica Sims

If you are interested in reviewing a book on this list, please contact Jessica Sims (bookrevieweditor@canadianfieldnaturalist.ca). This list covers a range of upcoming and new releases in field biology, ecology, and natural history. We also welcome your suggestions for new titles and offers to review unlisted books with a Canadian connection, including those on any species (native or non-native) that inhabits Canada, or books covering topics of global relevance, including climate change, biodiversity, species extinction, habitat loss, evolution, and field research experiences.

Please note: Books marked with a * have already been assigned to a *Canadian Field-Naturalist* reviewer. All other books are available for review and review copies of books marked with a † have been explicitly offered by publishers.

Currency Codes: CAD Canadian Dollars, AUD Australian Dollars, USD United States Dollars, EUR Euros, GBP British Pounds.

BIOLOGY

The Benefits of Imperfection: Biology, Society, and Beyond. By Olivier Hamant. 2024. CRC Press. 208 pages, 267.50 CAD, Hardcover.

The Catalyst: RNA and the Quest to Unlock Life's Deepest Secrets. By Thomas R. Cech. 2024. W.W. Norton. 304 pages, 38.99 CAD, Hardcover, 26.99 CAD, E-book.

Color in Nature. By Justin Marshall, Thomas Cronin, Sönke Johnsen, Ron Douglas, Anya Hurlbert, Jane Boddy, and Fabio Cortesi. 2024. Princeton University Press. 288 pages and 150+ colour illustrations, 44.00 CAD, Hardcover. Also available as an E-book.

The Emotional Lives of Animals: a Leading Scientist Explores Animal Joy, Sorrow, and Empathy—and Why They Matter. Edition, Revised and Updated. By Marc Bekoff. Foreword by Jane Goodall. 2024. New World Library. 272 pages, 30.50 CAD, Paper, 25.99 CAD, E-book.

Evolution Evolving: the Developmental Origins of Adaptation and Biodiversity. By Kevin N. Lala, Tobias Uller, Nathalie Feiner, Marcus Feldman, and Scott F. Gilbert. Illustrations by David Andrews. 2024. Princeton University Press. 440 pages and 19 black and white illustrations, 57.00 CAD, Hardcover. Also available as an E-book.

A Little Queer Natural History. By Josh L. Davis. 2024. University of Chicago Press. 128 pages, 20.95 CAD, Paper. Also available as an E-book.

Living on Earth: Forests, Corals, Consciousness, and the Making of the World. By Peter Godfrey-Smith. 2024. Farrar, Straus and Giroux. 336 pages, 39.00 CAD, Hardcover, 16.99 CAD, E-book.

Meet the Neighbors: Animal Minds and Life in a More-than-Human World. By Brandon Keim. 2024. W.W. Norton. 368 pages, 39.99 CAD, Hardcover, 30.99 CAD, E-book.

The Network of Life: a New View of Evolution. By David P. Mindell. 2024. Princeton University Press. 272 pages, 36 black and white illustrations, and 14 tables, 35.00 CAD, Hardcover. Also available as an E-book.

Sensory Systems of Animals: Biology and Behavior. By Mark Hollins. 2024. CRC Press. 304 pages, 349.99 CAD, Hardcover, 137.99 CAD, Paper.

The Well-Connected Animal: Social Networks and the Wondrous Complexity of Animal Societies. By Lee Alan Dugatkin. 2024. University of Chicago Press. 264 pages, 10 colour plates, and 6 halftones, 29.00 USD, Hardcover. Also available as an E-book.

Why Animals Talk: the New Science of Animal Communication. By Arik Kershenbaum. 2024. Penguin Press. 288 pages, 39.99 CAD, Hardcover, 16.99 CAD, E-book.

BOTANY

Do Plants Know Math? Unwinding the Story of Plant Spirals, from Leonardo da Vinci to Now. By Stéphane Douady, Jacques Dumais, Christophe Golé, and Nancy Pick. 2024. Princeton University Press. 352 pages and 208 colour illustrations, 35.00 CAD, Hardcover. Also available as an E-book.

The Heart of the Woods. By Wyl Menmuir. 2024. Aurum. 336 pages, 27.95 CAD, Hardcover.

How to be a Bad Botanist. By Simon Barnes. Illustrations by Cindy Lee Wright. 2024. Simon and Schuster. 288 pages, 16.99 GBP, Hardcover, 9.99 GBP, E-book.

**The Light Eaters: How the Unseen World of Plant Intelligence Offers a New Understanding of Life

on Earth. By Zoë Schlanger. 2024. HarperCollins. 304 pages, 36.99 CAD, Hardcover, 14.99 CAD, E-book.

Oaklore: Adventures in a World of Extraordinary Trees. By Jules Acton. 2024. Greystone Books. 272 pages, 32.95 CAD, Hardcover.

Our Green Heart: the Soul and Science of Forests. By Diana Beresford-Kroeger. 2024. Random House of Canada. 216 pages, 35.00 CAD, Hardcover, 16.99 CAD, E-book.

Plants and Fungi: the Definitive Visual Encyclopedia. DK Definitive Visual Encyclopedias. By DK. 2024. DK. 448 pages, 66.00 CAD, Hardcover. Also available as an E-book.

Poisonous Plants. Kew Pocketbooks. By Melanie-Jayne Howes and Eliot Jan-Smith. 2024. Royal Botanic Gardens, Kew. Distributed by University of Chicago Press. 96 pages and 40 colour plates, 19.50 CAD, Hardcover.

Redouté: Fabulous Flowers. By Pierre-Joseph Redouté. 2024. Dover Publications. 192 pages, 33.75 CAD, Hardcover. Also available as an E-book.

Rooted in Time: Living Fossils and Other Tenacious Plants. By Carole T. Gee. Illustrations by Channing Redford. 2024. Johns Hopkins University Press. 280 pages, 135 colour photos, and 12 black and white illustrations, 51.95 CAD, Hardcover. Also available as an E-book.

Smithsonian Trees of North America. By W. John Kress. Foreword by Lonnie G. Bunch and Margaret D. Lowman. 2024. Yale University Press. 800 pages, 3626 colour illustrations, and 300+ maps, 97.50 CAD, Hardcover.

†**Treewilding: Our Past, Present and Future Relationship with Forests.** By Jake M. Robinson. 2024. Pelagic Publishing. 336 pages, 37.00 CAD, Hardcover.

Wild Harvest: Edible Plants of the Pacific Northwest. By Terry Domico. 2024. Hancock House. 88 pages and 42 illustrations, 15.95 CAD, Paper.

CONSERVATION AND CLIMATE CHANGE

After Ice: Cold Humanities for a Warming Planet. Edited by Rafico Ruiz, Paula Schönach, and Rob Shields. Foreword by Emma Kowal and Joanna Radin. 2024. UBC Press. 280 pages and 20 black and white photos, 99.00 CAD, Hardcover.

The Age of Melt: What Glaciers, Ice Mummies, and Ancient Artifacts Teach Us about Climate, Culture, and a Future Without Ice. By Lisa Baril. 2024. Timber Press. 272 pages, 39.00 CAD, Hardcover, 19.99 CAD, E-book.

Bad Smoke, Good Smoke: a Texas Rancher's View of Wildfire. By John R. Erickson. 2024. Texas Tech University Press. 208 pages, 33.95 CAD, Hardcover, 26.95 CAD, Paper. Also available as an E-book.

Beautiful Beasts, Beautiful Lands: the Fall and Rise of an African National Park. By Mark Infield. 2024. Whittles Publishing. 240 pages, 31.95 CAD, Paper.

Before They Vanish: Saving Nature's Populations—and Ourselves. By Paul R. Ehrlich, Gerardo Ceballos, and Rodolfo Dirzo. Foreword by Jared Diamond. 2024. Johns Hopkins University Press. 384 pages, 38.95 CAD, Hardcover.

The Biology and Conservation of Animal Populations. By John A. Vucetich. 2024. Johns Hopkins University Press. 312 pages, 8 black and white photos, and 86 black and white illustrations, 97.95 CAD, Hardcover. Also available as an E-book.

Burn Scars: a Documentary History of Fire Suppression, from Colonial Origins to the Resurgence of Cultural Burning. By Char Miller. 2024. Oregon State University Press. 272 pages, 43.95 CAD, Paper.

Copout: How Governments Have Failed the People on Climate—an Insider's View of Climate Change Conferences, from Paris to Dubai. By Nick Breeze. 2024. Palazzo Editions. 240 pages, 22.99 CAD, Paper.

†**Cull of the Wild: Killing in the Name of Conservation.** By Hugh Warwick. 2024. Bloomsbury USA. 304 pages, 37.00 CAD, Hardcover, 20.99 CAD, E-book.

Flourishing in the Age of Climate Change. By William M. Throop. 2024. Cornell University Press. 224 pages, 30.95 CAD, Paper. Also available as an E-book.

The Great River: the Making and Unmaking of the Mississippi. By Boyce Upholt. 2024. W.W. Norton. 352 pages, 39.99 CAD, Hardcover, 30.99 CAD, E-book.

The Green Ages: Medieval Innovations in Sustainability. By Annette Kehnel. 2024. Brandeis University Press. Distributed by University of Chicago Press. 352 pages, 45.50 CAD, Hardcover.

Groundbreakers: the Return of Britain's Wild Boar. By Chantal Lyons. 2024. Bloomsbury USA. 288 pages, 37.00 CAD, Hardcover, 20.99 CAD, E-book.

The Heart of the Wild: Essays on Nature, Conservation, and the Human Future. Edited by Ben A. Minteer, Jonathan B. Losos, and Bill Adams. 2024. Princeton University Press. 280 pages and 26 black and white illustrations, 58.50 CAD, Hardcover. Also available as an E-book.

Heat, a History: Lessons from the Middle East for a Warming Planet. By On Barak. 2024. University of California Press. 322 pages, 119.00 CAD, Hardcover, 37.95 CAD, Paper. Also available as an E-book.

Intertwined: from Insects to Icebergs. By Michael Gross. 2024. Johns Hopkins University Press. 424 pages, 42.95 CAD, Hardcover. Also available as an E-book.

Into the Clear Blue Sky: the Path to Restoring Our Atmosphere. By Rob Jackson. 2024. Scribner. 304 pages, 39.99 CAD, Hardcover, 20.99 CAD, E-book.

The Land is Our Community: Aldo Leopold's Environmental Ethic for the New Millennium. By Roberta L. Millstein. 2024. University of Chicago Press. 184 pages, 149.50 CAD, Hardcover, 37.95 CAD, Paper. Also available as an E-book.

The Last Sunset in the West: Britain's Vanishing West Coast Orcas. By Natalie Sanders. 2024. Birlinn. 320 pages, 19.99 CAD, Paper.

Nature-First Cities: Restoring Relationships with Ecosystems and with Each Other. By Cam Brewer, Herb Hammond, and Sean Markey. Foreword by Faisal Moola and David Suzuki. 2024. UBC Press. 224 pages, 48 black and white photos, 9 illustrations, and 9 maps, 39.95 CAD, Paper.

Nature's Ghosts: the World We Lost and How to Bring It Back. By Sophie Yeo. 2024. HarperCollins. 320 pages, 36.99 CAD, Hardcover, 22.99 CAD, E-book.

Nuclear is Not the Solution: the Folly of Atomic Power in the Age of Climate Change. By M.V. Ramana. 2024. Verso Books. 272 pages, 35.95 CAD, Hardcover, 11.99 CAD, E-book.

One Garden against the World: In Search of Hope in a Changing Climate. By Kate Bradbury. 2024. Bloomsbury USA. 304 pages, 35.00 CAD, Hardcover, 19.99 CAD, E-book.

Philosopher Fish: Sturgeon, Caviar, and the Geography of Desire. Edition, Revised and Updated. By Richard Adams Carey. 2024. Brandeis University Press. Distributed by University of Chicago Press. 352 pages, 45.50 CAD, Paper.

Polar and Climate Change Education: Citizen Science and Sustainability. Research and Teaching in Environmental Studies. Edited by Gisele M. Arruda. 2024. Routledge. 176 pages and 76 black and white illustrations, 331.50 CAD, Hardcover.

Proven Climate Solutions: Leading Voices on How to Accelerate Change. Edited by B.F. Nagy. 2024. Rowman & Littlefield. 238 pages, 47.00 CAD, Hardcover.

Rewilding the Urban Frontier: River Conservation in the Anthropocene. Edited by Greg Gordon. 2024. University of Nebraska Press. 344 pages, 87.95 CAD, Hardcover.

River Profiles: the People Restoring Our Waterways. By Pete Hill. 2024. Columbia University Press. 288 pages, 156.00 CAD, Hardcover, 39.00 CAD, Paper. Also available as an E-book.

Saving the World: How Forests Inspired Global Efforts to Stop Climate Change. By Brett M. Bennett and Gregory A. Barton. 2024. Reaktion Books. Distributed by University of Chicago Press. 256 pages, 32.50 CAD, Hardcover. Also available as an E-book.

†**Sea Change: Charting a Sustainable Future for Oceans in Canada.** Sustainability and the Environment Series. Edited by Ussif Rashid Sumaila, Derek Armitage, Megan Bailey, and William W.L. Cheung. 2024. UBC Press. 276 pages, 45.00 CAD, Paper. Also available as an E-book.

A Sea Full of Turtles: the Search for Optimism in an Epoch of Extinction. By Bill Streever. 2024. Pegasus Books. 256 pages, 38.95 CAD, Hardcover.

The State of Fire: Why California Burns. By Obi Kaufmann. 2024. Heyday. 256 pages, 42.95 CAD, Hardcover.

Voices for the Islands: Thirty Years of Nature Conservation on the Salish Sea. By Sheila Harrington. Foreword by Briony Penn. 2024. Heritage House. 288 pages, 34.95 CAD, Paper, 11.99 CAD, E-book.

What We Leave Behind: a Birdwatcher's Dispatches from the Waste Catastrophe. By Stanislaw Lubienski. 2024. Hodder. 272 pages, 24.99 CAD, Paper, 5.99 CAD, E-book.

What the Wild Sea Can Be: the Future of the World's Ocean. By Helen Scales. 2024. Grove/Atlantic. 320 pages, 42.95 CAD, Hardcover.

When the Ice is Gone: What a Greenland Ice Core Reveals about Earth's Tumultuous History and Perilous Future. By Paul Bierman. 2024. W.W. Norton. 304 pages, 36.99 CAD, Hardcover, 26.99 CAD, E-book.

ECOLOGY

Hedgelands [US Edition]: a Wild Wander Around Britain's Greatest Habitat. By Christopher Hart. 2024. Chelsea Green Publishing. 208 pages, 33.95 CAD, Paper.

Into the Great Wide Ocean: Life in the Least Known Habitat on Earth. By Sönke Johnsen. 2024. Princeton University Press. 224 pages and 15 black and white illustrations, 32.00 CAD, Hardcover. Also available as an E-book.

James Prosek Grasslands: Painting the American Prairie. By James Prosek. Contributions by Andrew J. Walker, Andrew Graybill, Spencer Wigmore, Margaret Adler, and Matt White. 2024. Rizzoli. 160 pages, 60.00 CAD, Hardcover.

†Principles of Soundscape Ecology: Discovering Our Sonic World. By Bryan C. Pijanowski. 2024. University of Chicago Press. 456 pages, 80 halftones, and 28 tables, 214.50 CAD, Hardcover, 71.50 CAD, Paper. Also available as an E-book.

Sing Like Fish: How Sound Rules Life under Water. By Amorina Kingdon. 2024. Crown. 336 pages, 39.99 CAD, Hardcover, 16.99 CAD, E-book.

The World Atlas of Deserts and Drylands. Edited by David Thomas. 2024. Princeton University Press. 400 pages and 250+ colour illustrations, 75.00 CAD, Hardcover. Also available as an E-book.

ENTOMOLOGY

The Ant Collective: Inside the World of an Ant Colony. By Armin Schieb. 2024. Princeton University Press. 128 pages and 120 colour illustrations, 32.00 CAD, Hardcover, 24.99 CAD, E-book.

Conservation of Dragonflies: Sentinels for Freshwater Conservation. By Michael J. Samways. 2024. CABI. 640 pages, 253.50 CAD, Hardcover. Also available as an E-book.

Dragonflies of North America. By Ed Lam. 2024. Princeton University Press. 448 pages and 1850+ colour illustrations, 44.00 CAD, Paper. Also available as an E-book.

Heart of the Hive: Inside the Mind of the Honey Bee and the Incredible Life Force of the Colony. By Hilary Kearney. Photography by Eric Tourneret. 2024. Storey Publishing, LLC. 200 pages, 36.00 CAD, Hardcover.

The Honey Trap: How the Good Intentions of Urban Beekeepers Risk Ecological Disaster. By Dana Church. 2024. Sutherland House Books. 250 pages, 27.95 CAD, Paper.

The Lives of Bees: a Natural History of Our Planet's Bee Life. The Lives of the Natural World No. 9. By Christina Grozinger and Harland Patch. 2024. Princeton University Press. 288 pages and 150+ colour illustrations, 44.00 CAD, Paper. Also available as an E-book.

The Monarch Butterfly Migration: Its Rise and Fall. By Monika Maeckle. 2024. University of Oklahoma Press. 240 pages, 40.95 CAD, Hardcover.

Routledge Handbook of Insect Conservation. Routledge Environment and Sustainability Handbooks. Edited By James S. Pryke, Michael J. Samways, Tim R. New, Pedro Cardoso, and René Gaigher. 2024. Routledge. 586 pages and 74 colour illustrations, 399.95 CAD, Hardcover, 71.99 CAD, E-book.

Six-Legged Ghosts: the Insects of Aotearoa. By Lily Duval. 2024. Canterbury University Press. 296 pages and 100+ colour illustrations, 46.00 CAD, Hardcover.

†What Do Bees Think about? Animal Worlds Series. By Mathieu Lihoreau. Translated by Alison Duncan. 2024. Johns Hopkins University Press. 176 pages, 28.95 CAD, Paper, 21.99 CAD, E-book.

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Crocodiles, Alligators and Lizards: from Black Caimans to Komodo Dragons. By David Alderton. 2024. Amber Books. 224 pages, 38.99 CAD, Hardcover.

The Frog Book. The Nature Book Series. By Jo Byrne. 2024. Graffeg. 160 pages, 22.99 CAD, Hardcover.

Frog Day: a Story of 24 Hours and 24 Amphibian Lives. Earth Day Series. By Marty Crump. Illustrations by Tony Angell. 2024. University of Chicago Press. 200 pages and 24 halftones, 23.50 CAD, Hardcover. Also available as an E-book.

Incredible Lizards: One Hundred Species from Around the World. By Steve Wilson. 2024. New Holland Publishers. 216 pages, 47.00 CAD, Hardcover.

Our Sea Turtles: a Practical Guide for the Atlantic and Gulf, from Canada to Mexico. Second Edition. By Blair Witherington and Dawn Witherington. 2024. Globe Pequot. 296 pages, 38.95 CAD, Paper.

Reptiles. By Steve Wilson. 2024. New Holland Publishers. 208 pages, 53.99 CAD, Hardcover.

Salamanders of the Eastern United States. Wormsloe Foundation Nature Books. By Larry Wilson, Whit Gibbons, and Joe Mitchell. 2024. University of Georgia Press. 500 pages, 450 colour photos, and 80+ maps, 48.95 CAD, Paper.

†Tortoises of the World: Giants to Dwarfs. By George R. Zug and Devin A. Reese. 2024. Johns Hopkins University Press. 256 pages, 25 colour photos, 15 black and white photos, and 51 black and white illustrations, 64.95 CAD, Hardcover, 49.99 CAD, E-book.

ORNITHOLOGY

The Bird Book: the Stories, Science, and History of Birds. By DK. 2024. DK. 320 pages, 54.00 CAD, Hardcover, 19.99 CAD, E-book.

Bird Photographer of the Year: Collection 9. Edited by Bird Photographer of the Year Limited. Foreword by Simon King. 2024. Princeton University Press. 256 pages, 44.00 CAD, Hardcover. Also available as an E-book.

Birding for Boomers: and Everyone Else Brave Enough to Embrace the World's Most Rewarding and Frustrating Activity. By Sneed B. Collard III. Illustrations by Tanner Barkin. 2024. Mountaineers Books. 224 pages, 32.95 CAD, Paper.

Birds: the Art of Ornithology. By Jonathan Elphick. 2024. Natural History Museum, London. 224 pages, 33.99 CAD, Hardcover.

The Birds that Audubon Missed: Discovery and Desire in the American Wilderness. By Kenn Kaufman. 2024. Avid Reader Press/Simon & Schuster. 400 pages, 44.00 CAD, Hardcover, 33.99 CAD, E-book.

†Birds of North America: a Photographic Atlas. By Bruce M. Beehler. Photography edited by Brian E. Small. 2024. Johns Hopkins University Press. 560 pages, 1173 colour photos, 39 colour illustrations, and 735 maps, 77.95 CAD, Hardcover.

City Bird: Explore the Charming Metropolitan Melodies of Our Feathered Friends. By Angela Harrison Vinet and Janis Hatten Harrison. 2024. Epic Ink. 128 pages, 17.99 CAD, Hardcover.

Clinging to the Edge: a Year in the Life of a Little Tern Colony. By Richard Boon. 2024. Pelagic Publishing. 204 pages and colour illustrations, 45.00 USD, Paper. Also available as an E-book.

The Complete Language of Birds: a Definitive and Illustrated History. Complete Illustrated Encyclopedia No. 13. By Randi Minetor. 2024. WellFleet Press. 256 pages, 32.99 CAD, Hardcover.

Cuckoo. By Cynthia Chris. 2024. Reaktion Books. Distributed by University of Chicago Press. 168 pages, 80 colour plates, and 17 halftones, 28.95 CAD, Paper.

†Dare to Bird: Exploring the Joy and Healing Power of Birds. By Melissa Hafting. Photography by Melissa Hafting. 2024. Rocky Mountain Books (RMB). 224 pages, 45.00 CAD, Paper, 19.99 CAD, E-book.

The East Atlantic Flyway of Coastal Birds: 50 Years of Exciting Moments in Nature Conservation and Research. Edited by Peter Prokosch. 2024. Lynx Edicions. 232 pages, colour photos, colour illustrations, and colour maps, 29.00 EUR, Hardcover.

Feathered Entanglements: Human-Bird Relations in the Anthropocene. Edited by Scott Simon and Frédéric Laugrand. 2024. UBC Press. 340 pages, 31 black and white photos, 14 tables, 7 charts, and 4 maps, 99.00 CAD, Hardcover.

Ferdinand Bauer's Remarkable Birds. By Jonathan Elphick. 2024. Bodleian Library Publishing. Distributed by University of Chicago Press. 240 pages and 120 colour plates, 146.50 CAD, Hardcover.

The Golden Eagle Around the World: a Monograph on a Holarctic Raptor. Edited by Jesús Bautista and David H. Ellis. 2024. Hancock House. 928 pages and 1150 photos and illustrations, 99.95 CAD, Hardcover.

The Gull Guide: North America. By Amar Ayyash. 2024. Princeton University Press. 512 pages and 1800+ colour photos, 50.00 CAD, Paper. Also available as an E-book.

The New York Pigeon: Behind the Feathers. Second Edition. By Andrew Garn. 2024. powerHouse Books. 160 pages, 53.95 CAD, Hardcover.

Of a Feather. By Thaddeus Holownia and Harry Thurston. 2024. Anchorage Press. 56 pages, 45.00 CAD, Paper.

†**The Shorebirds of North America: a Natural History and Photographic Celebration.** By Pete Dunne and Kevin T. Karlson. 2024. Princeton University Press. 304 pages and 225 colour photos, 44.00 CAD, Hardcover. Also available as an E-book.

Shorebirds of the Northern Hemisphere. Helm Photographic Guides. By Richard Chandler. 2024. Bloomsbury. 448 pages, 700 colour photos, and 150 colour maps, 107.00 CAD, Paper.

Space for Birds: Patterns and Parallels of Beauty and Flight. By Roberta L. Bondar. 2024. Figure 1 Publishing. 256 pages, 55.00 CAD, Hardcover.

The Stokes Guide to Finches of the United States and Canada. By Lillian Q. Stokes and Matthew A. Young. 2024. Little, Brown and Company. 352 pages, 345+ colour photos, and 50+ maps, 28.99 CAD, Paper, 19.99 CAD, E-book.

Storm-Petrels. By Rob Thomas. 2024. Bloomsbury USA. 336 pages, 67.00 CAD, Paper.

Swirling Starlings. By Erik Hijweege. Text by Maartje van den Heuvel and Koos Dijksterhuis. Photography by Erik Hijweege. 2024. Waanders & de Kunst. 96 pages, 60.00 CAD, Hardcover.

The Wisdom of Birds: Essential Life Lessons for Positivity and Grace. By Alison Davies. 2024. Michael O'Mara. 128 pages, 22.99 CAD, Hardcover.

ZOOLOGY

A Beary Special April in Yellowstone. By Jonathan G. Way. 2024. Self-published. 596 pages and colour photos, Open Access URL (but please consider a 10.00 USD donation) at https://www.easterncoyoteresearch.com/downloads/BearySpecialAprilinYellowstone.pdf.

Eight-Legged Wonders: the Surprising Lives of Spiders. By James O'Hanlon. 2024. Greystone Books. 272 pages, 34.95 CAD, Hardcover.

Grizzly Confidential: an Astounding Journey into the Secret Life of North America's Most Fearsome Predator. By Kevin Grange. 2024. Harper Horizon. 272 pages, 36.99 CAD, Hardcover, 17.99 CAD, E-book.

How Primates Eat: a Synthesis of Nutritional Ecology across a Mammal Order. Edited by Joanna E. Lambert, Margaret A.H. Bryer, and Jessica M. Rothman. Foreword by T.H. Clutton-Brock. Afterword by Alison Richard. 2024. University of Chicago Press. 760 pages, 128 halftones, and 29 tables, 324.99 CAD, Hardcover. Also available as an E-book.

In Search of the Great Canadian Shark. By Chris Harvey-Clark. 2024. Pottersfield Press. 204 pages, 22.95 CAD, Paper.

The Little Book of Whales. Little Books of Nature Series. By Robert Young and Annalisa Berta. 2024. Princeton University Press. 160 pages and 140 colour illustrations, 19.99 CAD, Hardcover. Also available as an E-book.

The Lives of Spiders: a Natural History of the World's Spiders. The Lives of the Natural World No. 11. By Ximena Nelson. 2024. Princeton University Press. 288 pages and 150 colour illustrations, 44.00 CAD, Hardcover. Also available as an E-book.

Mammals of North America, Volume 1: Systematics and Taxonomy. By Sergio Ticul Alvarez-Castañeda. 2024. Springer. 643 pages, 584.99 CAD, Hardcover.

Mammals of North America, Volume 2: Systematics and Taxonomy. By Sergio Ticul Alvarez-Castañeda. 2024. Springer. 368 pages, 364.95 CAD, Hardcover.

Marine Fishes and Fisheries of New York. By Howard M. Reisman and Emerson C. Hasbrouck Jr. Photography by Christopher Paparo. 2024. Cornell University Press. 296 pages, 28 colour photos, and 158 black and white illustrations, 40.95 CAD, Paper.

The Pipestone Wolves: the Rise and Fall of a Wolf Family. By Günther Bloch. Photography by John E. Marriott. Foreword by Mike Gibeau. 2024. Rocky Mountain Books (RMB). 224 pages and colour photos, 35.00 CAD, Paper.

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The Secret History of Sharks: the Rise of the Ocean's Most Fearsome Predators. By John Long. 2024. Ballantine Books. 480 pages, 48.00 CAD, Hardcover, 18.99 CAD, E-book.

Slippery Beast: a True Crime Natural History, with Eels. By Ellen Ruppel Shell. 2024. Abrams Press. 304 pages, 35.00 CAD, Hardcover.

†**Stowaway: the Disreputable Exploits of the Rat.** By Joe Shute. 2024. Bloomsbury USA. 272 pages, 35.00 CAD, Hardcover, 19.99 CAD, E-book.

***Thinking Like a Wolf: Lessons from the Yellowstone Packs.** Alpha Wolves of Yellowstone Series. By Rick McIntyre. Foreword by Frans de Waal. 2024. Greystone Books. 272 pages, 34.95 CAD, Hardcover.

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What Walks This Way: Discovering the Wildlife Around Us through Their Tracks and Signs. By Sharman Apt Russell. 2024. Columbia University Press. 208 pages, 130.00 CAD, Hardcover, 31.00 CAD, Paper. Also available as an E-book.

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A Woman Among Wolves: My Journey through Forty Years of Wolf Recovery. By Diane K. Boyd. Foreword by Douglas H. Chadwick. 2024. Greystone Books. 240 pages, 34.95 CAD, Hardcover.

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Adventures in Volcanoland: What Volcanoes Tell Us about the World and Ourselves. By Tamsin Mather. 2024. Hanover Square Press. 384 pages, 41.00 CAD, Hardcover, 20.99 CAD, E-book.

Alexander von Humboldt: a Concise Biography. By Andreas W. Daum. Translated by Robert Savage. 2024. Princeton University Press. 214 pages, 32.00 CAD, Hardcover. Also available as an E-book.

Animals, Plants and Afterimages: the Art and Science of Representing Extinction. Edited by Valérie Bienvenue and Nicholas Chare. 2024. Berghahn Books. 460 pages, 40.99 CAD, Paper. Also available as an E-book.

Atlas Obscura: Wild Life—an Explorer's Guide to the World's Living Wonders. By Cara Giaimo and Joshua Foer. 2024. Workman Publishing Company. 464 pages, 50.00 CAD, Hardcover, 24.99 CAD, E-book.

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Earthly Bodies: Embracing Animal Nature. By Vanessa Chakour. 2024. Penguin Life. 336 pages, 27.99 CAD, Paper, 14.99 CAD, E-book.

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Field Guide to Newfoundland and Labrador. By Michael Collins. 2024. Breakwater Books Ltd. 480 pages, 34.95 CAD, Paper.

Forest Fungi: Biodiversity, Conservation, Mycoforestry and Biotechnology. Edited by Ahmed M. Abdel Azeem, Marieka Gryzenhout, Soumya Ghosh, and Teroj A. Mohammed. 2024. Academic Press. 550 pages, 259.99 CAD, Paper.

Going to See: 30 Writers on Nature, Inspiration, and the World of Barry Lopez. Edited by James Perrin Warren and Kurt Caswell. 2024. Mountaineers Books. 272 pages, 37.95 CAD, Paper, 24.99 CAD, E-book.

Impossible Monsters: Dinosaurs, Darwin, and the Battle between Science and Religion. By Michael Taylor. 2024. W.W. Norton. 496 pages, 43.99 CAD, Hardcover, 32.99 CAD, E-book.

Lichenpedia: a Brief Compendium. Pedia Books. By Kay Hurley. Illustrations by Susan Adele Edwards. 2024. Princeton University Press. 192 pages and 47 black and white illustrations, 22.99 CAD, Hardcover, 17.99 CAD, E-book.

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The Lives of Lichens: a Natural History. The Lives of the Natural World No. 10. By Robert Lücking and Toby Spribille. 2024. Princeton University Press. 288 pages and 150+ colour illustrations, 44.00 CAD, Hardcover. Also available as an E-book.

Mushrooms of Cascadia: an Illustrated Key to the Fungi of the Pacific Northwest. Second Edition. By Michael Beug. 2024. Clarkson Potter/Ten Speed. 352 pages, 37.99 CAD, Paper.

A Natural History of Empty Lots: Field Notes from Urban Edgelands, Back Alleys, and Other Wild Places. By Christopher Brown. 2024. Timber Press. 296 pages, 39.00 CAD, Hardcover, 19.99 CAD, E-book.

Nature's Writers: Mentored by the Land. By Donald S. Clark. Foreword by Bill McKibben. Preface by Camille Dungy. 2024. Rizzoli. 216 pages, 47.00 CAD, Hardcover.

Navigating Rocky Terrain: Caves, Karsts, and the Soul of Unseen Spaces. By Laurie Roath Frazier. 2024. Trinity University Press. 224 pages, 28.95 CAD, Paper.

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Origin Story: the Trials of Charles Darwin. By Howard Markel. 2024. W.W. Norton. 368 pages, 47.00 CAD, Hardcover, 35.99 CAD, E-book.

Otherworldly Antarctica: Ice, Rock, and Wind at the Polar Extreme. By Edmund Stump. 2024. University of Chicago Press. 168 pages and 144 colour plates, 36.50 CAD, Hardcover, 27.99 CAD, E-book.

Our Kindred Creatures: How Americans Came to Feel the Way They Do about Animals. By Bill Wasik and Monica Murphy. 2024. Knopf Doubleday. 464 pages, 48.00 CAD, Hardcover, 18.99 CAD, E-book.

Playing Possum: How Animals Understand Death. By Susana Monsó. 2024. Princeton University Press. 272 pages and 18 black and white illustrations, 38.00 CAD, Hardcover. Also available as an E-book.

Reclaiming the Don: an Environmental History of Toronto's Don River Valley. Second Edition. By Jennifer L. Bonnell. 2024. University of Toronto Press. 332 pages and 34 black and white illustrations, 44.95 CAD, Paper. Also available as an E-book.

Sharks Don't Sink: Adventures of a Rogue Shark Scientist. By Jasmin Graham. 2024. Knopf Doubleday. 224 pages, 37.99 CAD, Hardcover, 16.99 CAD, E-book.

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The Tame and the Wild: People and Animals After 1492. By Marcy Norton. 2024. Harvard University Press. 448 pages, 49.50 CAD, Hardcover, 39.99 CAD, E-book.

†The Tomb of the Mili Mongga: Fossils, Folklore, and Adventures at the Edge of Reality. By Samuel Turvey. 2024. Bloomsbury Sigma. 304 pages, 37.99 CAD, Hardcover, 20.99 CAD, E-book.

†Wildlife, Landscapes, and Geology: an Alberta and Saskatchewan Touring Guide. By Dale Leckie. 2024. Broken Poplars Publishing. 216 pages, 29.95 CAD, Paper.

The Canadian Field-Naturalist

News and Comment

Compiled by Amanda E. Martin

Upcoming Meetings and Workshops

Student Conference on Conservation Science (NY)

The 15th annual Student Conference on Conservation Science (NY) to be held 9–11 October 2024 as a hybrid event, with online content and an in-person meeting at the American Museum of Natural History, New York City, New York. Registration is currently open. More information is available at https://www.amnh.org/research/center-for-biodiversity-conservation/convening-and-connecting/sccs-ny.

BeeCon

BeeCon, Southern Ontario Bee Researchers' Symposium, to be held 17–18 October 2024 as a hybrid event, with online content and an in-person meeting at York University, Toronto, Ontario. Registration is currently open and is free, thanks to the sponsors: the Faculties of Science and Environmental and Urban Change and the Office of the VPRI. More information is available at https://www.yorku.ca/bees/beecon-2024/.

The Wildlife Society Annual Meeting

The 31st annual meeting of the Wildlife Society to be held 19–23 October 2024 at the Hilton Baltimore Inner Harbor, Baltimore, Maryland. Registration is currently open. More information is available at https://twsconference.org/.

Joint Annual Meeting of the Entomological Societies of Quebec and Canada 2024

The Joint Annual Meeting of the Entomological Societies of Quebec and Canada to be held 20–23 October 2024 at the Hotêl Le Concorde, Québec City, Quebec. The theme of the conference is: 'The Good, The Bad and The Ugly - A Matter of Perspective'. Registration is currently open. More information is available at https://event.fourwaves.com/seq-esc2024/pages.

Entomology 2024

Entomology 2024 to be held 10–13 November 2024 at the Phoenix Convention Center, Phoenix, Arizona. Registration is currently open. More information is available at https://www.entsoc.org/events/annual-meeting.

In Memoriam for Honorary Ottawa Field Naturalists' Club member J. Bruce Falls

J. Bruce Falls, 18 December 1923–27 April 2024. Professor Falls became an Honorary Member of The Ottawa Field-Naturalists Club in 2012 (OFNC 2013). He became a Member of the Order of Canada in November 2016 (The Governor General of Canada no date). His long tenure as a faculty member in the Department of Zoology at the University of Toronto (UoT) began in 1954 where his research included a 36-year study of small mammal population dynamics in Algonquin Provincial Park; he also pioneered the use of audio playback to study territoriality and breeding behaviour of birds (University of Toronto 2024a). More of his achievements are outlined in the establishment of the J. Bruce Fall scholarship at the UoT (University of Toronto 2024b). His obituary is available at https://www.legacy.com/ca/obituaries/theglobeandmail/name/bruce-falls-obituary?id=55026018.

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D.A.W. LEPITZKI
CFN EDITOR-IN-CHIEF

Erratum *The Canadian Field-Naturalist* 137(1–2)

Lepitzki, D.A.W. 2023. In Memoriam for four long-standing Ottawa Field-Naturalists' Club members. Canadian Field-Naturalist 137(1–2): 175.

The Canadian Field-Naturalist Special Issue by Reddoch and Reddoch was published in 1997, not 2010 as stated. The correct citation is:

Reddoch, J.M., and A.H. Reddoch. 1997. The orchids in the Ottawa District: floristics, phytogeography, population studies and historical review. Canadian Field-Naturalist Special Issue 111: 1–184. https://doi.org/10.5962/bhl.title.46794

Erratum *The Canadian Field-Naturalist* 137(3)

The caption accompanying the cover image for *The Canadian Field-Naturalist* 137(3) incorrectly stated the name of MARS as the Marine Animal Rescue Society. The correct caption is:

Marine Animal Response Society (MARS) responder, Andrew Reid, and a volunteer investigate a Cuvier's Beaked Whale (*Ziphius cavirostris*) that had stranded alive and subsequently died in Blandford, Nova Scotia on 7 February 2016. This was the first mainland stranding for the species in eastern Canada. See the article by McAlpine *et al.* (201–231). Photo: © Marine Animal Response Society.

The Canadian Field-Naturalist

Editors' Report for Volume 136 (2022)

Mailing dates for the four issues of *The Canadian Field-Naturalist* (CFN) in volume 136 were: 8 September 2022, 12 December 2022, 22 March 2023, and 17 July 2023; online posting dates are approximately four weeks before the mailing dates: 5 August, 8 November, 20 February, and 22 June, respectively. The time differential is because the print proofs need to be produced and then couriered from and back to the printer after they are checked by the *Editor-in-Chief* (EiC) before printing and then shipped to the mailer. In comparison, the mailing and online posting dates of the four issues in volume 135 ranged from 22 July 2021 to 25 May 2022 and 23 June to 29 April, respectively. Summaries of the distribution of paid subscribers to CFN for 2022 are shown in Table 1, and are compared to volume 135 for 2021. This list does not include free copies distributed to Honorary Ottawa Field-Naturalist' Club (OFNC) members or online access, which is included in OFNC membership dues and those provided to *Associate Editors* (AE). Institutional subscribers potentially represent many thousands of users. There was a decline (–18) in the number of paid subscribers for 2022 compared to 2021. This decline is largely because of a net decrease (–13) in OFNC members paying for a print copy: 26 members no longer received the print copy and 13 new members started receiving the print copy.

The number of articles published in volume 136 decreased by four relative to the number published in volume 135 while the number of notes increase by eight, resulting in four more manuscripts published in 2022 ($n = 38$) in comparison to 2021 (Table 2). Mammals and birds were the most popular subjects followed by amphibians and reptiles, then plants (Table 2). Our search for a new *Book Review Editor* after 135(2) was successful and we welcomed Jessica Sims beginning with 136(1). More book reviews (+2) and new titles (+122) were published in volume 136 in comparison to volume 135 (Table 3). The total number of pages published declined by 17 for volume 136 in comparison to volume 135 (Table 4) with fewer pages of articles (–91) but more pages of notes (+38), tributes (+10), Book Reviews/New Titles (+4), and News and Comment (+7) published. The News and Comment included a couple of in memoriams and in 136(2), two comments, one of which was several pages long about the lack of a biodiversity protection act in Canada (https://doi.org/10.22621/cfn.v136i2.3105). Once again, there were no thematic collections (editor-selected compilations of previously published contributions in both CFN and the regional OFNC publication, *Trail & Landscape*, on a central theme with internet links to each article) nor additional articles on Greatest Canadian Field Naturalists, the latter of which were included in News and Comment in volume 131 (for 2017).

One additional manuscript or enquiry about potential submissions ($n = 47$) was received in 2022 than

Table 1. The 2022 (2021) circulation of *The Canadian Field-Naturalist*. Compiled by Eleanor Zurbrigg from the subscription list for 136(4). This list does not include copies distributed to Honorary Members or online access which is included in the Ottawa Field-Naturalist' Club (OFNC) membership dues.

Subscriber type	Canada		USA		Other		Total	
OFNC Members	35	(45)*	0	(3)*	0	(0)	35	(48)
Subscriptions:								
Individual	26	(28)	12	(9)	0	(0)	38	(37)
Institutional	57	(58)	74	(79)	12	(12)	143	(149)
Total	118	(131)*	86	(91)*	12	(12)	216	(234)

*There was an error in the published table of subscribers for volume 135 for 2021 (https://doi.org/10.22621/cfn.v136i2.3097) with the correct numbers now being indicated above. Three OFNC members were erroneously attributed to being from the USA instead of Canada. Thus there were three not six subscribers from the USA in 2021, reducing the total number of subscribers from the USA from 94 to 91 in 2021. The corresponding numbers of Canadian OFNC member subscribers and total subscribers were increased to 45 (from 42) and 131 (from 128), respectively.

in 2021; since 2017, the number of annual submissions and enquiries has varied from 46 to 67 (Table 5). The single enquiry in 2022 did result in an informal submission in 2023 and it may eventually be published. Four of the 46 submissions were declined in 2022 meaning 91% of the submissions could eventually be published if suitably revised and then accepted for publication (Table 5).

Dwayne Lepitzki, EiC, initially reviewed the appropriateness of a submission and assigned an AE after William Halliday, *Online Journal Manager and Webmaster*, determined the completeness of the submission. Dwayne then reviewed the recommendation from the AE and reviewers and decided if and when the submitted and subsequently revised manuscript was accepted for publication. A *Copy Editor* (Sandra Garland or John Wilmshurst) was then assigned and once their work was reviewed by Dwayne and the authors, the manuscript was sent for layout and typesetting. *Assistant Editor* Amanda Martin edited content, proofread galleys (as did Dwayne), and sent and received author order and transfer of copyright forms; she also prepared the News and Comment. Robert Forsyth typeset galleys, provided corrections for page proofs, and created pdfs for online posting and printing. Jessica Sims requested books for review, selected reviewers, edited submitted reviews, and prepared the new titles listings for volume 136. Ken Young sent page charge invoices to authors and tracked the budget while Eleanor Zurbrigg managed subscriptions and mailed printed copies. William Halliday provided digital content to subscribers, posted tables of

TABLE 2. Number of research articles and notes published in *The Canadian Field-Naturalist*, volume 136 (volume 135), by major field of study.

Subject	Articles	Notes	Total
Mammals	7 (3)	5 (6)	12 (9)
Birds	5 (9)	4 (0)	9 (9)
Amphibians and Reptiles	5 (2)	2 (2)	7 (4)
Fishes	0 (1)	2 (0)	2 (1)
Plants	2 (6)	3 (0)	5 (6)
Insects	0 (2)	1 (1)	1 (3)
Non-insect invertebrates	1 (2)	0 (0)	1 (2)
Other	1 (0)	0 (0)	1 (0)
Total	21 (25)	17 (9)	38 (34)

TABLE 3. Number of reviews and new titles published in the Book Review section of *The Canadian Field-Naturalist*, volume 136 (volume 135), by topic.

	Reviews	New Titles
Zoology*	11 (12)	106 (70)
Botany	2 (3)	36 (29)
Miscellaneous†	8 (4)	216 (137)
Total	21 (19)	358 (236)

*Includes Entomology, Herpetology, Ornithology, and Zoology.

†Includes Biology, Conservation and Climate Change, Ecology, and Other.

TABLE 4. Number of pages per section published in *The Canadian Field-Naturalist*, volume 136 (135), by issue.

	Issue				Total
	1	2	3	4	
Editorials/Editors' Report	0 (0)	3 (4)	0 (0)	0 (0)	3 (4)
Articles	22 (58)	56 (74)	54 (91)	65 (65)	197 (288)
Notes	26 (9)	21 (12)	26 (5)	7 (16)	80 (42)
Thematic Collections	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Tributes	21 (10)	0 (0)	9 (0)	0 (0)	30 (10)
Book Reviews and New Titles	9 (20)	12 (12)	13 (9)	16 (5)	50 (46)
News and Comment*	4 (3)	7 (2)	3 (2)	2 (2)	16 (9)
Reports†	16 (16)	0 (0)	0 (0)	0 (0)	16 (16)
Errata	0 (0)	0 (0)	3 (0)	0 (0)	3 (0)
Blank page‡	2 (0)	1 (0)	1 (1)	0 (0)	4 (1)
Index	– (–)	– (–)	– (–)	6 (6)	6 (6)
Total	100 (116)	100 (104)	109 (108)	96 (94)	405 (422)

*Includes the James Fletcher Award for best paper published in the volume.

†Includes Annual Business Meeting Minutes, Annual Committee Reports, and OFNC Awards; Financial Statements are only available online beginning with 132.

‡Necessary to begin each issue with an odd numbered page.

TABLE 5. Number of submissions and inquiries about submissions to *The Canadian Field-Naturalist* from volume 131 to 136 and percent submissions accepted and/or undergoing revision or further review. Some of the enquiries result in later formal submissions.

Year (volume)	2017 (131)	2018 (132)	2019 (133)	2020 (134)	2021 (135)	2022 (136)
Number of submissions and enquiries	57*	67†	49	63	46	47‡
% submissions not declined and undergoing revision and further review§	90%	83%	85%	80%	89%	91%

*Includes 10 for the Special Issues 132(1) and 132(2) honouring Dr. Francis Cook.

†Includes 13 for the Special Issues 132(1) and 132(2) honouring Dr. Francis Cook.

‡Includes 11 for the Special Double Issue for 2023, volume 137(1–2).

§Not all of these submissions may be revised by the authors and resubmitted or eventually accepted and published.

contents, abstracts, and pdfs on the CFN website, and prepared the Index. Our AEs managed manuscripts, provided reviews and recommendations, and guided authors through the revisions process. Dave Seburn, our *Map Editor*, reviewed and provided suggestions for all the maps. The Publication Committee, chaired by Jeff Saarela and consisting of Annie Bélair, Carolyn Callaghan, Paul Catling, William Halliday, Diane Kitching, Dwayne Lepitzki, Amanda Martin, Karen McLachlan Hamilton, Ken Young, and Eleanor Zurbrigg effectively guided the operation of the journal. We are indebted to our very dedicated team.

The following AEs voluntarily managed, assessed, and reviewed manuscripts submitted in 2022 or published in volume 136: R. Brooks, University of Guelph, emeritus, Weymouth NS (2 manuscripts published); P.M. Catling, Agriculture and Agri-Food Canada, retired, Ottawa ON (3); F. Chapleau, University of Ottawa, Ottawa ON (1—stepped down as AE in 2021); J. Foote, Algoma University, Sault St. Marie ON (3 + 1 declined); G. Forbes, University of New Brunswick, Fredericton NB (4); W. Halliday, Wildlife Conservation Society Canada, Whitehorse YT and University of Victoria, Victoria BC (5); K. Ilves (1); T. Jung, Yukon Government, Whitehorse YT (1); D. McAlpine, New Brunswick Museum, Saint John NB (3 + 1 declined); G. Mowat, Government of British Columbia, Nelson BC (2); M. Obbard, Ontario Ministry of Natural Resources and Forestry, retired, Peterborough ON (2—stepped down as AE in 2022); J.M. Saarela, Canadian Museum of Nature, Ottawa ON (3); J. Skevington, Agriculture and Agri-food Canada, Ottawa ON (1); and D. Tozer, Birds Canada, Port Rowan ON (7 + 2 declined). B. Patterson, Ontario Ministry of Natural Resources and Forestry, Peterborough ON joined as an AE in 2022 with expertise in mammals; the first manuscript he handled was published in 2023.

As with many other journals, AEs are at times having difficulty finding suitable reviewers; without dedicated AEs and reviewers there would be no journal. As such, a heart-felt thanks and gratitude is extended to the following who voluntarily reviewed manuscripts published in volume 136 (number of manuscripts reviewed >1 in parentheses) or submitted in 2022: Christian Artuso, Canadian Wildlife Service; Cheryl Asa, Saint Louis Zoo; Ted Barney, Canadian Wildlife Service; James Baxter-Gilbert, Stellenbosch University; Marc Belisle, University of Sherbrooke; Andrew Bennett, Canadian National Collection of Insects, Arachnids and Nematodes; Diana Bizecki Robson, Manitoba Museum; Sean Boyd, Environment and Climate Change Canada; Catlin Bradbury, Saint Mary's University; Adrian Bradley, University of Queensland; Dan Brunton, Ottawa ON; Suzanne Carriere, Government of Northwest Territories; Kira Cassidy, United States National Park Service; Shane Conor White, British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development; John Cooley, Loon Preservation Committee; Joe Crowley, Ontario Ministry of Natural Resources and Forestry; Chris Darimont, University of Victoria; Jean-Yves Dubuisson, Sorbonne Université; Marc Dupuis-Désormeaux, York University; Mark Edwards, Royal Alberta Museum; Kristin Ellis, United States Geological Survey; Bruce Ford, University of Manitoba; Jean-Marc Gagnon, Canadian Museum of Nature; Sabrina Garcia, Alaska Department of Fish and Game; Lauren Gaudet, Saint Mary's University; Tiffany Grade, Loon Preservation Committee; David Green, McGill University; Gavin Hanke, Royal British Columbia Museum; Jim Harding, Michigan State University Museum; Howard Huynh, Carleton University; Thomas Jung, Government of Yukon; Page Klug, United States Department of Agriculture Animal and Plant Health Inspection Service's National Wildlife Research Center; Lina Lapointe, Université Laval; Karl Larsen, Thompson Rivers University (2); Randy Lauff, St. Francis Xavier University; Cori Lausen, Thompson Rivers University; Shelby Lawson, University of Illinois

Urbana-Champaign; Lee Lyman, University of Missouri; Jan Macek, National Museum Czeck Republic; Jeffrey Marliave, Vancouver Aquarium; Shelley Marshall, British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development; André Martel, Canadian Museum of Nature; Don McAlpine, New Brunswick Museum; L. David Mech, United States Geological Survey; Michael Melampy, Baldwin Wallace University; Aimee Mitchell, Coastal Partners in Conservation Society; Lucy Mitchell, Ghent University; Patrick Moldowan, University of Toronto (3); Damien Mullin, University of New Brunswick; Daniel Nickrent, Southern Illinois University-Carbondale (retired); Erica Nol, Trent University; Stephen Nowicki, Duke University; Michael Oldham, Ontario Natural Heritage Information Centre (2); Nikisha Patel, Trinity College; Brent Patterson, Ontario Ministry of Natural Resources and Forestry (2); Agnes Pelletier, British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development; Tim Poole, Wildlife and Fisheries Manitoba; Justin Ray, Wildlife Conservation Society Canada; Joyce Reddoch, Ottawa ON; John Reynolds, Waterloo ON; David Seburn, Seburn Ecological Services (3); Carolyn Shores, British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development; Paul Sokoloff, Canadian Museum of Nature; Mathew Sorum, United States National Park Service; Stephen Symes, Advisian; Ric Taylor, University of British Columbia; John Theberge, University of Waterloo (retired); Richard Thiel, Tomah WI; Rodger Titman, McGill University; Leanne Tol, Birds Canada; Cindy Tribuzio, National Oceanic and Atmospheric Administration Fisheries; Yves Turcotte, Collège de La Pocatière; Blaire van Valkenburgh, University of California Los Angeles; Winnie Wake, London Swiftwatch; Jon Way, Eastern Coyote/Coywolf Research; Adrian Wydeven, Department of Natural Resources Wisconsin (retired).

The journal was printed at Gilmore Printers, Ottawa. Thanks to Guylaine Duval of Gilmore Printers for overseeing production and printing. The COVID-19 pandemic resulted in supply chain issues with the coated paper stock normally used for printing in short supply and most likely at an increased cost if even available. Due to potential problems of ink bleeding into the alternative uncoated stock, we moved to a digital press beginning with 135(4); 136(1) also was printed using a digital press but we moved back to offset printing beginning with 136(2). We are grateful to the OFNC President Jakob Mueller and the Club's Board of Directors for their support of the journal. We are also grateful to all of the individual subscribers and authors who support our team as we strive to provide a high-quality scientific journal on natural history, field biology, and ecology. Finally, we thank our families/partners for their patience and support throughout many long days, evenings, and weekends of working on the journal.

DWAYNE A.W. LEPITZKI, *Editor-in-Chief*
AMANDA E. MARTIN, *Assistant Editor*

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Compiled by William Halliday

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