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COVER: "Observing", the Nuu-Chah-nulth art piece by Hawilh-Wayanis (Joshua Watts), documenting scratching behaviour of a Salmon Shark (*Lamna ditropis*) on floating anthropogenic debris in the proposed Tang.g̱wan-ḥačxʷiqak-Tsig̱is Marine Protected Area off northern Vancouver Island, British Columbia, Canada. See the note by Du Preez *et al.* (pp. 274–280) that describes two novel observations of sharks scratching in the open ocean and explains the traditional art.

The Canadian Field-Naturalist

Note

A fossil beech fern (cf. *Phegopteris* (C. Presl) Fée) from Driftwood Canyon Provincial Park, British Columbia

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Greenwood, D.R. 2022. A fossil beech fern (cf. *Phegopteris* (C. Presl) Fée) from Driftwood Canyon Provincial Park, British Columbia. Canadian Field-Naturalist 136(3): 201–205. https://doi.org/10.22621/cfn.v136i3.3001

Abstract

Ferns are important components of the biodiversity of wet forests across Canada, and the fossil record offers insights into the origins of fern diversity and biogeography. In 1967, Driftwood Canyon Provincial Park in north-central British Columbia was declared an Eocene Epoch plant, insect, fish, bird, and mammal fossil site of national scientific significance to preserve the Driftwood Creek fossil beds. The fossil plants from this important fossil site remain largely unknown. Here, a first record of a beech fern from the Eocene of British Columbia—morphologically comparable to the *Phegopteris connectilis* group—is illustrated, further revealing the past biodiversity of ancient British Columbia. The absence of sori and other key anatomical characters prevents definitive identification. Today, the circumpolar to temperate species Northern Beech Fern (*Phegopteris connectilis*) is widespread across British Columbia, occurring in wet coniferous forests; other members of the *P. connectilis* group also occur in temperate climates.

Key words: Beech fern; *Phegopteris*; fossil; Eocene; British Columbia; diversity

Today, British Columbia (BC) has ~60 species of native ferns (class Polypodiopsida, subclass Polypodiidae), excluding horsetails (*Equisetum* spp.) and the grape ferns and adders tongue ferns (subclass Ophioglossidae). They encompass ~10 families and ~23 genera, including the beech ferns (*Phegopteris* (C. Presl) Fée, Thelypteridaceae; Douglas *et al.* 2000, 2002; PPG I 2016). One tool for exploring the origins of fern diversity in BC and across North America is the fossil record (Arnold 1955; Rothwell and Stockey 1991; Stockey *et al.* 1999, 2006; Collinson 2001; Smith *et al.* 2006; Collinson *et al.* 2017; Pigg *et al.* 2021). A few fossil sites from BC dated to the Eocene Epoch (55–36 million years ago [Mya]) include fossil ferns, principally near Princeton and near Falkland in south-central BC, around metropolitan Vancouver, and in Driftwood Canyon Provincial Park (Figure 1) east of Smithers in north-central BC (Greenwood *et al.* 2005, 2016; Pigg *et al.* 2021). In 1967, Driftwood Canyon Provincial Park was declared to preserve the Driftwood Creek fossil beds, an Eocene Epoch plant, insect, fish, bird, and mammal fossil site of national scientific significance (Wilson 1977; Stockey 1984; Archibald *et al.* 2011; Eberle *et al.* 2014; Archibald and Makarkin 2017; Mayr *et al.* 2019), which are dated as 51.77 ± 0.34 Mya (Greenwood *et al.* 2016).

Here, I illustrate a small fossil fern from Driftwood Canyon Provincial Park as an exemplar of the, as yet, poorly documented diversity of the ancient Eocene forests of north-central BC. It is a close morphological match for extant beech ferns of the genus *Phegopteris* (Thelypteridaceae; Figure 2). The specimen is part of a public education display mounted on a wooden board housed in the BC Parks Smithers office and is lacquered, preventing detailed examination of the micromorphology of the specimen. Its date of collection and collector are unknown.

The Thelypteridaceae contains two subfamilies, Phegopteridoideae and Thelypteridoideae, with the former containing three genera, including *Phegopteris*, with seven species (PPG I 2016; Patel *et al.* 2019; Fujiwara *et al.* 2021). Laminal wings at the base of most pinnae are characteristic of *Phegopteris* and are present on the fossil fern leaf from Driftwood Canyon. *Phegopteris* is separable into two groups: the *Phegopteris connectilis* group—*Phegopteris connectilis* (Michaux) Watt (Northern Beech Fern), *Phegopteris excelsior* N.R. Patel & A.V. Gilman (Tall Beech

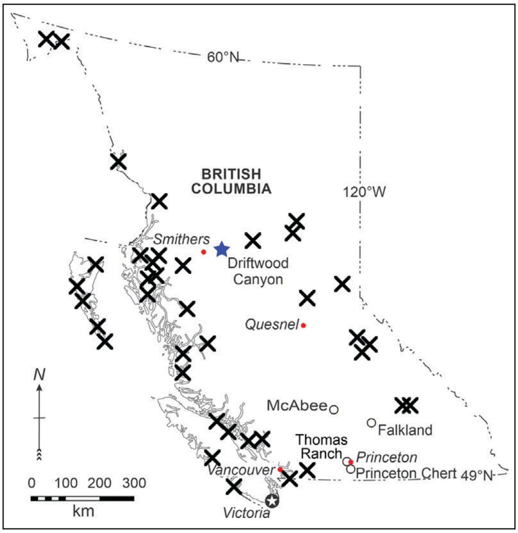

FIGURE 1. Map of British Columbia with overlay of current distribution (×) of Northern Beech Fern (*Phegopteris connectilis*; Klinkenberg 2020). Blue star indicates location of Driftwood Provincial Park. Other fossil localities mentioned in the text shown by open circles, and nearby cities and towns by red dots. Base map adapted from Greenwood *et al.* (2016).

Fern), *Phegopteris hexagonoptera* (Michaux) Fée (Broad Beech Fern), and *Phegopteris tibetica* Ching (no English common name; Patel *et al*. 2019), characterized by creeping rhizomes and deltoid (triangular) leaf blades; and the *Phegopteris decursive-pinnata* group with three species, *Phegopteris decursive-pinnata* (H.C. Hall) Fée (Japanese Beech Fern), *Phegopteris koreana* B.Y. Sun & C.H. Kim (no English common name), and *Phegopteris taiwaniana* T. Fujiw., Ogiso & Seriz. (no English common name), characterized by erect rhizomes and lanceolate leaf blades (Fujiwara *et al.* 2021). The fossil fern from Driftwood Canyon is deltoid and bipinnate–pinnatifid, consistent with the *P. connectilis* group.

The fossil beech fern shares with the Canadian species of *Phegopteris* (*P. connectilis*, *P. excelsior*, and *P. hexagonoptera*; Patel *et al.* 2019) a triangular pinnate–pinnatifid to bipinnate–pinnatifid frond (Figure 2a), with pinnae in the lower two thirds that are winged with the rachis both basioscopically and acroscopically, i.e., extending from the lower and upper edges of the pinna junction with the rachis (Figure 2b–d). The fossil has nine lanceolate, free, pinnae pairs on an incompletely preserved fossil leaf blade with the lowermost preserved pair also incomplete versus *P. connectilis*, *P. excelsior*, and *P. hexagonoptera* with 12–15 pairs. The distal portion of the fern blade in *P. connectilis* (Figure 2a), and less so in *P. excelsior*, narrows abruptly to a pinnatifid tip, whereas, in *P. hexagonoptera*, the blade narrows evenly toward the tip as seen in the fossil (Figure 2b). Patel *et al.* (2019) separated *P. connectilis* from *P. excelsior* on the basis of the "tear-shaped" outline of the whole blade versus the broadly deltoid shape of *P. excelsior* and from *P. hexagonoptera* by the prominent basioscopically (downward) pointing and asymmetric lowermost pair of pinnae in that species, with *P. connectilis* pinnae symmetrical and *P. excelsior* intermediate between these states. It is unclear whether the lowermost pair of pinnae is present on the fossil beech fern, and the attachment of the lowermost pinna to the rachis is poorly preserved (Figure 2b). However, if the lowermost pinna is interpreted as part of the lowermost pinna pair, it is symmetrical, as seen in *P. connectilis* (Patel *et al.* 2019), but lacks the basioscopic orientation (Figure 2a,b) typical of the *P. connectilis* group. It is unclear whether laminal wings joined this pinna to the one above it or whether the rachis was unwinged, as seen in *P. connectilis* and *P. excelsior* (Patel *et al*. 2019). Marginal exindusiate sori—diagnostic of *Phegopteris*—are absent on the specimen, preventing definitive assignment of the specimen to *Phegopteris* and to a species (e.g., Stockey *et al.* 2006). The presence of free dichotomously branching veins that extend to the pinnule margins in the fossil, however, is consistent with *Phegopteris*, as are the crenate margins of the pinnules and wings at the juncture of narrowly lanceolate pinnatifid pinnae with the rachis (Figure 2c,d). The overall size of the fossil, at 3.4 cm length × 1.9 cm width, is very small compared with fully developed fronds in all three extant Canadian species (e.g., *P. excelsior* 17–44 cm long × 14–29 cm wide; Patel *et al.* 2019) and may reflect a frond from a young or stunted plant.

Onoclea L. and *Woodwardia* Smith, genera known from the western Canadian Paleocene and Eocene (Rothwell and Stockey 1991; Greenwood *et al.* 2016; Pigg *et al.* 2021), share with the Driftwood fern a winged rachis, but unlike the fossil, these genera have netted venation. The Paleocene fossil, *Speirseopteris orbiculata* Stockey, Lantz & Rothwell (Thelypteridaceae), from Alberta shares with the Driftwood Canyon specimen a deltoid pinnate–pinnatifid lamina and pinnules with free branched venation, although Stockey *et al.* (2006) note key differences between their fossil species and *Phegopteris*. *Speirseopteris orbiculata*, however, is much larger (ca. 16 cm) than the Driftwood Canyon specimen, lacks laminal wings basal to the pinnae, has pinnules with narrowly triangular apices rather than rounded in the Driftwood Canyon specimen, and has preserved sori, so I do not consider these fossils congeneric. Collinson (2001) and Stockey *et al.* (2006) caution against assigning fossil

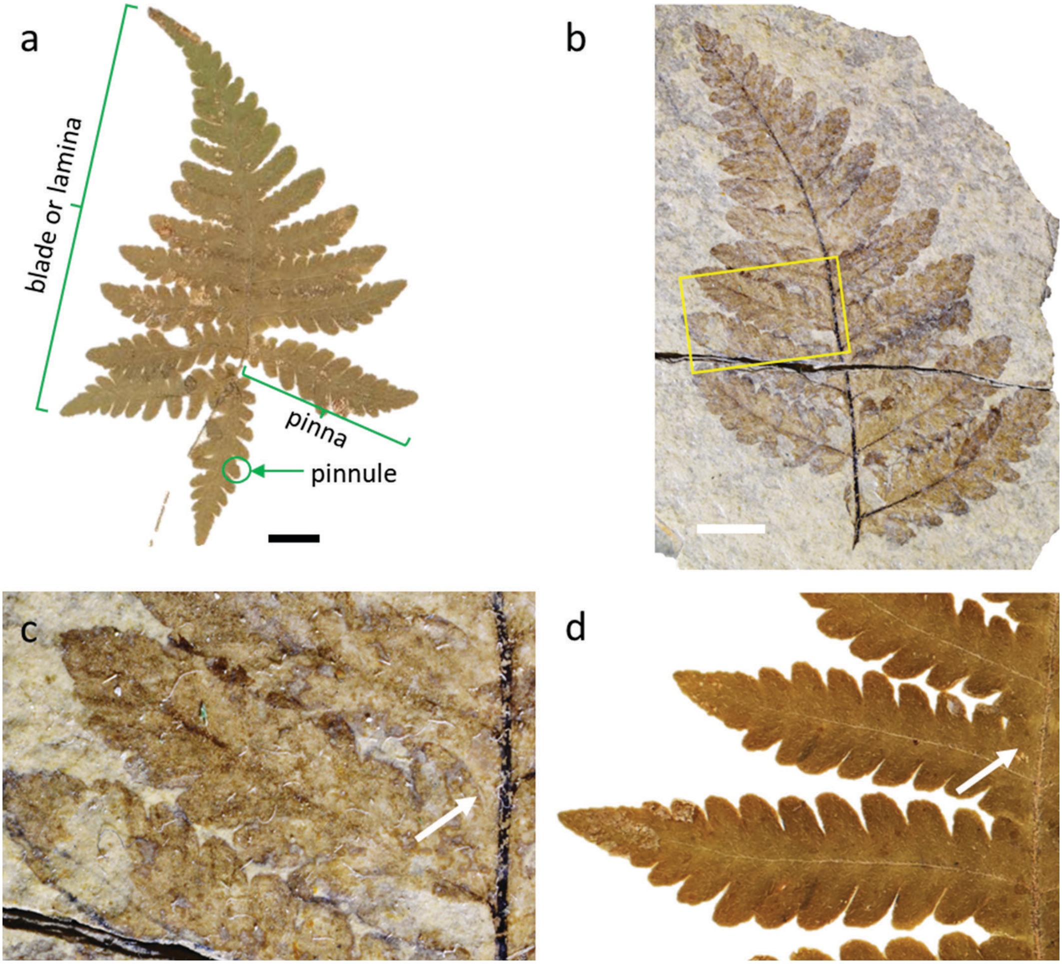

FIGURE 2. a. Whole leaf of Northern Beech Fern (*Phegopteris connectilis*; 1 cm scale bar) versus b. whole leaf of the fossil (0.5 cm scale bar). c. Close-up of fossil showing winged rachis (arrow) and pinnae with free, branching venation. d**.** Close-up of extant *P. connectilis* showing winged rachis characteristic of *Phegopteris*. Images have been digitally brightened by 20% to better show pinnae features. Photos a and d: used under CC BY-SA from the Carnegie Museum Herbarium, specimen CM007315 (Mid-Atlantic Herbaria Consortium 2022). Photos b and c: D.R. Greenwood.

ferns to extant families and genera in the absence of key characters, including those associated with sori. Therefore, while the Driftwood Canyon specimen is a close morphological match to members of the *P. connectilis* group, assignment to the family Thelypteridaceae and genus *Phegopteris* is tentative.

Phegopteris connectilis is a circumboreal species found across Canada. In BC, it is found mostly in the coastal wet forests, but also grows in wet mixed conifer–broadleaf forests of the interior, including areas east of Driftwood Canyon (Figure 1; Douglas *et al.* 2000). Both *P. excelsior* and *P. hexagonoptera* are restricted to northeastern North America, including southern Ontario, New Brunswick, and Nova Scotia in Canada (Patel *et al.* 2019). Schneider *et al.* (2013) place the evolutionary diversification of *Phegopteris* from other Thelypteridaceae in the Eocene to Oligocene (ca. 43 ± 13 Mya), and they estimate that the temperate-climate *P. connectilis* group originated during the Oligocene, about 30 ± 6 Mya. Multiple studies have constructed dated fern phylogenies using the few well-dated fossil fern taxa (Pigg *et al.* 2021 and references they cite). If the Driftwood fern is a member of the *P. connectilis* group, its early Eocene age (~52 Mya) re-dates origination of the *P. connectilis* group as 28–16 Mya older and closer in age to the calculated diversification of *Phegopteris* from other Thelypteridaceae than estimated by Schneider *et al.* (2013).

The original forest community of the cf. *Phegopteris* fossil from the Driftwood Creek fossil beds has been interpreted as a mixed conifer–broadleaf forest community with cedars and redwoods (Cupressaceae: *Chamaecyparis* and/or *Thuja*, *Metasequoia*, and *Sequoia*), and other conifers including fir (*Abies*), larch (*Larix*), spruce (*Picea*), pines (*Pinus driftwoodensis* Stockey), golden larch (*Pseudolarix*), as well as rare *Ginkgo*, and the broadleaf deciduous angiosperms alder (*Alnus*), birch (*Betula*), Sassafras (*Sassafras hesperia* (Berry) Wolfe et Wehr), elms (*Ulmus*), oak family (Fagaceae), and many as yet unidentified plant fossils (Stockey 1984; Greenwood *et al*. 2005, 2016). A diverse insect fauna is known from the Driftwood Creek beds, together with fish, birds, and two mammals, a primitive hedgehog and tapir (Wilson 1977; Archibald *et al.* 2011; Eberle *et al.* 2014; Greenwood *et al*. 2016; Archibald and Makarkin 2017; Mayr *et al.* 2019). The climate was reconstructed as temperate and wet, with mean annual temperature ~10–15°C and mean annual precipitation ~100 cm with little or no winter freezing (Greenwood *et al*. 2005; Eberle *et al.* 2014). The environmental interpretation of the early Eocene forest setting for the cf. *Phegopteris* fossil frond is comparable to that of the present-day southern range of *P. connectilis* (e.g., Vancouver and Ontario and adjoining United States states).

Several BC Eocene fossil sites have recorded the floating fern *Azolla* (Arnold 1955; Greenwood *et al.* 2005, 2016; Collinson *et al.* 2017), a genus occurring today in southern BC but generally considered a subtropical–tropical fern (Douglas *et al.* 2000; Collinson *et al.* 2017; Klinkenberg 2020). Apart from *Azolla*, however, ferns have only rarely been reported from BC Eocene fossil floras (e.g., Driftwood Canyon, Falkland, McAbee, and Thomas Ranch; Greenwood *et al.* 2016; Pigg *et al.* 2021), although five fern taxa have been described from the Princeton chert (Pigg and DeVore 2016). From Falkland (Figure 1), Pigg *et al.* (2021) described the fossil fern *Dennstaedtia christophellii* Pigg, Greenwood, Sundue, & DeVore (Dennstaedtiaceae), a relative of the bracken fern (*Pteridium* spp.) allied to extant Neotropical *Dennstaedtia* species. *Dennstaedtia* has one extant species in eastern Canada, Hay-scented Fern (*Dennstaedtia punctilobula* (Michaux) T. Moore), but this genus is absent from the present-day BC native flora (Douglas *et al.* 2000). The beech fern from Driftwood Canyon occurs within the circumboreal distribution of *P. connectilis* today. Discoveries of past fern diversity from the fossil record highlight past biogeographical linkages between the fern flora of BC and both warmer climate areas to the south (*Azolla*, *Dennstaedtia*) and potentially across the Northern Hemisphere (*P. connectilis* group).

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Note

A late Pleistocene Wood Turtle (*Glyptemys insculpta*) from Iowa, USA: response of the taxon to glaciation and formation of the current range

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Hill, M.G. 2022. A late Pleistocene Wood Turtle (*Glyptemys insculpta*) from Iowa, USA: response of the taxon to glaciation and formation of the current range. Canadian Field-Naturalist 136(3): 206–212. https://doi.org/10.22621/cfn.v136i3.2705

Abstract

The partial shell of a Wood Turtle (*Glyptemys insculpta*) was collected from the West Branch of the East Nishnabotna River in southwestern Iowa, near Malvern. By direct accelerator mass spectrometry, it radiocarbon dates to the late Pleistocene (10 220 ± 30 years before present [BP], 11 975–11 813 calibrated years [cal] BP). Other subfossil evidence indicates that Wood Turtles moved far south of their current range, into the southeastern United States, in response to late Pleistocene glaciation. The specimen suggests that the species also moved south and west, into a previously undocumented western range, where favourable habitat and, in particular, somewhat cooler summer temperatures prevailed until ~10 200 cal BP. My assessment of the Holocene subfossil record suggests that establishment of the western portion of the current range may have occurred within the past 1000 years. Phylogenetic analysis and direct radiometric dating of subfossil specimens are needed to determine additional details about the late Pleistocene dispersal of Wood Turtle and the postglacial formation of their current range.

Key words: Range formation; paleozoology; reptile; paleoclimate; herpetofauna

Résumé

La carapace partielle d'une Tortue des bois (*Glyptemys insculpta*) a été collectée du bras ouest de la Rivière Est Nishnabotna (East Nishnabotna River) au sud-ouest de l'Iowa, près de Malvern. Sa datation radiocarbone par spectrométrie de masse par accélérateur remonte au Pléistocène tardif (10 220 ± 30 avant le présent [AP], 11 975–11 813 calibré [cal] AP). Une autre évidence subfossile montre que les Tortues des bois se sont déplacées loin au sud de leur aire de répartition actuelle, au sud-est des Etats-Unis, suite à la période glaciaire du Pléistocène tardif. Le spécimen montre que les espèces se sont aussi déplacées au sud et à l'ouest, dans une aire de répartition occidentale non documentée auparavant, où un habitat favorable et, en particulier, des températures estivales un peu plus fraîches prédominaient jusqu'à ~10 200 cal AP. Mon évaluation du registre subfossile de l'Holocène suggère que l'établissement de la partie ouest de l'aire de répartition actuelle s'est peut-être produit au cours des 1000 dernières années. L'analyse phylogénétique et la datation radiométrique directe des spécimens subfossiles sont nécessaires pour déterminer des détails supplémentaires sur la dispersion de la Tortue des bois pendant le Pléistocène tardif et la formation postglaciaire de leur aire de répartition actuelle.

Mots-clés : habitat, paléozoologie, reptile, paléoclimat, herpétofaune

Quaternary temporal and geographic distributions of extant and extinct fauna are routinely used to reconstruct environment and community architecture as well as to profile how biota differentially respond to climate change (Holman 1992; Bell *et al.* 2010; Williams *et al.* 2018). The recovery of the partial shell of a Wood Turtle (*Glyptemys insculpta*; formerly *Clemmys insculpta*) from southwest Iowa in 2019 (Figure 1), directly radiocarbon dated to ~12 000 calibrated years (cal) before present (BP), provides the opportunity to examine response of the taxon to climate change, the character of the regional late Pleistocene environment, and the establishment of the species' current range.

Wood Turtle is a medium-sized, semi-terrestrial turtle that currently ranges across the northern Great Lakes, northeastern United States, and southeastern Canada (Ernst and Lovich 2009; Jones *et al.* 2021;

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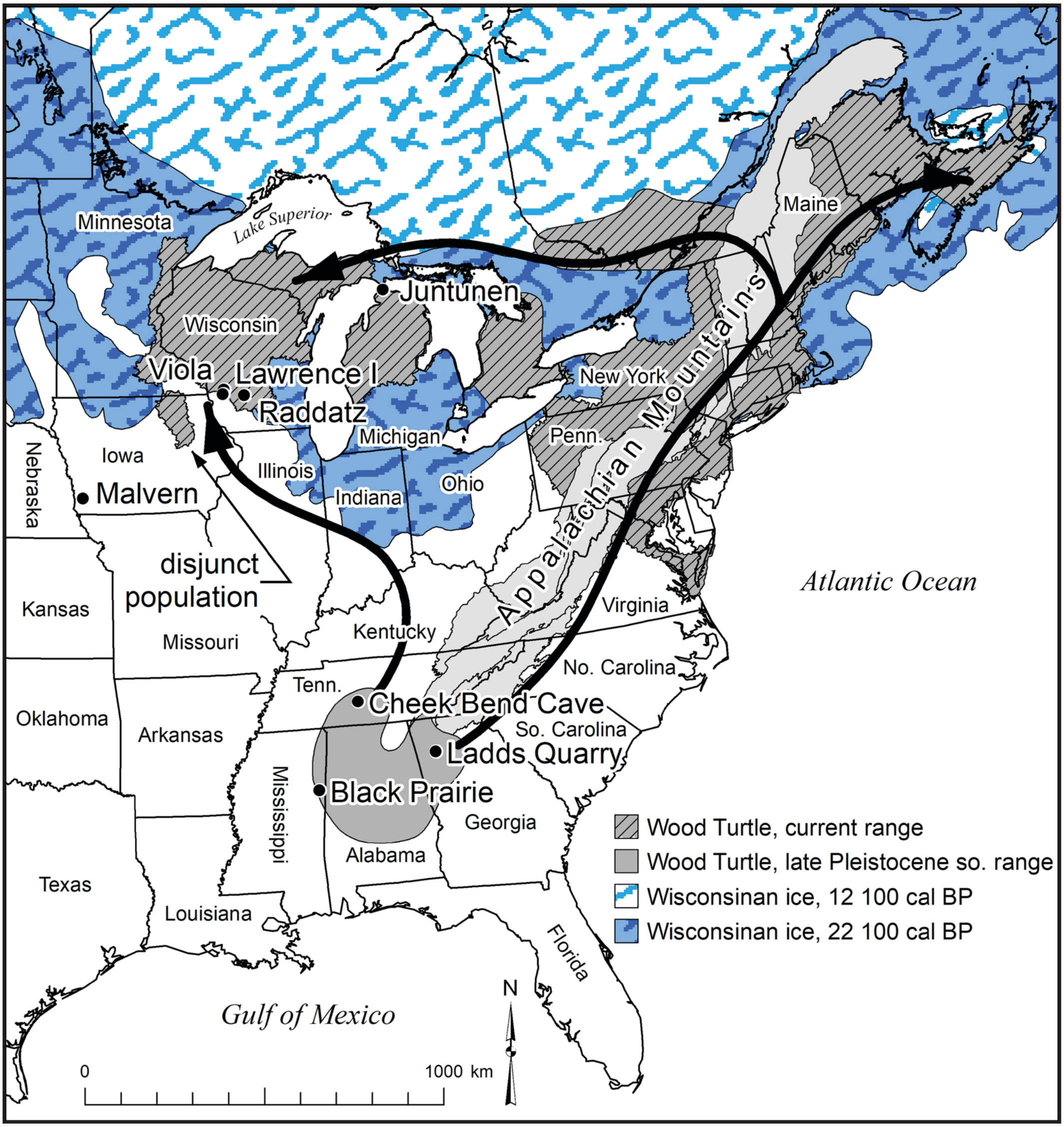

FIGURE 1. Current range of Wood Turtle (*Glyptemys insculpta*) in the contiguous United States and Canada (Ernst and Lovich 2009: 251; USGS 2018), including the location of extra-limital records, relative to the position of the ice margin during the last glacial maximum (22 100 calibrated years before present [cal BP]) and at 12 100 cal BP (Dalton *et al.* 2020), when the taxon was present in southwest Iowa. Also included are the proposed recolonization routes from the late Pleistocene southern range from Jones *et al.* (2021) as originally proposed by Amato *et al.* (2008).

Figure 1). A small, disjunct, and genetically isolated population occurs in the Cedar River basin in northeastern Iowa and crosses the state border into southeastern Minnesota (Spradling *et al.* 2010; Lapin *et al.* 2019). In general, Wood Turtle is found north of the 29°C (85°F) isotherm for normal daily maximum July temperature (Parmalee and Klippel 1981). It is a habitat generalist that occurs in hard-bottomed (e.g., sand, gravel, or cobble substrates) rivers and streams adjacent to forested riparian areas that contain foraging and nesting habitat (Lapin *et al.* 2019). Wood Turtles hibernate in fast-flowing water with high levels of dissolved oxygen, and lotic water sources are central to individual home ranges (Otten 2017). Although some individuals become more terrestrial during summer, in Iowa, they are usually not found farther than 300 m from lotic habitat (Tamplin 2016, 2019). Wood Turtles are opportunistic omnivores; earthworms, snails, slugs, and plant material are primary foods (Ernst and Lovich 2009).

Previously found late Pleistocene remains from Black Prairie, Mississippi (Phillips 2006), Ladds Quarry, Georgia (Holman 1967, 1985), and Cheek Bend Cave, Tennessee (Parmalee and Klippel 1981; Klippel and Parmalee 1982; Figure 1) indicate that the taxon survived late Wisconsinian glaciation by dispersing southward ~1000 km south of the present range. Concomitant with retreat of the Laurentide ice sheet, genetic profiles of modern specimens show that the turtle rapidly recolonized the area that ultimately resulted in its current range by taking two routes northward (Amato *et al.* 2008). One population dispersed from Alabama–Georgia, moving northward along the eastern seaboard into New Brunswick and Nova Scotia (Figure 1), with a tentacle then moving west across the Great Lakes region, possibly as far west as northern Wisconsin. The Ladds Quarry material appears to support this interpretation of the genetic evidence. Another population originated somewhat south and west of the Appalachian Mountains and recolonized Wisconsin, Minnesota, and lower Michigan (Figure 1). The remains from Cheek Bend Cave and Black Prairie support this route.

The subfossil turtle shell described here (Figure 2) was collected in July 2019 from a sand-and-gravel bar on the west branch of the East Nishnabotna River, near the city of Malvern, Mills County, Iowa (41.005403°N, 95.529881°W). It is now curated in the Paleontological Repository, Department of Earth and Environmental Sciences, University of Iowa (cat no. SUI – 148451). The specimen consists of about 50% of the anterior carapace and plastron (fused), including all of the left plastral bones. The left half of the plastron, which is complete, is 20 cm in maximum length. Except for subtle geological rounding of recent fracture edges, natural margins, and topographic highs, the physical condition of the specimen is excellent. The carapace is keeled and heavily sculpted, while the plastron is deeply concave and smooth. These features indicate it was an adult male Wood Turtle ≥25 years old when it died (Ernst and Lovich 2009; J.W. Tamplin pers. comm. 19 February 2020). A sample of plastron submitted for radiocarbon dating produced a median age of 11 889 cal BP (Table 1) and indicates the specimen is very late Pleistocene in age, hovering over the Pleistocene–Holocene boundary (Rasmussen *et al.* 2014).

The shell is somewhat similar to that of several turtles that share a modern range with Wood Turtles: Blanding's Turtle (*Emydoidea blandingii*), Common Map Turtle (*Graptemys geographica*), and False Map Turtle (*Graptemys pseudogeographica*). Although distinguishing these taxa can be difficult when only isolated pieces are available (Holman and Clouthier 1995), the identity of the Malvern shell is unquestionable and based on hands-on comparison with modern turtle material in my personal collection, published descriptions of Wood Turtle shell morphology, and feedback from specialists who examined digital images of the specimen (see Acknowledgements).

The Malvern record extends the late Pleistocene range of Wood Turtle several hundred kilometres south and west of the modern range (Figure 1) and suggests that somewhat cooler summer temperatures prevailed in southwest Iowa and adjacent areas of northwest Missouri, northeast Kansas, and eastern Nebraska until at least ~12 000 cal BP. Unfortunately, there are no vegetation or pollen studies from this area from that period to corroborate my assumption. Marshes, bogs and oxbow lakes, and wet meadows flanking rivers and streams, common landscape features today, were also abundant at the end of the Pleistocene. By 10 200 cal BP, summers were probably too warm and the environment too dry (Baker *et al.* 2000) to support Wood Turtles.

The specimen also suggests the existence of a previously undocumented, late Pleistocene western range for Wood Turtle. Although the extent of this range is unknown, it probably stretched into adjacent states. The potential for other subfossil specimens from these areas is high. Alternatively, the specimen may provide support for two rapid reinfiltration routes from the southern range. One population of turtles moved along the eastern seaboard, while another—involving the Malvern turtle—moved through the interior highlands, interior plateau, and central lowlands into the southern and western Great Lakes states. Assuming favourable preservation of ancient DNA, phylogenetic analysis of the Malvern specimen—ideally in conjunction with analyses of specimens from the southeast—could address these possibilities as well as determine additional details about the taxon's late Wisconsinan dispersal and the formation of its current range.

The current range of Wood Turtle covers the Upper Peninsula of Michigan, northern lower Michigan, most of Wisconsin, and parts of southeast Minnesota and northeast Iowa. Holocene subfossils in these areas—loosely, the western range—are absent or rare. To date, there are no Holocene records west of the Mississippi River (border between Illinois and Iowa) and only one from Michigan and three from Wisconsin, all from archaeological contexts (Figure 1). (I exclude a late Holocene record in western Wisconsin [Penman and Yerkes 1992] cited in the Neotoma database [Williams *et al.* 2018], because the three specimens were assigned to a different taxon in the final faunal report [Styles and White 1994].) The Juntunen,

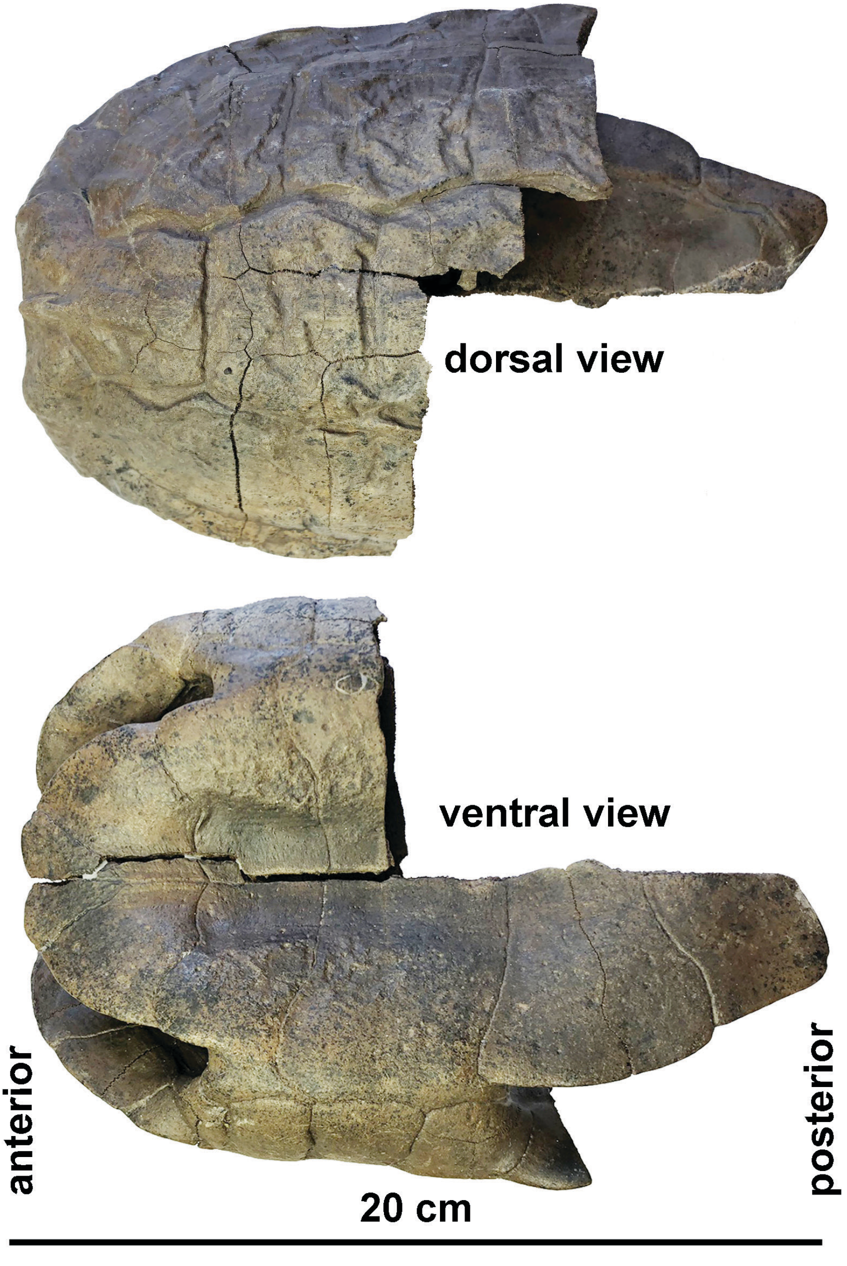

FIGURE 2. Subfossil Wood Turtle (*Glyptemys insculpta*) shell from near Malvern, Mills County, Iowa (cat no. SUI – 148451). Photo: Matthew G. Hill.

Michigan, record is very late Holocene (about ≤1000 cal BP; Cleland 1966); the skeletal basis of identification is not specified (Adler 1968). Two of the Wisconsin records are also late Holocene. The first is a nuchal (the most anterior carapace element), from the Middle Woodland component (1810 ± 80 years BP, 1890–1535 cal BP) at Viola rock shelter (Theler 1989; Steventon and Kutzbach 1990; J.L. Theler pers. comm. 21 August 2020). It is possible that this record is much older or much younger than the indirect date derived from dating the associated charcoal; rock shelter deposits are notoriously complex and direct

TABLE 1. Accelerator mass spectrometry (AMS) radiometric and isotopic results for the subfossil Wood Turtle (*Glyptemys insculpta*) shell from near Malvern, Mills County, Iowa, as determined by the Keck-Carbon Cycle AMS Facility, University of California, Irvine, USA.

	Laboratory no. 231586
Age ^{14}C years BP ± 1 sigma	10 220 ± 30
Calibrated age, ^{14}C years BP, cal BP, 2 sigma range (median)*	11 975–11 813 (11 889)
Fraction modern	0.2802 ± 0.0010
δ^{13}C‰ (PBD)	−21.3
δ^{15}N‰ (PBD)	6.8

* BP = before present, PBD = Pee Dee Belemnite. OxCal 4.4 (Bronk Ramsey and Lee 2016) and IntCal20 (Reimer *et al.* 2020) were used to calibrate the measured radiocarbon age.

dating is required to resolve this issue.

The second record consists of two carapace elements (a peripheral no. 7 and a proneural) from the late Middle Woodland–Late Woodland component at Lawrence I rock shelter (Berwick 1975). The taxonomic identification of these specimens requires verification because, as noted above, isolated carapace pieces from several taxa that co-occur in the region can be difficult to distinguish. Unfortunately, they could not be relocated in the collections at the Wisconsin Historical Society (WHS).

The third record is a complete nuchal from Raddatz rock shelter (Adler 1968), which I verified using digital images provided by WHS personnel. Parmalee (1959: Table 2) and Cleland (1966: Table 7) do not list the specimen in their enumerations of the site fauna; it is possibly tallied in the sample of indistinguishable Painted Turtle (*Chrysemys picta*), Blanding's Turtle, and/or map turtle (*Graptemys* spp.) remains. However, in part, because of the long, complicated history of custody and use of the collection (Speth *et al.* 2017), exact provenance has been lost, which muddles where the specimen falls in time. Summary data provided by Cleland (1966: Table 7), combined with his (opaque) discussion of the stratigraphy (1966: 104–105), indicates it was recovered from deposits dating to either the early-late Holocene (level 3, ~3500 cal BP) or the middle Holocene (level 11, ~7500–5000 cal BP). Regionally, these were the two warmest and driest intervals of time since deglaciation (Maher 1982; Winkler *et al.* 1986; Keen and Shane 1990), conditions that stand in contrast to current Wood Turtle range, which is well to the north, suggesting that Wood Turtle prefer much cooler habitats. Direct accelerator mass spectrometry dating of the specimen will be required to resolve this seeming discrepancy.

If Wood Turtles were present in the western half of the current range during the Holocene, then it is unusual that their remains have not been recovered more often at archaeological sites, as is the case with other turtle taxa (Theler 2000: Table 5). Faunal preservation at open human habitations and in rock shelters across the region is generally excellent, and many large faunal samples with high taxonomic diversity have been reported (Parmalee 1959, 1960, 1963; Cleland 1966, 1970; Styles and White 1993, 1994, 1995; Theler 1993, 2000; Kuehn 1998; Baker and Theler 2005; Kuehn and Clark 2012). The geographic locations of the known records and the lack of Wood Turtles at other archeological sites suggests that the formation of the western range occurred relatively recently, perhaps within the past 1000 years. In this scenario, the western Wisconsin rock shelter records represent a now-extinct, Holocene population that may be more closely related to those animals that recolonized the region from the south following deglaciation, with the caveat that the Lawrence I record requires checking (assuming the material is relocated) and that the Raddatz rock shelter record requires direct dating. Direct dating of the Viola and Lawrence I records would also shed light on this supposition. Furthermore, the current western range may have been shaped by a very late Holocene population that spread across the northern Great Lakes and into Wisconsin, Minnesota, and possibly, Iowa.

In conclusion, Wood Turtles inhabited some areas of the southeast and eastern Central Plains at the end of the Pleistocene, presumably migrating to these locations from a more northern, ancestral range that had become inhospitable due to advancing Laurentide ice. A general, northward movement of these populations attended subsequent deglaciation and environmental amelioration. Formation of the current range, particularly that which stretches across the northern Great Lakes region into northern and southwestern Wisconsin, may have occurred during the very late Holocene. The extant population in northeast Iowa, and possibly that which also inhabits southwest Wisconsin, may be most closely related to the aforementioned Central Plains population.

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Tabusintac Bay (New Brunswick, Canada): an important spring migratory stopover for Atlantic Brant (*Branta bernicla hrota*)

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Abstract

Atlantic Brant (*Branta bernicla hrota*) is an Arctic-breeding migratory waterfowl that relies heavily on Common Eelgrass (*Zostera marina*) for food during migration and overwintering. Although the abundance of Atlantic Brant along the coasts of the Maritime provinces has declined drastically over the past decades, some flocks continue to migrate through the area in spring. Here, we present field observations of Atlantic Brant spring staging in the Tabusintac Bay, New Brunswick, Canada. We surveyed the Tabusintac Bay seven times between 26 May and 6 June 2018. We observed a maximum daily count of 1259 individuals, which is comparable to high counts from the 1970s. These spring surveys indicate the continuing importance of Tabusintac Bay to Atlantic Brant for spring staging. There is a pressing need to increase monitoring and research in the region and to preserve or enhance the quality of the area for spring staging brant.

Key words: Atlantic Brant; *Branta bernicla hrota;* spring migration; Common Eelgrass; *Zostera marina*; Tabusintac

Introduction

Brant (*Branta bernicla*) is an Arctic-breeding migratory waterfowl species that relies heavily on native seagrasses (*Zostera* spp.) for food during migration and overwintering (Reed *et al*. 1996; Ganter 2000; Kollars *et al.* 2017). Four distinct populations are recognized in North America, including Atlantic Brant (*Branta bernicla hrota*; CWSWC 2022). Atlantic Brant nests on Southampton Island and around the Foxe Basin in the eastern Canadian Arctic and overwinters along the eastern coast of the United States, from Massachusetts to North Carolina (Ganter 2000). The Atlantic Brant population has been decreasing since 2000, but has remained stable over the last five years, with an estimated population size of 106 000 in 2019 (CWSWC 2022). This population was subject to a significant decline in the early 1930s following a widespread and drastic decline in Common Eelgrass (*Zostera marina*) along the Atlantic coast caused by the pathogenic slime mold *Labyrinthula zosterae* (Cottam *et al.* 1944). Before the decline of eelgrass, Atlantic Brant commonly used to migrate through the Maritime provinces of Canada during the fall and spring. However, since the 1940s, a greater portion of the Atlantic Brant population takes a more direct path between their breeding and wintering grounds, flying directly to eastern James Bay (Quebec, Canada), and fewer individuals pass through the Maritimes (Erskine 1988; Castelli *et al.* 2010). Once abundant and widely distributed along the coasts of the Maritimes, Atlantic Brant are now observed in lower numbers and in a limited number of locations (Hanson 2004; McAskill 2019). Unlike other species of geese, Atlantic Brant are dependent on native seagrasses during migration, preferring coastal estuaries, shorelines, and lagoons for feeding (Ladin *et al.* 2011; CWSWC 2022). As a result, the identification and conservation of eelgrass meadows, as important coastal foraging areas, is important for the management of this species in eastern Canada.

Here, we present field observations of spring staging Atlantic Brant in the Tabusintac Bay, on the east coast of New Brunswick, Canada (47.3407°N, 64.9452°W). These field observations were part of a larger project that used unmanned aerial vehicles to detect Atlantic Brant (LaRocque *et al.* 2021). The area has been identified as critically important to waterfowl and shorebirds and is recognized under the Ramsar Convention as a Wetland of International Importance (RAMSAR 2017) and by Bird Life International as an Important Bird Area (IBA Canada 2021). The area has long been used by Atlantic Brant as a stopover site during migration (Erskine 1988; Hanson 2004), and they spend a few weeks in the bay in the spring (from mid-May to early June; B.J. Fowler pers. comm. 15 April 2018).

Methods

Spring staging Atlantic Brant were surveyed from 26 May to 6 June 2018 in six areas covering the entire Tabusintac Bay (Figure 1a). The bay is protected from the Gulf of St. Lawrence by a natural beach barrier and contains extensive monospecific beds of eelgrass (Figure 1b; Forsey *et al.* 2020; Leblanc *et al.* 2021). One observer used a spotting scope to observe Atlantic Brant at a survey station within a particular survey area. The entire bay was surveyed seven times between 26 May and 6 June 2018. To avoid double counting of flocks, the observer would begin surveying the birds at either the northern or southern end of the estuary and keep track of flocks already surveyed while moving to the next station. Each survey day, the observer would alternate the starting point between the northern and southern ends of the estuary. Surveys were not conducted during heavy rain or fog when light conditions were poor. To determine the flock's position from the survey stations, the observer took a bearing with a compass and estimated the flock's distance from the main coast or beach barrier. The global positioning system coordinates of the survey stations, bearings, the distance from landmarks (with known coordinates) within the survey area, and distances were then used to estimate the position of flocks using ArcGIS 10.5.1 software (Esri, Redlands, California, USA).

Results and Discussion

The seven spring surveys resulted in 5326 brant observations. Daily counts ranged from 205 to 1259 individuals (Figure 2), with a daily average of 761 ±122 SE. The number of Atlantic Brant observed in a given area of the bay ranged from two to 643, and the average flock size was 88 ± 19 SE. The largest Atlantic Brant flocks (277–643) were mostly found in

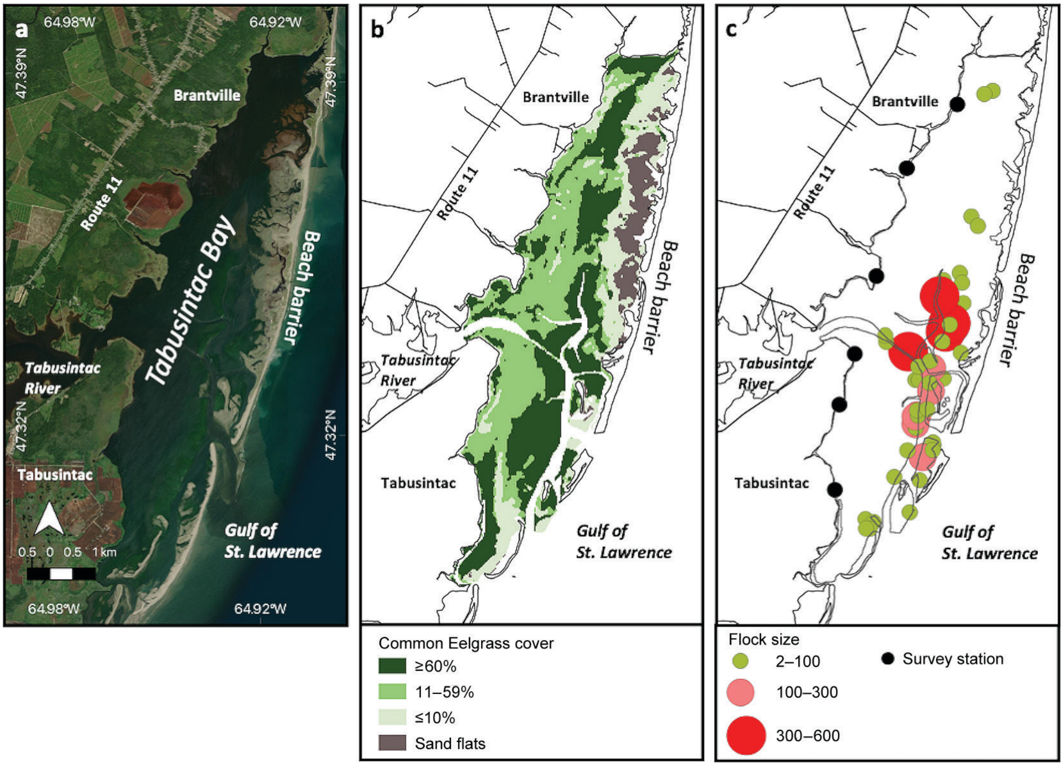

FIGURE 1. a. Study area at Tabusintac Bay, northeastern New Brunswick, Canada. b. Distribution of Common Eelgrass (*Zostera marina*) in Tabusintac Bay, generated using a Landsat image acquired in 2017 (Leblanc *et al.* 2021). c. Flock size of spring staging Atlantic Brant (*Branta bernicla hrota*) in Tabusintac Bay, New Brunswick, Canada, from 26 May to 6 June 2018.

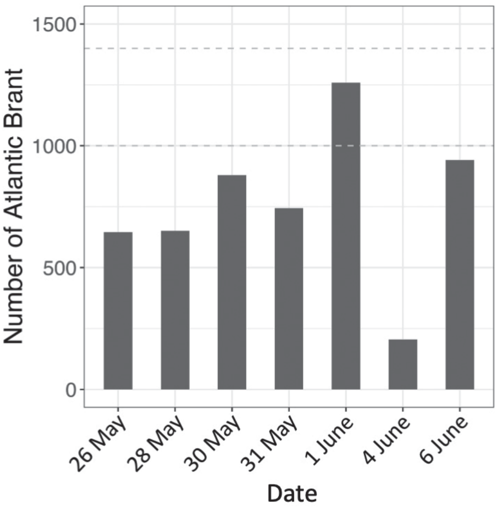

FIGURE 2. Counts of spring staging Atlantic Brant (*Branta bernicla hrota*) in Tabusintac Bay, New Brunswick, Canada, in 2018. The dashed lines represent the minimum (1000) and maximum (1400) number of Atlantic Brant observed in Tabusintac in the 1970s (Erskine 1988).

the mid-section of the bay, near the beach barrier and dense eelgrass beds (eelgrass beds with cover ≥60%, Figure 1c). The largest flocks were also observed foraging relatively near the Tabusintac Bay's channel. Smaller flocks (2–92) were generally seen in the bay's northern and southern portions.

In eastern North America, the primary stopover sites of migrating Atlantic Brant are around the James Bay region. During spring migration, brant concentrate initially in the southern section of James Bay (Ruppert Bay), then travel to the northwest of the James Bay coast before moving to the Foxe Basin region (Castelli *et al.* 2010). However, there have been reports of some brant still using a coastal migration route though the Maritimes in the spring, stopping at Grand Manan Island, New Brunswick, and Cape Sable Island, Nova Scotia (Castelli *et al*. 2010). Our preliminary findings indicate that the Tabusintac Bay continues to be an important spring staging area for Atlantic Brant. During aerial surveys conducted across the whole Tabusintac Bay in the spring in the mid 1970s, 1000 Atlantic Brant were observed in 1974 and 1400 in 1977 (Erskine 1988). The largest daily count in 2018 (1259 individuals) is comparable to those in the 1970s, suggesting that the bay continues to be a significant stopover site in New Brunswick. Although the Tabusintac Bay harbours extensive eelgrass beds, a recent study has found that eelgrass is declining in some areas (Leblanc *et al.* 2021). Continued decline of eelgrass beds in the Tabusintac Bay could jeopardize the critical ecological services they provide, including important feeding sites for Atlantic Brant and other migratory waterfowl. As a result, there is a pressing need to increase monitoring and research efforts in the region and preserve or enhance the quality of the area for spring staging brant. The spring surveys in 2018 provide valuable current population data that can be used to guide future studies on Atlantic Brant habitat use in relation to eelgrass abundance and quality in the Tabusintac Bay.

Author Contributions

Writing – Original Draft: M.-L.L.; Review & Editing: A.H., B.L., A.L., and M.M.H.; Conceptualization: M.-L.L.; Investigation: M.-L.L.; Methodology: M.-L.L.; Formal Analysis: M.-L.L.; Funding Acquisition: M.-L.L. and B.L.

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Impact of grazing and conservation opportunities for nesting grassland birds in a community pasture

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Abstract

Multiple bird species-at-risk nest on the ground in hayfields and pastures, making nests susceptible to inadvertent destruction from agricultural activity (e.g., trampling by livestock). To better understand the impact of Domestic Cattle (*Bos taurus*) grazing, we assessed the distribution and breeding status of nesting grassland birds in 2019 and 2020 at the Grey Dufferin Community Pasture, a ~234 ha pasture in southern Ontario, Canada. We estimated there were 86 male Bobolink (*Dolichonyx oryzivorus*) in the community pasture in 2019 and 100 in 2020 before grazing began; observed abundance decreased by 73% in fields after grazing in 2020. Eastern Meadowlark (*Sturnella magna*) maintained territories after grazing and fledged young in 67% ($n = 21$) of territories. Savannah Sparrow (*Passerculus sandwichensis*) was common across the community pasture before and after grazing occurred. We detected evidence of nesting more frequently in Bobolink and Savannah Sparrow territories in ungrazed than in grazed fields. Our results support previous research indicating nesting Bobolink often disperse from moderately to heavily grazed fields, whereas Eastern Meadowlark and Savannah Sparrow largely remain and renest. Despite the inadvertent negative impacts of cattle stepping or laying on nests and consuming vegetative cover, the community pasture provides areas for successful nesting, with Eastern Meadowlark faring better than Bobolink. Flexibility in the timing and duration of grazing in rotational grazing systems may enable strategic management in target fields (e.g., maintaining enough vegetation for nesting Bobolink). Information about the distribution and abundance of birds can be used to target particular fields for conservation.

Key words: Distance sampling; nest monitoring; range management; regenerative agriculture; spot mapping; stocking rate; Vickery index

Introduction

Temperate grassland is the terrestrial biome of greatest conservation risk for wildlife worldwide because 46% of the land has been converted to other uses and only 5% are in protected areas (Hoekstra *et al.* 2005). A substantial portion of temperate grasslands in North America has been converted from native grassland to farmland (Samson and Knopf 1994; Hoekstra *et al.* 2005). In addition to providing food, fibre, and fuel for the human population and contributing to the economy, farmland also provides wildlife habitat (Kremen and Merenlender 2018). In eastern North America, where temperate grasslands were rare before European colonization, agricultural grasslands were created through the conversion of other land-cover types, such as forest, to farmland. These agricultural grasslands (i.e., hayfields and pastures) are currently the most common type of grassland in the region, providing important wildlife habitat. Thus, collaboration between conservation biologists and farmers is essential for identifying ways to support grassland species that are compatible with farm management.

Populations of birds that nest in grasslands (e.g., Bobolink [*Dolichonyx oryzivorus*]) have been declining in North America since at least the first half of the 20th century, based on observations of naturalists and ornithologists (Forbush 1907; Bent 1958). Grassland bird populations decreased by 53% in North America between 1970 and 2017, more than birds in any other biome (Rosenberg *et al.* 2019). These population declines have led to conservation concern for multiple species that nest in grasslands (i.e., hayfields, pastures, fallow or old fields, native grasslands, restored grasslands). Bobolink and Eastern Meadowlark (*Sturnella magna*), which nest on the ground exclusively in grasslands, are listed as Threatened in Canada (Government of Canada 2017); their populations declined by 73% and 88%, respectively, between 1970 and 2019 (Smith *et al.* 2020). Savannah

Sparrow (*Passerculus sandwichensis*), which is not a grassland obligate but frequently nests in grasslands, is considered a conservation priority in some regions (Environment Canada 2014). Its population declined by 38% in Canada between 1970 and 2019 (Smith *et al.* 2020).

Habitat loss and a decrease in habitat quality are likely the two most important factors contributing to population declines in grassland birds on their breeding grounds (COSEWIC 2010, 2011; McCracken *et al.* 2013; MECP 2015). Habitat loss has occurred because of the conversion of hayfields, pastures, and native grasslands to other types of landcover (Samson and Knopf 1994; Smith 2015). In hayfields and pastures, early and frequent hay harvests and intensive livestock grazing result in poor habitat quality for nesting birds by creating an ecological trap (Schlaepfer *et al.* 2002). Nests can be destroyed, and young birds can be killed directly (e.g., nests crushed by mowing [Tews *et al.* 2013] or trampled by livestock) or indirectly (e.g., exposure to predators; Bollinger *et al.* 1990; Perlut *et al.* 2006; MacDonald and Nol 2017). Stewardship practices on farms meant to benefit nesting grassland birds often involve delaying grazing or hay harvest until birds finish nesting, typically in July (COSEWIC 2010; McCracken *et al.* 2013; MECP 2015; OSCIA 2020). Unfortunately, these stewardship practices often have negative impacts on farm production. For example, the protein content of unharvested forage decreases across June and July, reducing nutritional quality for livestock (Brown and Nocera 2017).

Research is needed to better understand how the needs of nesting grassland birds can be incorporated into farm management, while minimizing negative impacts on farm production. Management of grasslands in Ontario, Canada, where Bobolink and Eastern Meadowlark are listed as Threatened provincially (MECP 2010, 2012), is important for the conservation of grassland birds. For example, ~10% of the global Bobolink population breeds in the province (Partners in Flight 2020). There are ~525 000 ha of various pasture types in Ontario (OMAFRA 2016), which can potentially provide productive nesting habitat for grassland birds under particular conditions.

Our overall goal was to improve our understanding of the impacts of the rotational grazing of Domestic Cattle (*Bos taurus*) on nesting grassland birds. Rotational grazing is promoted as a best management practice for agricultural production and typically entails moving livestock through at least three fields during the grazing season (OMAFRA 2012). The Grey Dufferin Community Pasture provided a unique opportunity to monitor the impacts of rotational grazing on multiple species of grassland birds in a large block of grassland. Improving our knowledge about the status of grassland birds in pastures and the impact of management practices (e.g., rotational grazing) may help guide future conservation efforts to provide the greatest positive impacts for grassland birds in agricultural grasslands. Our objectives were to assess: (1) Bobolink abundance before and after grazing occurred and the impact of grazing on breeding status, (2) Eastern Meadowlark distribution, abundance, and breeding success throughout the breeding season, and (3) Savannah Sparrow distribution before and after grazing occurred and the impact of grazing on breeding status.

Study Area

We monitored grassland birds in 2019 and 2020 at the Grey Dufferin Community Pasture (hereafter community pasture), in Grey County, southern Ontario, Canada (44.094°N, 80.440°W). Grey County is in the Mount Forest ecodistrict within the Mixedwood Plains ecozone (Ontario GeoHub 2012). The ~868 000 ha ecodistrict is primarily rural, consisting of 72% pasture and cropland, and 20% forest (Wester *et al.* 2018). The community pasture is privately owned and managed by a committee to provide grazing opportunities to local farmers for beef cattle. The property includes ~234 ha of pasture (predominantly open grassland with some wooded areas) which supports ~600 cattle through rotational grazing each spring and summer. It also provides a significant amount of wildlife habitat, primarily for grassland species, although the property also includes forested, wetland, and riparian areas. There are permanently fenced fields in the community pasture, some of which are further subdivided with temporary fencing to enable rotational grazing throughout the grazing season. For our study, we identified 21 fields (2.6–20.5 ha); these field boundaries largely followed permanent fencing. In 2019, 430 steers and 250 heifers were rotated through the pasture as separate groups beginning on 28 May. In 2020, 325 steers and 271 heifers were rotated through the pasture as separate groups beginning on 27 May. Each field was grazed once or twice by the end of July and was grazed for about 1–12 days each time cattle entered the field. After the first grazing occasion, each field was rested for about four to five weeks in 2019 and about six to seven weeks in 2020 before being grazed a second time.

Methods

Transect surveys

We used transects to survey the number of Bobolink before and after grazing occurred in 2019 and 2020. Additionally, we used transects to detect the presence of Savannah Sparrow in each field in 2020. We placed one transect in each of the 21 fields using a geographic information system (QGIS version 3.4; QGIS Development Team 2019) and aerial photographs. The length of each transect varied based on the number of 100 m sections that fit in each field (200–600 m). We visited each transect four times each year, except for transects in fields being grazed by cattle on the day of a survey. In both years, visits one and two occurred before grazing began (22–29 May) in 20 fields; one field was grazed before we could complete surveys. Visits three and four occurred from 20 to 25 June in both years. During visits three and four in 2019, we surveyed 17 grazed and one ungrazed field(s). During visits three and four in 2020, we surveyed nine grazed and eight ungrazed fields. The number of ungrazed fields surveyed was larger in 2020 because cattle were rotated through fields more slowly compared to 2019.

During each survey, we walked the transect at a pace of one step/sec. We recorded detections of Bobolink within 75 m of either side of the transect line. When we detected a Bobolink, we noted how we detected the individual (i.e., by song, call, or visually), the sex of the individual (if possible), and perpendicular distance from the transect line to the individual when it was first detected. Because Savannah Sparrow was abundant across the pasture, we did not record detections of individuals. Instead, we noted if we detected the species on each 100 m section of the transect. We conducted all surveys between sunrise and 0940 during appropriate weather conditions for detecting birds (i.e., not during rain or strong wind).

Spot mapping

We used spot mapping (*sensu* Wiens 1969) to collect data on grassland bird territories. We collected spot mapping data differently in each year and for each species. Bobolink, Eastern Meadowlark, and Savannah Sparrow are migratory songbirds. Males typically arrive on breeding grounds before females and establish individual breeding territories that they defend to exclude conspecific males (Jaster *et al.* 2020; Renfrew *et al.* 2020; Wheelwright and Rising 2020). It is common for >1 adult female to breed in a territory (Jaster *et al.* 2020; Renfrew *et al.* 2020; Wheelwright and Rising 2020). We used spot mapping to assess the breeding status of Bobolink in 2019 and 2020 in grazed and ungrazed fields from 20 to 28 June. We selected this time period to coincide with when most Bobolink in the study area have mature nestlings or young fledglings (Campomizzi *et al.* 2020). We used detections of Bobolink on the third and fourth transect visit to guide territory sampling and distributed sampled territories across as many fields as possible. We attempted to sample 10 territories in grazed fields and 10 territories in ungrazed fields in each year. Because many Bobolink had dispersed due to grazing by late June, there was a scarcity of territories to spot map. As a result, we sampled 19 territories in grazed fields and 18 in ungrazed fields across 2019 and 2020. We visited each territory once.

Similarly, we used spot mapping to assess the breeding status of Savannah Sparrow, in 2020 only, in grazed and ungrazed fields. We visited sampled territories once from 14 to 16 June because Savannah Sparrow arrives (Renfrew *et al.* 2020; Wheelwright and Rising 2020) and starts breeding earlier than Bobolink (Peck and James 1987). We randomly selected a sample of 10 territories in grazed fields and 10 in ungrazed fields by walking into a field and spot mapping the first individual we detected. We distributed sampled territories across as many fields as possible.

In 2020, we also used spot mapping to assess distribution, abundance, and evidence of breeding of Eastern Meadowlark throughout the breeding season. We visited each field about once per week from 21 May to 5 August to monitor Eastern Meadowlark. We were unable to begin spot mapping in April when Eastern Meadowlark arrive because of government restrictions due to the COVID-19 pandemic, which delayed the start of field work.

Once we located birds in a target territory, we observed Bobolink and Savannah Sparrow for a maximum of 30 min and Eastern Meadowlark for up to 60 min. For Bobolink and Savannah Sparrow, we ended a spot mapping visit early if we detected evidence of nesting or fledged young. For Eastern Meadowlark, we used observations of evidence of nesting to help locate nests (see below). On each visit to a territory for all three species, we recorded the coordinates of three to six locations used by the birds on a hand-held global positioning system (GPS) unit (eTrex 20 and GPSMAP 78; Garmin International Inc., Olathe, Kansas, USA). At each location, we noted the behaviour of the birds, prioritizing behaviours that indicated nesting or fledged young. For Bobolink, we considered observations of nest building, incubating eggs, faecal sac carry from a nest, food carry to a nest, and agitated alarm calling as evidence of nesting, and food carry to fledglings or dependent fledglings as evidence of fledged young. We considered all other behaviours (i.e., loafing, vocalizing, foraging, territorial behaviour, courtship) to not indicate evidence of nesting or fledged young. For Savannah Sparrow and Eastern Meadowlark, we used the same criteria except we did not record the agitated alarm calling behaviour.

Nest monitoring

In 2020, we searched for and monitored Eastern Meadowlark nests about once per week from 21

May to mid-August, during and after spot mapping. We also monitored Savannah Sparrow and Bobolink nests, located opportunistically, about once per week over the same time period.

For Eastern Meadowlark, we used behavioural cues and systematic searching to locate nests (Martin and Geupel 1993; Winter *et al.* 2003). For Savannah Sparrow and Bobolink, we located nests opportunistically from behavioural cues observed while in the community pasture (e.g., a female flushing from a nest as we walked nearby).

We did not approach nests when females were building to minimize the risk of nest abandonment. Once females were incubating eggs, we visited nests approximately once per week until a nest was no longer active. On each visit, we recorded the number of eggs, number of young, age of young, condition of the nest, and adult behaviour. We considered a nest to have fledged young if we had evidence of ≥1 young leaving the nest (e.g., presence of flightless dependent fledglings, adults alarm calling or carrying food); otherwise, we considered the nest to have failed. We considered a nest predated if we found a nest empty after the nest contained eggs or nestlings on the previous visit and we did not observe evidence of fledged young. We considered a nest failed due to trampling if we found evidence of livestock movements around the nest location (i.e., flattened and grazed vegetation) and either saw a flattened nest or did not observe the adult birds tending to a nest we were unable to relocate. Because birds were unmarked and we visited nests about once per week and did not visit fields that were being actively grazed, we were occasionally unable to determine nest outcome or reason for nest failure even when we suspected failure due to trampling.

Vegetation sampling

We measured vegetation height to assess differences between grazed and ungrazed fields and Bobolink use of fields from 21 to 26 June to coincide with Bobolink spot mapping. Each year, we used QGIS to generate 90 random sampling locations in each of three field types: 30 in ungrazed fields, 30 in grazed fields where we detected Bobolink on the third or fourth transect visit, and 30 in grazed fields where we did not detect Bobolink on the third or fourth transect visit.

Analyses

We conducted all analyses in program R (version 4.0.3; R Core Team 2020) and considered resulting P values < 0.05 statistically significant. Except for distance sampling, we used fairly simple statistical tests to address our objectives because sample sizes were small and not conducive to complex modelling (e.g., models with hierarchical structure).

We used distance sampling (Buckland *et al.* 1993a) to estimate the number of male Bobolink across the 205 ha of open pasture in each year (excluding forested areas where Bobolink territories would not occur). We used data from the first and second transect visit, which occurred before grazing began. Distance sampling provides estimates of abundance, density, and detection probability based on the distance from the survey location to the detected individual. Estimating detection probability addresses the imperfect detection of birds on surveys (e.g., some individuals go undetected because, for example, a male may not vocalize during the survey; MacKenzie *et al.* 2002). We used the "Distance" package in R for the distance sampling analysis (Miller 2019). We ran four models for each year: uniform key function with cosine adjustments, half-normal key function with cosine adjustments, half-normal key function with Hermite polynomial adjustments, and hazard-rate key function with polynomial adjustments, following recommendations by Thomas *et al.* (2010). Key functions provide a baseline shape of the relationship between detection probability and distance from survey location. We truncated the distance to 55 m (excluding males detected 56–75 m) to improve model performance while retaining sufficient detections (i.e., 64 in 2019, 68 in 2020). Because our sample size was small, we did not include covariates in models. We compared relative model performance using AICc (Akaike 1974; Burnham and Anderson 2002) and considered models with ΔAICc <7 to have some support compared to the best-supported model (Burnham *et al.* 2011). We calculated ΔAICc using the *aictabCustom* function in the R package "AICcmodavg" (Mazerolle 2019). We used the *gof_ds* function to apply the Cramer-von Mises test to evaluate goodness-of-fit and considered P values < 0.05 as evidence of poor model fit. We used transect length and the area of open pasture in the distance sampling analysis to enable estimates of male Bobolink abundance for the area of open pasture. We include estimates of male Bobolink density for future use by other researchers.

For comparison with results from the distance sampling analysis, we summed the maximum number of males detected ≤75 m on either side of the transect line in each field across the first and second transect visit in 20 fields because Campomizzi *et al.* (2020) found the maximum number of males detected was a reasonable estimate of the number of Bobolink territories in a surveyed area.

We did not detect enough males on the third and fourth transect visit to estimate abundance with distance sampling (Buckland *et al.* 1993b) because most

Bobolink had dispersed after grazing. Thus, for comparison with the first and second transect visit in 2019, we summed the maximum number of males detected ≤75 m on either side of the transect line in each field across the third and fourth transect visit in grazed and ungrazed fields because there was only one ungrazed field. In 2020, we used a before-after-control-impact design (Morrison *et al.* 2008) with males detected ≤75 m on either side of the transect line because about half of fields had been grazed when we made the third and fourth transect visit. For the 17 fields with comparable data in 2020, we summed the maximum number of males detected in each field across the first and second transect visit to provide data before the grazing impact occurred separately for fields that remained ungrazed and those that were grazed by the third and fourth visit. We also summed the maximum number of males detected in each field across the third and fourth transect visit to provide data after the grazing impact occurred separately for fields that were ungrazed and grazed at that time. We used two Wilcox paired-sample tests (Zar 1999), the first to assess if the maximum number of male Bobolink detected differed between visits one and two compared to visits three and four for fields that remained ungrazed (controls) and the second test for those that had been grazed (impact) by transect visit three and four. Although this approach did not model the imperfect detection of birds on surveys, it provided direct comparisons and an index of abundance based on a fixed distance from the transect line (Johnson 2008; Hutto 2016).

Repeat visits to spot map Eastern Meadowlark territories enabled us to determine the number of territories across the pasture based on GPS location clusters and the number of individuals detected on each visit. We combined observations of evidence of nesting and fledging from spot mapping with nest monitoring data to provide an estimate of the number of territories that had nests and fledged young. For Bobolink and Savannah Sparrow, we used Fisher's exact tests to assess if the proportion of territories with evidence of nesting from spot mapping was different between territories in grazed and ungrazed fields for each species (Zar 1999). We did not assess the relationship between the spatial distribution of breeding territories and field and landscape variables.

For each Eastern Meadowlark nest with sufficient data, we estimated first-egg date (n = 12) and fledge date (n = 7) based on our observations and the literature (one egg laid/day, average clutch size of five eggs, 14 days of incubation, 11 days from hatch to fledge; Jaster *et al.* 2020). For each Savannah Sparrow nest with sufficient data, we estimated first-egg date (n = 21) and fledge date (n = 6) based on our observations and the literature (one egg laid/day, average clutch size of four eggs, 12 days of incubation, 10 days from hatch to fledge; Wheelwright *et al.* 2020). For each Bobolink nest with sufficient data, we estimated first-egg date (n = 3) based on our observations and the literature (one egg laid/day, average clutch size of five eggs, 12 days of incubation, 11 days from hatch to fledge; Renfrew *et al.* 2020). We did not monitor any Bobolink nests that were confirmed to have fledged young. Results herein are observed nest success uncorrected for exposure days (Mayfield 1961; Dinsmore *et al.* 2002).

We report median vegetation height to assess differences among ungrazed fields, grazed fields with Bobolink, and grazed fields without Bobolink. We used a t-test for each year to test if mean vegetation height was different between grazed fields with Bobolink and grazed fields without Bobolink (Zar 1999).

Results

Observed abundance and occurrence

The sum of the maximum number of male Bobolink we detected in each field was 68 in 2019 and 58 in 2020 across the first and second transect visit before grazing occurred in 20 fields. These 20 fields contained 69, 100 m transect sections. In both years, Bobolink was unevenly distributed across the pasture. During the third and fourth transect visit, the maximum number of male Bobolink we detected was lower in grazed fields than in ungrazed fields. On the third and fourth visits in 2019, we detected two males on three 100 m transect sections in an ungrazed field and 10 males on 56 transect sections in 16 grazed fields. In 2020, the number of males detected decreased by 73% (26 to seven males on 32 transect sections) in fields that were grazed by transect visit three and four (P = 0.013). In contrast, the number of males detected in fields that remained ungrazed was similar across visits one and two compared to visits three and four (19 to 24 males on 24 transect sections; P = 0.281).

In 2020, we detected Savannah Sparrow on 83% of transect sections during visit one and 76% during visit two (n = 71 100-m transect sections). On the third transect visit, we detected Savannah Sparrow on 100% of transect sections in ungrazed fields (n = 30 transect sections) and 91% in grazed fields (n = 34 transect sections). On the fourth transect visit, we detected Savannah Sparrow on 100% of transect sections in ungrazed fields (n = 25 transect sections) and 92% in grazed fields (n = 37 transect sections).

Estimated Bobolink abundance

In 2019, the only acceptable distance sampling model (goodness-of-fit test P = 0.119) had a hazard-rate key function and polynomial adjustment (scale coefficient 4.231, SE 0.125; shape coefficient 3.754, SE 3.747); other models had SEs that were orders of magnitude higher than coefficients. Based on the only acceptable model, detection probability was 1.0 and the estimated number of male Bobolink across the 205 ha of open pasture was 86 (95% CI 67–112; Figure 1). Estimated density of male Bobolink in 2019 was 0.42/ ha, based on this model.

In 2020, both distance sampling models with a half-normal key function were simplified to remove adjustments based on the internal model selection process of the distance sampling function, resulting in only one half-normal model being used. Multiple models had some support because the three models used had ΔAICc < 7 (Table 1). However, results were fairly consistent among the three models; detection probability was 0.92–1.0 and estimated abundance of male Bobolink in the 205 ha of open pasture was 92–100 (Table 1). The best-supported model had a uniform key function, a cosine adjustment coefficient of 0.088 (SE 0.169), and 95% CI for male abundance was 67–148 (Figure 1). Estimated density of male Bobolink was 0.45–0.49/ha in 2020, based on the three models receiving some support.

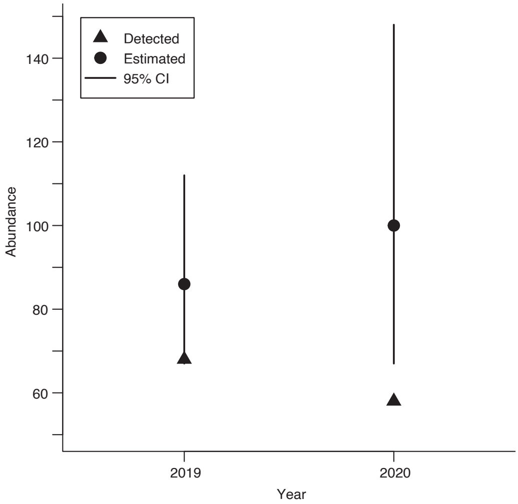

FIGURE 1. The number of male Bobolink (*Dolichonyx oryzivorus*) detected and estimated in 2019 and 2020 in the Grey Dufferin Community Pasture, southern Ontario, Canada. The number detected was based on the maximum number of males detected in each of 20 fields across two visits to transect surveys each year. The estimated abundance was based on the best-supported distance sampling model from analysis of transect survey data, specified for the 205 ha of open pasture each year.

Spot mapping

We detected evidence of nesting more frequently in Bobolink territories in ungrazed fields (50%, *n* = 18 territories) than in grazed fields (16%, *n* = 19 territories; *P* = 0.038; Figure 2). Similarly, we detected evidence of nesting more frequently in Savannah Sparrow territories in ungrazed fields (60%, *n* = 10 territories) than in grazed fields (0%, *n* = 10 territories; *P* = 0.011; Figure 2b). We did not detect evidence of fledging from one visit to each sampled Bobolink and Savannah Sparrow territory for spot mapping.

We estimated 21 Eastern Meadowlark territories across the community pasture. Weekly visits to fields indicated that the number and distribution of Eastern Meadowlark territories was fairly consistent throughout the breeding season. Eastern Meadowlark continued to use and nest in fields that had been grazed, even after nests failed to fledge young. We confirmed the presence of two nesting females in six of the territories and suspected a second female in another three territories; however, these were unconfirmed. We found evidence of nesting in all Eastern Meadowlark territories and evidence of fledged young in 67% (*n* = 21) of territories, based on spot mapping and nest monitoring.

Nest monitoring

We monitored 16 Eastern Meadowlark nests, 26 Savannah Sparrow nests, and three Bobolink nests across the community pasture in 2020 (Table 2). First-egg dates ranged from 5 May to 13 July (*n* = 12) for Eastern Meadowlark, 22 May to 14 July (*n* = 21) for Savannah Sparrow, and 30 May to 10 June (*n* = 3) for Bobolink. Our infrequent visits to nests resulted in few nests with estimated fledge dates. Fledge dates ranged from 3 June to 30 July (*n* = 7) for Eastern

TABLE 1. Model results for distance sampling from transect surveys for male Bobolink (*Dolichonyx oryzivorus*) in the Grey Dufferin Community Pasture, southern Ontario, Canada in 2020.

Key function	Adjustment	*K**	ΔAICc†	*P*‡	Detection§	Abundance‖
Uniform	Cosine	2	0.00	0.95	0.92	100
Half-normal	None	2	0.22	0.89	0.97	95
Hazard-rate	None	3	2.23	0.78	1.00	92

*Number of parameters in model.
†AICc for best-supported model = 548.91.
‡Cramer-von Mises goodness-of-fit test.
§Estimated average probability of detection for male Bobolink on transect surveys.
‖Estimated abundance of male Bobolink in the 205 ha of open pasture.

Meadowlark and 14 June to 3 July ($n = 6$) for Savannah Sparrow. We observed evidence of nesting activity for all three species throughout the pasture before any grazing occurred; however, we located few Bobolink and Savannah Sparrow nests relative to the number of individuals in the pasture because we were not actively searching for their nests.

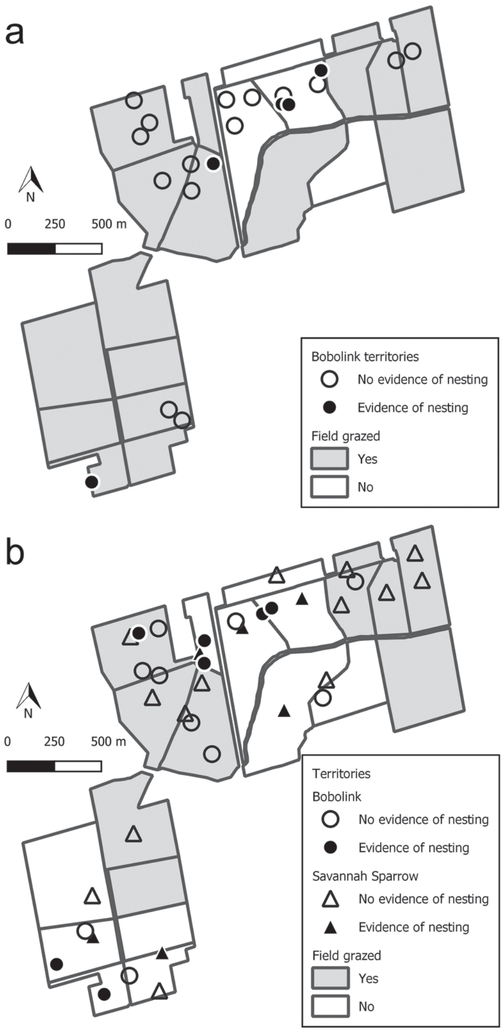

Figure 2. Approximate locations of Bobolink (*Dolichonyx oryzivorus*) territories selected for sampling of breeding status at the Grey Dufferin Community Pasture, southern Ontario, Canada in a. 2019 and b. 2020, also showing locations of Savannah Sparrow (*Passerculus sandwichensis*) territories selected for sampling. We visited each sampled territory once and used behavioural observations to assess if there was evidence of nesting. Symbols show locations of sampled territories, not territory size; sampled territories were distributed across fields as much as possible, but not all fields had territories when sampling occurred. We indicate whether a field had been grazed as of when we sampled each territory: a: 21–28 June or by 28 June for fields where we did not sample territories; b: 14–16 June for Savannah Sparrow and 20–25 June for Bobolink or by 25 June for fields where we did not sample territories.

Predation was the most common reason for nest failure ($n = 14$; Table 2) that we were able to identify across all monitored nests; we are uncertain of the predator species, but occasionally detected potential mammalian and avian nest predators in the community pasture. We suspect grazing caused a substantial amount of nest failure, but infrequent visits to check nests (~once per week) and our inability to check nests in fields where cattle were actively grazing resulted in some nests with unknown outcome ($n = 11$; Table 2) or unknown reason for failure ($n = 3$; Table 2).

Vegetation

In 2019, median vegetation height in the only ungrazed field was 0.70 m. Vegetation in 2019 was 32% taller in grazed fields where we detected Bobolink (0.58 m) compared to grazed fields without Bobolink detections (0.44 m; $t_{50} = 2.95$, $P = 0.005$). In 2020, median vegetation height in ungrazed fields was 0.72 m. Vegetation in 2020 was 16% taller in grazed fields where we detected Bobolink (0.52 m) compared to grazed fields without Bobolink detections (0.45 m; $t_{57} = 2.36$, $P = 0.022$).

Discussion

The community pasture provides nesting habitat for ground-nesting grassland birds. Despite the negative impacts of grazing on nests and the response to grazing varying by species, our results show that some birds are nesting successfully under the current management strategy. Additionally, rotational grazing creates opportunities to increase nest success at the community pasture by adjusting management in target fields with a higher abundance of nesting birds.

Our results provide empirical evidence of the impact of cattle grazing on multiple species of nesting grassland birds and the conditions under which nesting can occur in rotationally grazed pasture. Few Bobolink remained in fields after the first grazing occasion and they remained in fields where vegetation was taller compared to other grazed fields. In contrast, the number of Eastern Meadowlark territories did not change due to grazing. Most territories remained throughout the breeding season and pairs attempted to re-nest after suspected failure due to grazing. However, after grazing, some Eastern Meadowlark territory boundaries shifted, and some territories were apparently temporarily absent. We did not monitor Savannah Sparrow closely enough to assess their response to grazing; however, they continued to occur in most fields after grazing occurred.

TABLE 2. Summary of grassland bird nests monitored and reasons for nest failure at the Grey Dufferin Community Pasture, southern Ontario, Canada in 2020.

Species	No. (%) of nests				No. of failed nests			
	Monitored	Fledged	Failed	Outcome unknown	Predated	Trampled	Abandoned	Unknown
Savannah Sparrow (*Passerculus sandwichensis*)	26	6 (23)	11 (42)	9 (35)	8	1	2	0
Eastern Meadowlark (*Sturnella magna*)	16	7 (44)	8 (50)	1 (6)	5	0	0	3
Bobolink (*Dolichonyx oryzivorus*)	3	0 (0)	2 (67)	1 (33)	1	0	1	0

Our observations are consistent with previous research showing that nesting Eastern Meadowlark are better able to tolerate vegetation changes due to grazing than Bobolink and typically do not disperse from fields that are grazed at a light or moderate intensity. There is evidence that Eastern Meadowlark nested in pastures that were lightly to moderately grazed in Missouri, suggesting they remained after grazing occurred (Skinner 1975). In contrast, Campomizzi *et al.* (2019) reported that nesting Bobolink typically dispersed after their nests were trampled by cattle in fields that were moderately to heavily grazed in rotationally grazed pastures in eastern Ontario. Although some female Bobolink renested after grazing occurred in rotationally grazed pastures in a study in Vermont, most did not renest (Perlut *et al.* 2006). The response of nesting Bobolink to grazing undoubtedly depends on the grazing intensity and vegetation conditions, as supported by our results showing vegetation was taller in grazed fields where we detected Bobolink than in fields without Bobolink detections after grazing occurred. Although nesting Eastern Meadowlark can tolerate some grazing, there is evidence that they disperse from breeding territories following mowing of restored grassland in the Great Plains (Granfors *et al.* 1996). Of the three species we studied, Savannah Sparrow appears the most tolerant of grazing; they renested shortly after grazing occurred in rotationally grazed pasture and even after haying in a study in Vermont (Perlut *et al.* 2006). Understanding how nesting grassland birds respond to grazing is important for conservation efforts because the response varies by species, depends on when grazing occurs during the nesting season, and depends on how much vegetation remains after a field is grazed.

We are uncertain if Eastern Meadowlark in the community pasture are producing enough young to maintain a stable population, which has conservation implications. Although we observed evidence of fledged young in 67% of territories, we did not collect information about fecundity to understand population dynamics. In contrast to our results that show if young fledged in each territory, breeding success is often presented as a percent of nests that fledge ≥1 young or nest survival (both of which also have limitations; Mayfield 1961; Jones *et al.* 2005). For example, a large study that included active agricultural fields reported 18% of 170 Eastern Meadowlark nests fledged young in pasture compared to 38% of 280 nests in other landcover types, including hayfield and fallow fields (Roseberry and Klimstra 1970). Additionally, Eastern Meadowlark females commonly attempt to raise two broods of young per breeding season (Jaster *et al.* 2020). A study on land enrolled in the Conservation Reserve Program in Missouri estimated that Eastern Meadowlark would need to fledge 1.03–1.57 female offspring/adult female/year to sustain the population, given various assumptions including two broods attempted/female/year (McCoy *et al.* 1999). Although we did not monitor Eastern Meadowlark nesting closely enough to document all nesting attempts in the community pasture in 2020, we observed multiple nesting attempts by the same female in several territories. We documented only one instance of a female fledging two broods; however, the first successful brood was only a partial brood because some of the young were trampled by cattle. More detailed information about the number of young fledged/breeding female and multiple broods is needed to better understand how well Eastern Meadowlark is reproducing in the community pasture in particular and in pastures that are rotationally grazed by beef cattle in general.

Our evidence of more frequent nesting in ungrazed than grazed fields supports previous research on Bobolink and Savannah Sparrow. It is fairly common for cattle to cause nest failure in Bobolink and Savannah Sparrow in rotationally grazed fields in eastern North America (Perlut *et al.* 2006; MacDonald and Nol 2017; Campomizzi *et al.* 2019; Fromberger *et al.* 2020). Although we did not monitor nests frequently enough to assess reasons for nest failure as well as previous studies, we suspect grazing was the second most common reason for nest failure after predation. Additionally, we did not study the impact of reduced vegetation cover from grazing on the risk of nest predation because it was beyond the scope of our study. Lastly, we did not assess other factors that may have influenced nesting success, such as weather. Our results from nest monitoring at the community pasture should be interpreted with caution because sample sizes were small, visits to nests were too infrequent to determine nest fate in some cases, and we reported observed nest success, which can be biased because it is uncorrected for exposure days (Mayfield 1961; Dinsmore *et al.* 2002).

Conservation implications

In addition to their intended purpose of providing forage for livestock, pastures rotationally grazed by beef cattle can provide successful nesting habitat for ground-nesting grassland birds, under particular conditions. Rotational grazing enables targetting particular fields for conservation (e.g., those with higher abundance of nesting grassland birds) if there is some flexibility in the timing and duration of grazing. Fields with a higher abundance of nesting grassland birds can be placed last in the order of grazing rotation to delay grazing as long as possible, potentially giving birds time to fledge young. Additionally, because we found that vegetation was taller in fields where Bobolink remained after grazing compared to fields without detections, modifying the timing and intensity of grazing during the nesting season could benefit Bobolink. For example, grazing fields lightly in spring, leaving enough vegetation for Bobolink to remain and renest if nests are trampled, could be an effective strategy (Campomizzi *et al.* 2019). Ensuring enough vegetation remains for nesting Bobolink after light spring grazing occurs is challenging because of a lack of data about vegetation height and density. Rest period is also an important consideration to ensure birds have enough time to renest before subsequent grazing occurs. A rest period of six weeks or more should provide ample time for renesting, based on anecdotal observations and Bobolink nesting phenology, although information on the response of grassland birds to rest period is limited. Light spring grazing and typical rotational grazing have some compatibility with nesting Eastern Meadowlark. However, as with Bobolink, some nests are trampled by cattle and a sufficient rest period (e.g., six weeks) is needed to provide enough time for birds to fledge young from renesting attempts before a second grazing occurs. The conservation implications of our research will vary across geographic regions and depend on particular circumstances, including annual fluctuations in weather and vegetation growth.

Author Contributions

Conceptualization: Z.M.L. and A.J.C.; Data Curation: A.J.C. and Z.M.L.; Formal Analysis: A.J.C.; Funding Acquisition: Z.M.L. and A.J.C.; Investigation: Z.M.L. and A.J.C.; Methodology: A.J.C. and Z.M.L.; Project Administration: Z.M.L. and A.J.C.; Resources: Z.M.L. and A.J.C.; Supervision: Z.M.L. and A.J.C.; Validation: A.J.C. and Z.M.L.; Visualization: A.J.C. and Z.M.L.; Writing – Original Draft: A.J.C.; Writing – Review & Editing: A.J.C. and Z.M.L.

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Natural and human-made nesting habitat use by Bank Swallow (*Riparia riparia*) in Canada

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Abstract

Bank Swallow (*Riparia riparia*) is a Threatened migratory bird in Canada that nests colonially in burrows excavated in both human-made and natural banks. Until the mid-20th century, nest record cards reported 60% of Bank Swallows in Canada nested in human-made habitats. Here we provide an update on the proportion of Bank Swallow nesting colonies in natural and human-made habitats in Canada's provinces and territories based on data from a variety of sources including breeding bird atlases and eBird. Bank Swallow nesting colonies reported from 2001 to 2017 throughout Canada indicate a reversal in the dominant type of habitat used for nesting, with a 56% probability that nesting occurrences are now found in natural habitats. We discuss possible mechanisms responsible for the apparent reversal and recommend that natural nesting habitat be formally protected and restored where it has been altered, especially where co-benefits include climate change resiliency. With the support of landowners and industry, active colonies in human-made habitats will likely make an important contribution to a resilient Bank Swallow population, the majority of which presently appears to nest in natural habitats across the country.

Key words: Bank Swallow; nesting habitat; *Riparia*; anthropogenic habitat; natural habitat; migratory bird; species-at-risk

Résumé

L'Hirondelle de rivage (*Riparia riparia*) est un oiseau migrateur au statut menacé au Canada qui niche de façon coloniale dans des terriers creusés dans des fronts de talus tant naturels qu'artificiels. Jusqu'au milieu du 20e siècle, les fiches de nidification indiquaient que 60 % des Hirondelles de rivage au Canada nichaient dans des habitats artificiels. Nous présentons ici une mise à jour de la proportion des colonies d'Hirondelles de rivage nichant dans des habitats naturels et artificiels dans les provinces et territoires du Canada, en nous basant sur des données provenant de diverses sources, dont les atlas des oiseaux nicheurs et eBird. Les colonies de nidification d'Hirondelles de rivage signalées de 2001 à 2017 dans l'ensemble du Canada indiquent un renversement du type dominant d'habitat utilisé pour la nidification, avec une probabilité de 56 % que les occurrences de nidification se trouvent maintenant dans des habitats naturels. Nous discutons des mécanismes possibles responsables de ce renversement apparent et recommandons que l'habitat naturel de nidification soit officiellement protégé et restauré là où il a été altéré, surtout lorsque les co-bénéfices incluent la résilience au changement climatique. Avec le soutien des propriétaires fonciers et de l'industrie, les colonies actives dans les habitats artificiels contribueront probablement de manière importante à la résilience de la population d'Hirondelles de rivage, dont la majorité semble actuellement nicher dans des habitats naturels à travers le pays.

Mots-clés : Hirondelle de rivage; habitat de nidification; *Riparia*; habitat artificiel; habitat naturel; oiseau migrateur; espèce en péril

Introduction

Bank Swallow (*Riparia riparia*) is a colonial migratory bird whose breeding range in Canada extends to all provinces and territories except Nunavut. The species nests in burrows dug in vertical or near-vertical banks. Nesting burrows are excavated in friable soils with small particles, such as mixtures of sand and silt (Bols 2017; Garrison and Turner 2020). The presence of this type of substrate is associated with areas where alluvial soils are exposed or near the ground surface (COSEWIC 2013; Bols 2017; Burke 2017; Falardeau 2019). In natural environments, Bank Swallows nest on the banks of water bodies where hydrologic forces expose the soft sediments of the slopes. These sites are relatively ephemeral in nature due to the dynamic erosion of the slopes (Cadman and Lebrun-Southcott 2013). Some human activities re-create, incidentally, the conditions conducive to Bank Swallow nesting (Ghent 2001; Bols 2017; Burke 2017). The species nests in aggregate pits (e.g., sand or gravel), road cuts, and piles of unconsolidated material (Erskine 1979; Peck and James 1987; Campbell *et al.* 1997; Bols 2017). Structures specifically designed to mimic nesting habitat, e.g., a vertical wall with openings, have been colonized by Bank Swallows (Laberge and Houde 2015). In both natural and human-made nesting environments, Bank Swallows feed on insects captured on the wing in open habitats near the colony, such as wetlands, grasslands, and cropland (Falconer *et al.* 2016; Saldanha 2016; Garrison and Turner 2020).

Due to a population decline of 31% from 2001 to 2011 (COSEWIC 2013; a substantial 98% decline from 1970–2011), Bank Swallow was listed as a Threatened species in Canada under the *Species at Risk Act* in 2017 (SARA Registry 2021). A more recent estimate suggests a 93% population decline from 1970 to 2019 (Smith *et al.* 2020). Reports on the use of different habitat types by Bank Swallows have been published (Peck and James 1987; Campbell *et al.* 1997), but the only nationwide study is over 40 years old (Erskine 1979; see COSEWIC 2013). Based on data reported to the Nest Record Scheme through 1974 (starting in 1955 in British Columbia and in the late 1960s in Quebec; Downes 2000), only 40% of Bank Swallow nests were located in natural habitat and 60% were in human-made settings in Canada (Erskine 1979). The proportion of nests in natural sites was greater in the Maritimes, where coastal cliffs are abundant. The proportion of nests in human-made habitat was greater in British Columbia, Quebec, and Ontario, where the human population was larger and landscape alteration was greater. The highest proportion of nests in human-made habitats observed by Erskine (1979) was in British Columbia. Campbell *et al.* (1997) reported 815 colony observations from the Nest Record Scheme in British Columbia, of which 59% of the 481 colonies assigned to a habitat type were in human-made habitat. In Ontario, the Nest Record Scheme reported 48% of nesting occurrences (colonies or isolated nests) in human-made habitats and 52% in natural habitats (Peck and James 1987). Information on the recent, nationwide and regional distribution of the species' breeding population in relation to human-made versus natural nesting habitat is unknown, but would be useful for the conservation of the species.

Our goal is to update the proportion of Bank Swallow nesting colonies found in natural compared to human-made habitats in Canada. We compiled observations of Bank Swallow nesting colonies made between 2001 and 2017 from a variety of sources, including breeding bird atlases and eBird, and assigned each colony observation as being in natural or human-made habitat. We discuss possible mechanisms responsible for the apparent patterns we uncovered and we end by using our findings to make conservation recommendations to assist with the species' recovery in Canada.

Methods

Data acquisition

Data used are observations of colonies (active or inactive) of Bank Swallow or other evidence of confirmed nesting (such as adults leaving or entering nest sites, or adults carrying food for young), reported from 2001 to 2017 in Canadian provinces and territories. This period begins with the formal onset of the second Alberta (a pilot field season was held in 2000) and Ontario breeding bird atlases. Colony observations were obtained through an extensive search of data sources in Canada, including provincial conservation data centres, the NatureCounts database managed by Birds Canada, eBird checklists, and species-specific inventories from regional offices of the Canadian Wildlife Service (see Acknowledgements). Data from the breeding bird atlases indicating a specific nesting site for rare or colonial species were included in the analysis, but not the nesting indices reported at the scale of 10 km × 10 km atlas squares. eBird records were screened in a three-step process. First, records with blank checklist or species remark fields were excluded, as they did not provide information on nest habitat or bird behaviour. Second, records submitted using the eBird smartphone application were retained and assigned either a 100 m spatial uncertainty for stationary, casual, historical, or incidental protocols, or the travel distance plus 100 m for the travelling protocol. Third, remaining eBird records not submitted using a smartphone were assessed for nest habitat location remarks, validated on a map (see *Assignment of nesting habitat type*), and assigned a 100 m spatial uncertainty. The retained eBird and other data occurrences were required to have a spatial uncertainty of no more than 700 m. We limited this spatial uncertainty distance to the sum of a minimum foraging distance of 500 m (Falconer *et al.* 2016) and the detection distance class of 200 m assigned to Bank Swallow (Blancher *et al.* 2013). The assessment of data quality described above was implemented in addition to the initial vetting of data conducted by regional eBird experts or atlas coordinators. No data meeting the criteria for analysis were available for Nunavut. Following Erskine's (1979) methodology, observations from the same site within a single year were consolidated to a single colony observation for analysis, but observations from the same site between years were retained as separate colony observations in each year. In addition, observations indicating burrow clusters within the same colony were simplified to one colony observation per year by merging occurrences within ~10 m, or four decimal places of degree coordinates. The dataset contains 1898 unique colony observations.

Assignment of nesting habitat type

Each colony was assigned to a natural or human-made nesting habitat. Most observations could be assigned based on a habitat description. Key words such as gravel, pit, aggregate, dirt, pile, quarry, roadside, and construction, or their equivalent in French suggested nesting in a human-made site. Key words such as shoreline, cliff and river, or their equivalent in French suggested nesting in a natural site. The assignment of habitat type was validated by overlaying observations on aerial images in Google Earth (version 7.3.3.7786, California, USA; Figure S1). Data that did not specify the type of nesting habitat or for which visual examination of the site was inconclusive were classified as "unknown habitat".

Analyses

For a given province or territory, the proportion of colonies in each nesting habitat type represents the number of known colonies per habitat type divided by the total number of known colonies (excluding colonies classified as unknown habitat type) in that province or territory (Table S1). Erskine (1979) presented Nest Record Scheme data by grouping the provinces into four regions: Maritimes (excluding limited data from Newfoundland), Quebec and Ontario, Prairies, and British Columbia. For comparison with historical data, recent colony occurrences have been grouped according to these regions (Figure 1). These data exclude Newfoundland and Labrador, Yukon, and the Northwest Territories.

An important limitation of the dataset is the variable quality or lack of information on the number of breeding pairs in each colony. Bank Swallow colony size can vary from a few to several thousand nests (Peck and James 1987) and is highly variable by region, size of nesting habitat, and habitat type (Cadman and Lebrun-Southcott 2013; Bols 2017;

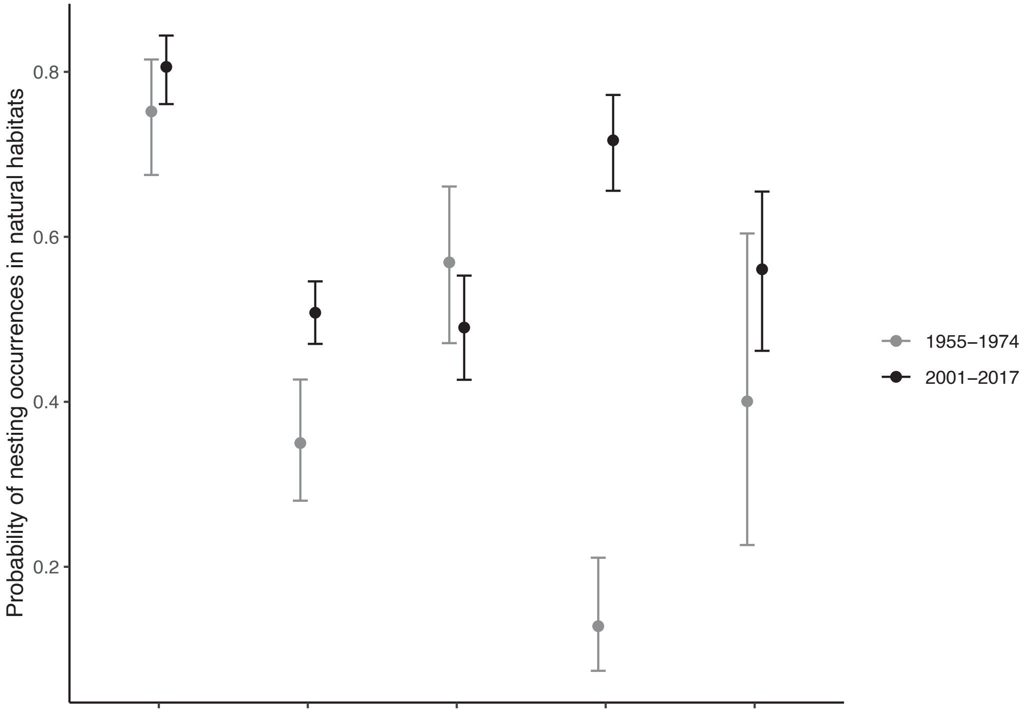

FIGURE 1. Probability of finding Bank Swallow (*Riparia riparia*) colonies in natural settings in the Maritimes, Quebec and Ontario, the Prairies, British Columbia, and nationally (excluding Yukon, Northwest Territories, and Newfoundland and Labrador). Probabilities are shown with their 95% CIs from the binomial model resulting from the sample size and Partners in Flight confidence limits.

Burke 2017). Thus, the proportions of colonies are not directly comparable to the proportions of nests by habitat type reported by Erskine (1979). The latter is a better indicator of the actual proportion of the breeding population using a habitat type, provided that the sample of nests assigned to habitat types is representative of the species' distribution. The historical data presents the number of nests assigned to each nesting habitat type and the average colony size by region (Erskine 1979). To allow comparison with our data, we divided the number of nests by the average colony size reported by Erskine (1979) in a given region to estimate the number of colonies found in each habitat type (Table S2). This conversion assumes equal median colony sizes in natural and human-made settings, although evidence from Ontario suggests colonies in natural settings can be 4.5 times larger than in human-made settings (Burke 2017).

We estimated a national probability of colonies being in natural settings by weighting regional colony occurrences with proportions of the Bank Swallow population in each region based on Partners in Flight (PIF) estimates (Population Estimates Database, Version 3.1; Partners in Flight 2020). We applied those proportions to both historical and present-day datasets, assuming a negligible change in distribution of the Bank Swallow population between regions.

We conducted a binomial generalized linear model with a logit link function to determine how time period, region, and their interaction affected the probability of a colony having been located in natural habitat. An ANOVA was used to identify that the time period/region effect in the model was significant. We then performed a least square means *post-hoc* test to determine which regions were significantly different between time periods using the "lsmeans" package (Lenth 2016). All analyses were performed in R version 4.1.0 (R Core Team 2021). Statistical significance was accepted at $P < 0.05$.

Results

Nationally, our dataset contains a total of 1802 colonies assigned to nesting habitat type (i.e., natural or human-made). At the national level, excluding Yukon, Northwest Territories, and Newfoundland and Labrador, we found that the probability of finding Bank Swallow colonies in natural settings increased from 40% (95% CI: 23–60%; historical data from Erskine 1979) to 56% (95% CI: 46–65%; 2001–2017 data). However this change is not statistically significant (Figure 1). The proportions of Bank Swallow colonies in natural and human-made habitats vary greatly among provinces and territories (Table 1). Saskatchewan had the fewest observations available ($n = 17$; no unassigned observations). Ontario had the most observations ($n = 391$; 39 unassigned observations). Yukon, Northwest Territories, British Columbia, Alberta, Saskatchewan, Ontario, New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland and Labrador have a higher proportion of colonies in natural settings than in human-made settings. Manitoba and Quebec are the only two provinces where the proportion of colonies is larger in human-made settings.

We found some significant differences in the proportion of colonies found in natural habitat across regions, and the magnitude of those regional differences has changed between the historical and the current dataset ($\chi^2_3 = 74.92$, $P < 0.001$). The proportion of colonies found in natural habitat increased over time in British Columbia ($z = 8.343$, $P < 0.0001$) and

Table 1. Number of Bank Swallow (*Riparia riparia*) colonies in human-made or natural settings reported between 2001 and 2017 in Canada.

Region	Human-made habitat	Natural habitat	Total number of assigned colonies	Number of colonies in unknown habitat
Yukon Territory	50	199	249	2
Northwest Territories	12	41	53	0
British Columbia	65	165	230	20
Alberta	6	59	65	8
Saskatchewan	7	10	17	0
Manitoba	109	48	157	7
Ontario	173	218	391	39
Quebec	150	116	266	6
New Brunswick	28	111	139	4
Nova Scotia	36	52	88	5
Prince Edward Island	4	119	123	4
Newfoundland and Labrador	11	13	24	1
National	651	1151	1802	96

the Quebec–Ontario region ($z = 3.562$, $P = 0.0004$), but has not changed significantly in the Prairies ($z = -1.336$, $P = 0.1816$) and the Maritimes ($z = 1.339$, $P = 0.1806$; Figure 1).

Discussion

Our more recent data from 2001 to 2017 indicate that a larger proportion of Bank Swallows now nest in natural habitats than in human-made habitats on a national scale, whereas the reverse was apparent based on Erskine's historical data from 1955 to 1971 (see *Sources of bias* below). The proportions of colonies suggest a recent reversal from the historical occupancy of these two nesting habitats. The switch to natural nesting habitats is stronger when all provinces and territories are considered, with a proportion of 63.9% of colonies in natural settings. However, this proportion must be considered in light of the regional distribution of the Bank Swallow breeding population. In comparison to Erskine's (1979) historical data, the probability of finding Bank Swallow colonies in natural settings increased in the Maritimes, Quebec and Ontario, and British Columbia, but not on the Prairies (Figure 1).

Data from Ontario (Peck and James 1987) and British Columbia (Campbell *et al.* 1997) suggest a transition in the proportions of habitat use over time. Peck and James (1987) found 48% of colonies in human-made settings using the Ontario Nest Record Scheme, compared with 44.2% of colonies in our dataset, which contrasts with nearly two-thirds of nests reported in human-made settings in Quebec and Ontario (Erskine 1979). In British Columbia, the proportion of the breeding population reported in human-made settings decreased from 87% (Erskine 1979) to 59% (Campbell *et al.* 1997) and then to 28.3% (our dataset).

The large change in habitat use over time could be explained by a change in survey efforts in natural and/or human-made settings (bias), and/or a change in the availability of habitat types (actual change). Humans tend to frequent human-modified landscapes and make observations there while natural habitats are often harder to access leading to a historical underrepresentation of natural colonies. Status reports and recovery strategies for Bank Swallows in Canada indicate an overall loss of natural and human-made habitats over the past several decades (COSEWIC 2013; Falconer *et al.* 2016). In Europe, regional Bank Swallow declines have been associated with changes in aggregate resource extraction industry practices (Lind *et al.* 2002; Heneberg 2013). For example, in Italy, inactive quarries do not provide adequate nesting habitat for Bank Swallows if not restored (Masoero *et al.* 2019). In populated areas of Canada, measures to control hydrological regimes and shoreline erosion continue to be implemented and could contribute to the loss of natural nesting habitat (COSEWIC 2013; Falconer *et al.* 2016). On the Atlantic coast, the increased risk of erosion associated with climate change may accelerate shoreline stabilization by heavy engineering structures (Boyer-Villemaire *et al.* 2016) leading to a permanent decrease in nesting habitat.

The availability of human-made habitats has probably changed markedly since the 1970s and reduced the proportion of colonies found in this type of habitat. Notable changes surrounding the aggregate resource industry are attributable to the introduction of regulations on the development and rehabilitation of aggregate pits. In Ontario, the first regulations came into effect in 1971 with the *Pits and Quarry Control Act* (Falconer *et al.* 2016). Under this Act, rehabilitation measures such as slope grading and erosion control were implemented, reducing the habitat available for Bank Swallow (Falconer *et al.* 2016). Legislation was strengthened in 1990 with the *Aggregate Resources Act*, leading to increased rehabilitation measures and the closure of many pits and quarries (Falconer *et al.* 2016). In Quebec, similar requirements were established under the *Environment Quality Act* in 1981 (COSEWIC 2013). In several Canadian jurisdictions, workplace safety standards require the grading of aggregate pit walls at the angle of repose of the sediments, i.e., an angle of 70° or less, reducing the risk of sediment slumping. Following the closure of extraction sites, slopes generally slump and stabilize within a few years. Maintenance and reclamation requirements for aggregate pits likely reduce the period when the slopes are suitable for nesting.

Historically, road cuts were the most common nesting habitat used by Bank Swallows in British Columbia (Erskine 1979; Campbell *et al.* 1997) and in Ontario they accounted for one-quarter of nest occurrences in the 1930s (Falconer *et al.* 2016). In Newfoundland and Labrador, road construction in the 1960s and 1970s is believed to have temporarily created suitable nesting habitat for Bank Swallows (Munro 2009). However, modern industry standards for transportation corridor development require the grading of slopes along roads and railroads (Transportation Association of Canada 2017), diminishing the attractiveness of these sites as nesting habitat. For example, in Ontario, no occurrences of Bank Swallow in roadside trenches have been reported since the 1990s (Falconer *et al.* 2016). Our data indicate a negligible proportion of colonies located in roadside trenches compared to aggregate pits. We note that in the Columbia and Kootenay River valleys of British Columbia, some road and railroad cut faces have been occupied by Bank Swallow colonies for several decades (Campbell *et al.* 1997) despite the lack of historical human intervention to create or enhance vertical walls along the railroads. It appears that the nesting habitat of colonies historically assigned to human-made habitat can be maintained naturally over several decades in the presence of wind or rain erosion. For comparison with historical records, we assigned such occurrences to human-made settings. However this habitat may be considered in the future as a type of natural habitat (e.g., because a railway company may have incidentally enhanced Bank Swallow habitat that was previously there) and receive a similar level of protection as other natural nesting habitats.

Finally, the increase in the proportion of Bank Swallows nesting in natural settings does not necessarily represent an absolute increase in the number of birds in this type of habitat. In Ontario, monitoring of colonies in natural settings shows that the long-term variation in colony size does not reflect the provincial decline in the Bank Swallow population suggested by Breeding Bird Survey data (Falconer *et al.* 2016). Data from the Breeding Bird Survey, a roadside survey, are probably very sensitive to changes in the availability of Bank Swallow human-made habitat for nesting. Our results suggest that a transition of the breeding population from human-made to natural settings would maintain colony size in natural settings despite the sharp decline in the population at the provincial level since the 1970s.

Sources of bias

Our study updates the previous national study (Erskine 1979) on the use of natural versus human-made nesting habitats by Bank Swallows in Canada. Our analysis includes fewer unassigned colonies to habitat (5.1%) than Erskine's (1979: 29%). Furthermore, we consider our assignment to habitat type to be very robust, because occurrences had to be spatially precise and were assigned based on both written descriptions and aerial image overlay. Erskine (1979) suspected a bias in favour of human-made habitats in the nest record schemes because Bank Swallow colonies are more easily accessible in human-made settings than in natural settings. Such an inventory bias is probably less important in our study for two reasons. First, our data come from an exhaustive search of data sources in Canada that includes diverse and flexible observation methods, some of which allow confirmation of nesting at a distance from the colony. In addition, we suspect that a greater effort to survey natural colonies was made in the years 2001 to 2017 compared to the nest records analyzed by Erskine (1979). During the second breeding bird atlases, a greater emphasis on recording breeding occurrences in less accessible areas might have increased the number of recorded colonies in natural settings compared to nest record scheme data collected prior to 1979. Despite this increased survey effort, occurrences of Bank Swallow colonies are likely to be underrepresented at the northern portion of the species' range.

The substantial decline of the Bank Swallow population in Canada since the 1970s may have prompted more colony surveys in natural settings than in human-made settings. Six data sources in our dataset reported only natural setting occurrences, compared to a single source reporting observations in only human-made settings. It is possible that colonies in natural settings are better represented in recent data, whereas they were underrepresented historically, providing a more accurate picture of recent nesting habitat use. The increased survey effort may also have led to the identification of colonies in human-made habitat that are difficult to access. For instance, in southeastern British Columbia where human-made habitat was created by a railroad, several colonies were only recently identified because they are in a relatively inaccessible location requiring boat access. These potential sources of bias should be kept in mind when interpreting any of the proportional changes we presented between historical and recent time periods.

Conclusions and implications for conservation

Canada is responsible for conserving the nesting habitats of nearly 400 migratory birds, including Bank Swallow, which has one of the steepest population declines in recent decades. Protection of Bank Swallow nesting habitat is essential for this species' conservation (Howie 2015; Falconer *et al.* 2016), although its limiting factors are still not well understood (Falconer *et al.* 2016; Berzins 2020). Historical evidence suggests that Bank Swallow has expanded its range in Canada as a result of the development of aggregate pits and transportation corridors (Erskine 1979; Bols 2017) and the conversion of forest habitat to open foraging habitat (Erskine 1979; Campbell *et al.* 1997). Across Canada, a substantial proportion of Bank Swallows continue to nest in human-made settings that, according to our data, remain the dominant nesting habitat in Manitoba and Quebec. Human-made habitats are conducive to nesting only through continuous intervention that maintains vertical or near-vertical faces (Hjertaas 1984), so the recovery of Bank Swallows should not be based on the long-term maintenance of this type of habitat at broad scales. Faced with limited conservation resources, the protection and maintenance of suitable faces in human-made settings could be counterproductive if these measures are implemented at the expense of the protection and rehabilitation of natural nesting environments.

In existing human-made habitats occupied by Bank Swallows, beneficial management practices can support the recruitment of individuals into the population by minimizing colony disturbance and the risk of incidental mortality. Inactive or abandoned extraction sites are attractive nesting habitats for Bank Swallows, but colonies may be disturbed or destroyed by the presence of all-terrain vehicles or walkers (COSEWIC 2013). Aggregate pit managers can play a key role in Bank Swallow conservation by implementing beneficial management practices (OMNRF 2017; ECCC 2022), but also by restricting public access to these sites. Known nesting sites in human-made settings should be monitored by authorities to enforce prohibitions under the *Migratory Birds Convention Act, 1994* and the *Species at Risk Act*.

Our study, however, shows that preservation of natural nesting habitats is critical to the recovery and conservation of Bank Swallows in Canada. The availability of natural nesting habitat may have decreased in recent decades, although Erskine (1979) estimated that human activities had a negligible influence on the availability of natural nesting sites. With increasing levels (and different types) of human recreational activities occurring on water bodies, we recommend that further work assess how these activities might negatively impact natural colonies. For instance, wake surf boats have been observed to travel close to colonies in British Columbia (R.D. pers. obs.). The boats produce a large wake (for surfing) that may be eroding banks at an alarming and unnatural rate during the breeding season, which may be causing nests to fail when banks erode.

Potential effects on nesting success resulting from these types of recreational activities are unknown. Moreover, human modifications of the environment through shoreline and coastal erosion control measures, hydroelectric development, and the construction of water-level control structures reduce the availability or quality of natural nesting habitat in Canada (COSEWIC 2013; Falconer *et al.* 2016; Bols 2017). Shoreline and erosion control that account for the needs of Bank Swallows could help to maintain adequate nesting habitat for the species in Canada over the long term. In California, shoreline rehabilitation through the removal of erosion control measures on the Sacramento River has been associated with an increase in Bank Swallow population viability (Girvetz 2010). Similar analyses would help guide shoreline erosion control measures to maximize the viability of Bank Swallow populations in Canada.

In coastal areas and shores of the Great Lakes where light engineering or interventions without hard structures are preferred (Boyer-Villemaire *et al.* 2016), conservation of Bank Swallow nesting habitat may be part of the solution to climate change adaptation. For example, new infrastructure could be built at a greater setback distance from cliffs occupied by Bank Swallows, the presence of which indicates active erosion processes, rather than implementing costly erosion control measures. Regarding human-made habitats, we recommend that further work include a spatial analysis of regional population changes relative to changes in aggregate pit availability. Finally, to ensure effective monitoring of the breeding population of Bank Swallow in Canada and to facilitate subsequent analyses, we recommend that Bank Swallow colony observations include the number of active nests and a precise description of the type of nesting habitat. We encourage the scientific community to determine nesting habitat use in the rest of the North American nesting range, particularly at a scale that would allow an assessment of the impact on population trends. Such an effort would contribute to a better understanding of the causes of the decline in the Bank Swallow population.

Author Contributions

Writing – Original Draft: N.P. and M.C.; Writing – Review & Editing: N.P., J.E.A., R.D., and M.C.; Resources: J.E.A. and R.D.; Methodology: M.C.; Formal Analysis: M.C.; Funding Acquisition: M.C.

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SUPPLEMENTARY MATERIALS:

Figure S1. Aerial images with centre representative of the habitat types assigned to Bank Swallow (*Riparia riparia*) occurrences for human-made settings (a), natural settings (b), and unknown settings (c) and (d).

Table S1. Confirmed nesting occurrences of Bank Swallow (*Riparia riparia*) recorded from 2001 to 2017 with associated bird conservation region, province or territory, and nest habitat type.

Table S2. Number of Bank Swallow colonies reported during the 1955–1971 (transformed from Erskine 1979) and 2001–2017 periods in anthropogenic, natural or unassigned settings in the Maritimes, Quebec and Ontario, the Prairies, British Columbia, and nationally (excluding Yukon, Northwest Territories, and Newfoundland and Labrador).

The Canadian Field-Naturalist

Gray Wolves (*Canis lupus*) consume free-ranging horses (*Equus ferus caballus*) on the Chilcotin plateau, British Columbia

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Abstract

We analyzed 122 Gray Wolf (*Canis lupus*) scats, collected at all seasons during 2013–2017, to determine what wolves were eating in two adjacent study areas of the Chilcotin region, British Columbia: Brittany Triangle and Nemiah Valley. Free-ranging horses (*Equus ferus caballus*), Mule Deer (*Odocoileus hemionus*), Moose (*Alces americanus*), and small mammals contributed to wolf diet throughout the year. In both study areas, horse appeared more frequently than other species in occurrence-per-faeces (OF) and occurrence-per-item (OI) analyses. Horse occurred in 58 of 97 wolf scats from Brittany (OF 59.8%, OI 52.7%), deer in 26 (OF 26.8%, OI 23.6%), small mammals in 17 (OF 17.5%, OI 17.3%), Moose in four (OF 4.1%, OI 3.6%), and bird and fish minimally (both OF <2.5%, OI <2.5%). The sample size in the more human-developed Nemiah Valley was too small to estimate reliable patterns, but results suggest a similar ranking of dietary items. Domestic Cattle (*Bos taurus*), available in both study areas, appeared infrequently (combined area OF <3.5%, OI <3.0%). Based on our scat findings, free-ranging horses were a regular dietary item for wolves in the area. Studies elsewhere have found that, where wolves and free-ranging horses are sympatric, a predator–prey relationship exists.

Key words: Gray Wolf; *Canis lupus*; wolves; free-ranging horse; *Equus ferus caballus*; predator; prey; scat; diet; hunt; scavenge

Introduction

Wolves (*Canis* spp.) and horses (*Equus* spp.) have coexisted for millennia in North America, Europe, and Asia (Savage 1969; Cohen 2002; Furrer *et al.* 2007; Germonpré *et al.* 2009; Hayes 2010). Despite the long history of overlapping ranges, few contemporary scientific studies have examined the dynamics of this formerly ancient, widespread, but now remnant predator–prey relationship, and none exist for British Columbia (BC). However, there are anecdotal reports of Gray Wolves (*Canis lupus*) chasing free-ranging horses (*Equus ferus caballus*) in the West Chilcotin (Davis 2009), attacking domestic horses in the Nemiah Valley (J. Tanis pers. comm. 2 June 2013), and approaching and testing free-ranging horses in the Brittany Triangle (D. Williams pers. comm. 28 February 2017).

Globally, wolves have flexible foraging patterns and strategies (Zlatanova *et al.* 2014; Newsome *et al.* 2016; Muhly *et al.* 2019). In North America, the diet of Gray Wolves is dominated by large and medium-sized wild ungulates (Newsome *et al*. 2016). Gray Wolves in Alberta's Rocky Mountain Forest Reserve are known to hunt free-ranging horses (Webb 2009; Webb *et al*. 2009). Studies in Europe (Patalano and Lovari 1993; Meriggi and Lovari 1996; Vos 2000; Lagos and Bárcena 2018) and Asia (van Duyne *et al.* 2009; Dorj and Namkhai 2013; Newsome *et al*. 2016; Chetri *et al.* 2019) also report wolves hunting free-ranging horses and/or ponies.

Our objective was to examine the annual diet of Gray Wolf in the Chilcotin (Tŝilhqot'in) region on the Interior Plateau of BC, near the Xeni Gwet'in First Nation community in the Nemiah Valley and determine whether free-ranging horses and Domestic Cattle (*Bos taurus*) were included and, if so, to what extent. (Note we use the anglicized spelling Chilcotin to refer to the geographic region and Tŝilhqot'in to refer to First Nation people.) Because wolves are known to consume free-ranging horses and/or ponies in other areas, as previously noted, we hypothesized that horse would be a part of wolf diet in our study area. Further, we hypothesized that cattle would be a part of the wolf diet given anecdotal information (McCrory 2002; Card 2010; Lamb-Yorkski 2015).

Although others commonly refer to free-ranging horses as Feral Horses (the terms are often used interchangeably), we prefer and use the term "free-ranging" for the horses in our study area. This term better reflects a species that lives in an area less dominated by humans and that has endured natural selective pressures for more than 300 years; McCrory (2002), Bhattacharyya *et al.* (2011), Cothran and McCrory (2014), Bhattacharyya and Murphy (2015), and Bhattacharyya and Slocombe (2017) document the presence and history of the Brittany Triangle horses.

Study Area

Our two adjacent study areas (Brittany Triangle, ~155 000 ha, and the Nemiah Valley, ~38 000 ha), each with different anthropogenic influences, are in the West Chilcotin region of the interior of BC (Figure 1) within the traditional territory of the Tŝilhqot'in Xeni Gwet'in First Nation and their ?Elegasi Qayus Wild Horse Preserve (Eagle Lake Henry Cayuse Wild Horse Preserve; Bhattacharyya *et al.* 2011; Bhattacharyya 2012). The Xeni Gwet'in have never signed treaties. In 2014, the Supreme Court of Canada recognized their rights and title (Supreme Court of Canada 2014) to the area that covers most of our study area and also includes Dasiqox Nexwagwez?an—a land, water, and wildlife protected conservation area and expression of Indigenous governance initiated in 2014 by the Xeni Gwet'in and Yuneŝit'in governments and supported by the Tŝilhqot'in National Government. A part of the Brittany Triangle is also in Nunsti Provincial Park. Most of the area is roadless and unlogged.

These areas are in the Interior Douglas Fir biogeoclimatic zone (IDFdk4; Meidinger and Pojar 1991) and include the eastern ranges and foothills of the Coast Mountains. The Chilcotin is characterized by semiarid grasslands and dry forests of Lodgepole Pine (*Pinus contorta* Douglas ex Loudon) with stands of Engelmann Spruce (*Picea engelmannii* Engelmann), as well as sedge meadows and wetlands (Grasslands Conservation Council of British Columbia 2010, as cited in Bhattacharyya *et al.* 2011). It is unique in that it is one of two regions in North America where free-ranging horses still coexist with a complete guild of large carnivores, the other region being the Rocky Mountain Foothills west of Sundre, Alberta (see Downer 2015; McCrory 2015; Zomorodi and Walker 2019). A small population of free-ranging horses also occurs in Saskatchewan's west-central Bronson Forest (Government of Saskatchewan 2009) where they are sympatric with wolves (Brown 2012), although other large carnivores, including Grizzly Bear (*Ursus arctos*) and Wolverine (*Gulo gulo*), have been extirpated there (COSEWIC 2012 and 2014, respectively).

Most data were collected in the Brittany Triangle, which supports one of the three self-sustaining free-ranging horse populations in Canada (McCrory 2002). The others include the horses in the foothills of Alberta and those on Nova Scotia's Sable Island, an offshore island in the North Atlantic and a national park reserve (Parks Canada 2021). The "triangle" is formed by the natural boundaries of the Chilko and Taseko Rivers on the north, east, and west, and by the Nemiah Valley on the south. The Brittany Triangle remains largely undisturbed by industry or anthropogenic influences, although a few small herds (<80 head) of cattle free-range from spring to fall on the west side (S.P. and W.P.M. pers. obs.). Of the estimated 2787 free-ranging horses in the greater Chilcotin plateau region (Environmental Dynamics Inc. 2019), ~150–215 live in the Brittany Triangle (G. Cothran and W.P.M. unpubl. data). Genetics indicate that the free-ranging horses of the Brittany Triangle are semi-isolated from adjacent horse populations. Both the Canadian Horse and, to a lesser degree, possibly East Russia/Yakut Horses contributed to the ancestry of Brittany horses (Cothran and McCrory 2014; G. Cothran and W.P.M. unpubl. data) whereas the Chilcotin horses to the east and north of the Brittany Triangle are largely of Spanish Iberian ancestry (G. Cothran and W.P.M. unpubl. data; L. Orlando pers. comm. 19 March 2020).

The Nemiah Valley, at the south end of the Brittany Triangle, is the home and official community centre for most of the Xeni Gwet'in, one of six member nations of the Tŝilhqot'in Nation (Bhattacharyya *et al.* 2011). The Nemiah Valley has ~400 residents (Bhattacharyya and Slocombe 2017) with a few tourism businesses and a few small ranches with cattle (S.P. and W.P.M. pers. obs.). A continuum of free-ranging horses occurs in the Nemiah Valley, varying from domestic (branded and halter-broke) to those that have never been handled by humans (Bhattacharyya and Larson 2014). Horse and cattle carcasses are sometimes left on the range in Nemiah after they die. Horse and cattle numbers in the Nemiah Valley were not determined for this study.

Besides free-ranging horses and cattle, other potential dietary items for wolves in both areas included Moose (*Alces americanus*), Mule Deer (*Odocoileus hemionus*), American Beaver (*Castor canadensis*), a variety of small mammals, and autumn runs of spawning wild Pacific salmon (*Oncorhynchus* spp.). A telemetry study of a small number of male Mule Deer in the Bridge River area to the south of our study area showed that most migrated from lower elevation winter and spring range to distant summer range to

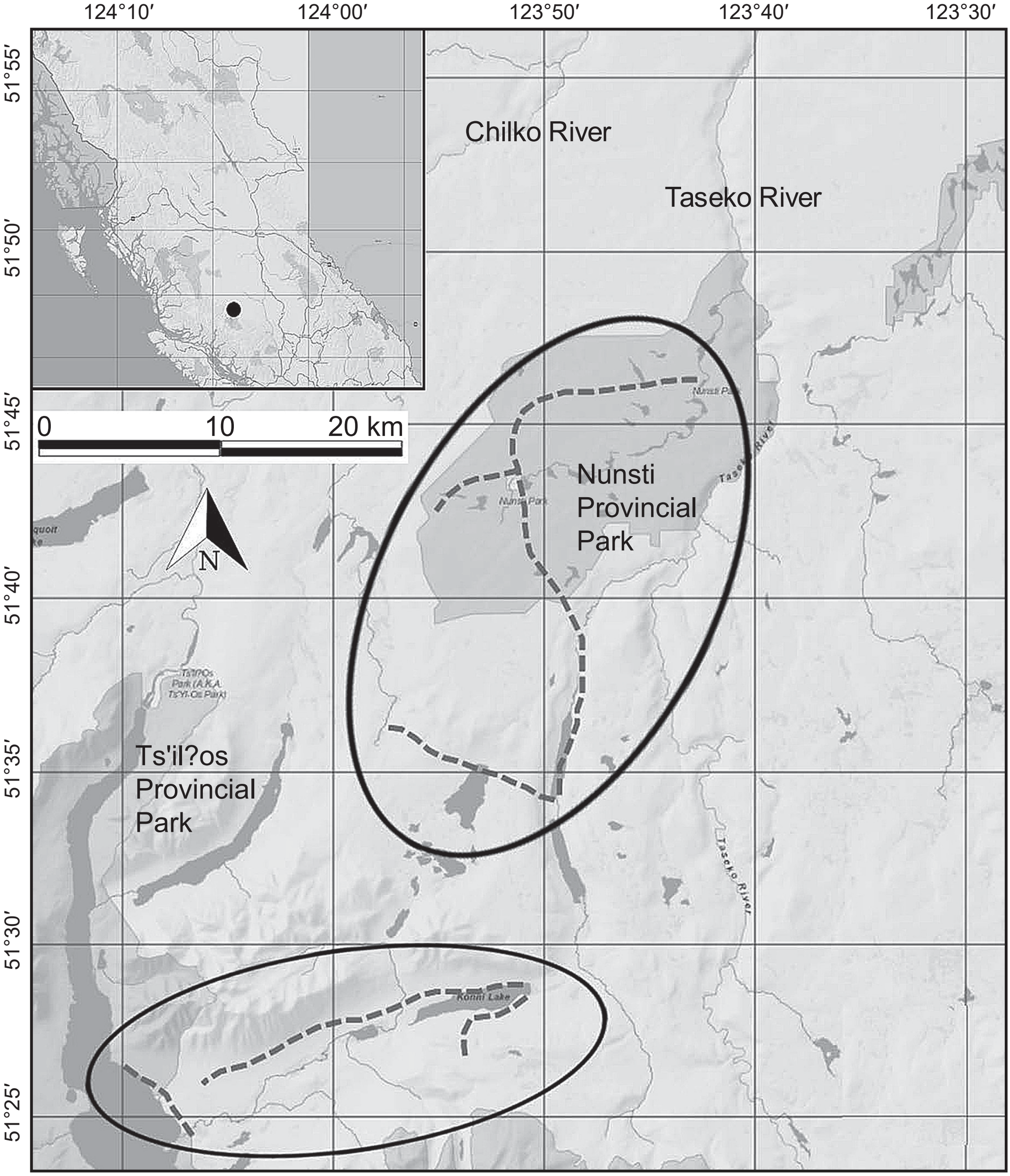

Figure 1. Approximate study areas on Chilcotin plateau, British Columbia, with transects shown as dashed lines. Top oval indicates Brittany Triangle study area and lower oval indicates Nemiah Valley area. The map inset shows the approximate location of the study area (dark circle) in British Columbia.

the west (Proctor and Iredale 2014), and Mule Deer in the study area are generally known to migrate annually to less harsh winter habitats at lower elevations along the Fraser River (Chilko Lake Study Team 1993; McCrory 2002; McCrory *et al.* 2014), leaving Moose and horse as the dominant ungulates available to predators in winter (McCrory 2002). Besides Gray Wolf, both areas host other large carnivores known to hunt free-ranging horses and large ungulates including Grizzly Bear (Clevenger *et al.* 1994; Pereira *et al.* 2021) and Cougar (*Puma concolor*; Turner *et al.* 1992; Greger and Romney 1999; Turner and Morrison 2001; Knopff 2010; Andreasen *et al*. 2021). Other resident carnivores include American Black Bear

(*Ursus americanus*), Wolverine, Coyote (*Canis latrans*), and Canada Lynx (*Lynx canadensis*).

Methods

Our study took place over five years (2013–2017) during which ~300 field days were spent collecting wolf scats. Scats were collected while walking along established transects four times each year, with each sampling period ranging from two to four weeks each season. Seasons were: spring (March 1–May 31), summer (June 1–August 31), autumn (September 1–November 30), and winter (December 1–February 28). Transects were selected non-randomly to ensure even distribution and to represent areas of wolf use identified through winter tracking; they consisted of dirt roads, bush roads, old wagon trails, horse trails, meadows, and human-made firebreaks (Figure 1). Wolf scats that appeared to be less than a week old were collected along transects and opportunistically within the study area. Unless tracks could verify wolf presence, only scats >30 mm in diameter were collected to avoid collecting Coyote faeces (Urton 2004). A handheld global positioning system unit (Garmin GPS 60, Taiwan, China) was used to record the universal transverse Mercator locations of scats. Scats were stored in labelled (date and location) bags that were frozen until analysis. To roughly estimate wolf numbers and to determine whether wolves travelled between the two study areas, we recorded wolf tracks along transects in our winter field observations and did incidental backtracking when wolf tracks crossed transects.

In the lab, scats were autoclaved at 130°C for 30 min to minimize the risk of parasite transmission. A compound microscope was used to identify guard hairs to the species level, when possible, by comparing scale and medulla patterns with hair keys from the University of Calgary (U of C) Geography Department, and voucher specimens of beaver, cattle, deer, horse, and Moose collected from the study area and stored at the U of C, and reference guides (Adorjan and Kolenosky 1969; Kennedy and Carbyn 1981). Diet items were classified into eight categories: horse, cattle, deer, Moose, beaver, small mammal (including rodents, lagomorphs), bird, and fish. Beaver was classified separately from small mammals, which were identified to the lowest taxonomic level at which confidence remained high, with less-common items identified only to family/order level (Lukasik and Alexander 2011). Only S.P. analyzed each scat sample after training by two professionals from the U of C Canid Ecology Lab; ~10% were randomly re-analyzed by an independent third party trained in scat analysis at U of C, yielding a 100% rate of precision. We did not retain voucher hair specimens from our scat analyses.

We used two indices to estimate wolf scat contents: occurrence per faeces (OF) and occurrence per item (OI; Urton 2004). Occurrence per faeces is the frequency with which a dietary category occurs in all scat samples or a subset thereof (e.g., by season or area), with the sample size being the total number of scats examined. To account for multiple species occurring in one scat, OI was used to determine the frequency with which a dietary category occurs among all dietary categories identified (Urton 2004). Sample size for OI is thus the total number of all dietary categories found in each subset of scat analyzed.

Results

Winter tracking, remote cameras, and direct sightings (S.P. and W.P.M. unpubl. data) suggested that at least some wolves travelled between the two study areas and that there was one or possibly two wolf packs in the combined study area; the number of wolves was not determined. Very little sign of deer was observed in winter, while direct sightings and sign of horse and Moose were more frequent (S.P. and W.P.M. unpubl. data).

We identified a variety of dietary items (Table 1) in the 122 wolf scats collected in the study area, which we grouped by season and area (Table 1). Horse, deer, Moose, and small mammal occurred in all four seasons (Figure 2a), although horse was absent from the two scats collected in the summer from the Brittany Triangle (Figure 2b). The OF for horse was largest in winter in both study areas combined (64.9%) and in the Brittany Triangle (75.0%). Overall, horse occurred in more than half of the 97 scats from the Brittany Triangle (OF = 59.8%, OI = 52.7%; Table 1, Figure 3). Only 25 wolf scats were collected from Nemiah Valley (Table 1); horse occurred there in each of the four seasons. Beaver and cattle occurred in scats only from the Nemiah Valley, and only minimally (Table 1).

Discussion

Despite extensive ground efforts, our sample size was small and varied among years and seasons, limiting our conclusions. Gable *et al.* (2017) recommended that, to accurately estimate wolf population diet, sample sizes of 10–20 adult scats/pack/month from home sites and/or opportunistically from packs are needed to minimize the potential temporal, interpack, and age-class biases. Although we collected only 122 scat samples over five years, our analysis does show that Gray Wolves are consuming horses year-round in our study area, which includes western Canada's first wild horse preserve.

Although relative densities of ungulates were unknown, and much of these data are lacking, the

Table 1. Food items identified in Gray Wolf (*Canis lupus*) scats collected 2013–2017 in combined area (C), Brittany Triangle (BT), and Nemiah Valley (NV) study areas, British Columbia, Canada, by season.

	Food items occurring in wolf scats								Total
	Horse	Deer	Moose	Small mammal*	Beaver	Cattle	Fish	Bird	
Study area									
C (*n* = 122)	65	30	5	32	1	4	2	1	140
BT (*n* = 97)	58	26	4	18	0	0	2	1	109
NV (*n* = 25)	7	4	1	14	1	4	0	0	31
Study area and season									
C spring (*n* = 25)	13	6	1	6	0	0	1	0	27
C summer (*n* = 9)	2	1	2	6	0	0	0	0	11
C autumn (*n* = 32)	13	10	1	16	0	0	1	0	41
C winter (*n* = 56)	37	13	1	5	1	4	0	1	62
BT spring (*n* = 24)	12	6	1	6	0	0	1	0	26
BT summer (*n* = 2)	0	1	1	0	0	0	0	0	2
BT autumn (*n* = 23)	10	8	1	10	0	0	1	0	30
BT winter (*n* = 48)	36	11	1	3	0	0	0	1	52
NV spring (*n* =1)	1	0	0	0	0	0	0	0	1
NV summer (*n* = 7)	2	0	1	6	0	0	0	0	9
NV autumn (*n* = 9)	3	2	0	6	0	0	0	0	11
NV winter (*n* = 8)	1	2	0	2	1	4	0	0	10

*Includes orders Rodentia and Lagomorpha.

timing of our research coincides with a declining Moose population trend documented for 1996–2015 in central BC (Kuzyk *et al.* 2018) and a relatively stable (i.e., unchanged) population of free-ranging horses in the Chilcotin between 2009 and 2019 (Environmental Dynamics Inc. 2019). Based on anecdotal animal sightings and observations of sign, higher densities of horse than Moose were apparent in our study area throughout the year (S.P. pers. obs.). Although deer, Moose, and small mammals were eaten throughout the year, we speculate that if our modest data set is representative of broader patterns throughout seasons and years, horse may be an important diet item for wolves, while cattle are not, although there were few scat samples from summer, when more vulnerable calves occur on the landscape. Few cattle appear to have been lost to wolves in this area; during the study, S.P. was in regular contact with local ranchers in the Nemiah Valley area, as well as with the Xeni Gwet'in Government, a Xeni Gwet'in Wild Horse Ranger, and Xeni Gwet'in Land Rangers who were informed of local events involving predators.

Scat analysis is also unable to reveal whether feeding occurred through predation or scavenging. Despite the strong possibility of wolves scavenging horses that died of other causes (i.e., scavenging is less risky than predation), predation of winter-weakened or newborn horses by wolves is likely. Predation could be expected, given the deep evolutionary history of wolves as predators of ungulates (Mech *et al.* 2015), the occurrence of horse in scats throughout the year in our combined study areas, and the documentation of wolves hunting free-ranging horses and/or ponies elsewhere (Patalano and Lovari 1993; Meriggi and Lovari 1996; Vos 2000; van Duyne *et al.* 2009; Webb 2009; Dorj and Namkhai 2013; Newsome *et al.* 2016; Lagos and Bárcena 2018; Chetri *et al.* 2019). Thus, we hypothesize that at least some of the horse in the wolf diet is from predation. Predation may also be more likely in the Brittany study area because horses there do not receive care or protection from humans. However, the details of wolves' horse-hunting behaviour remain to be studied.

Another bias arising from repeated scavenging of a carcass in one season is also possible. In addition, cattle and domestic horse carcasses left on the landscape in the Nemiah Valley may have confounded our results. Nonetheless, we found that cattle, although present in both study areas, were consumed by wolves minimally during our study. Of interest, some ranchers have suggested that free-ranging horses or ponies help minimize wolf predation on cattle (Card 2010; López-Bao *et al.* 2013). It is worth noting that although wild Pacific salmon are an important seasonal dietary resource for Gray Wolf on the BC coast (Darimont and Reimchen 2002; Darimont *et*

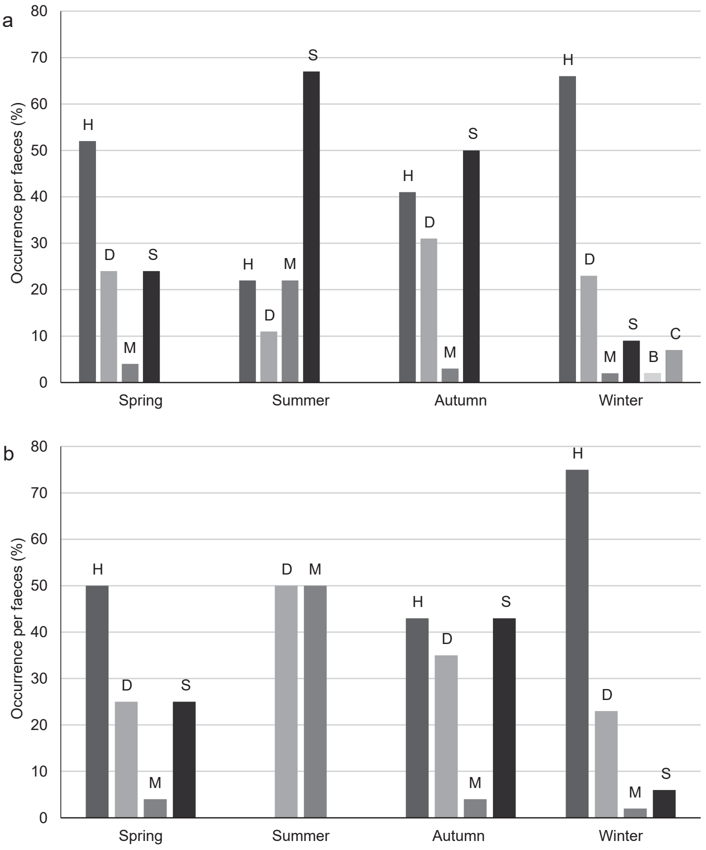

FIGURE 2. Seasonal variability in food items identified as occurrence per faeces (OF) in Gray Wolf (*Canis lupus*) scats collected 2013–2017 in a. combined area (spring n = 25, summer n = 9, autumn n = 32, winter n = 56); b. Brittany Triangle (spring n = 24, summer n = 2, autumn n = 23, winter n = 48), Chilcotin plateau, British Columbia. Only species with OF > 1% are included. Note: H = horse, D = deer, M = Moose, S = small mammal, B = beaver, C = cattle.

al. 2008) and are available in both study areas, minimal fish were detected in scats during annual spawning periods.

Finally, because our study included only a small number of wolves belonging to one or two packs, it is possible that the consistent consumption of horse we detected only reflects the habits of these specific packs and/or individuals. We also note that our study occurred over a brief period, whereas wolf prey use can vary substantially among years depending on a multitude of factors (Mattioli *et al.* 2011; Davis *et al.* 2012).

Potential implications for management of free-ranging horse populations

While acknowledging that concerns have been raised about the ecological interactions involving free-ranging horses and predators and the potential implications for biodiversity conservation (Boyce and McLoughlin 2021), namely through indirect competitive relationships (Wittmer et *al.* 2013; Gooch *et al.* 2017; Hall *et al.* 2018; Boyce and McLoughlin 2021), Duncan (1992) suggests that predation and horse social dynamics may be more important factors in regulating free-ranging horse populations than food supply. Based on our scat findings and given the minimum 300+ years that horses have been in this area (Storrar *et al.* 1977; McCrory 2002; Bhattacharyya *et al.* 2011; Bhattacharyya and Larson 2014; G. Cothran and W.P.M. unpubl. data) compared with millennia-scale evolutionary interactions between wolves and horses more generally, we postulate that Gray Wolves are potentially contributing as a top-down vector in limiting the size of the semi-isolated free-ranging horse population in the Brittany Triangle. Although this horse population might be influenced by a host of ecological factors, such as the harsh Chilcotin winters and other predators, it appears that wolves are consuming horses in our study area throughout all or most of the year.

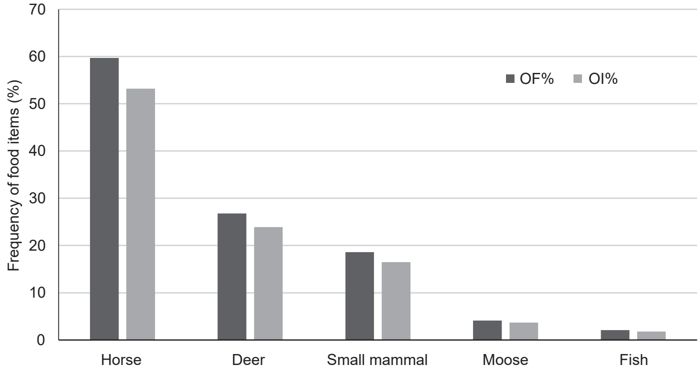

Figure 3. Occurrence per faeces (OF, *n* = 97) and occurrence per incidence (OI, *n* = 109) of food items detected in Gray Wolf (*Canis lupus*) scats collected in Brittany Triangle 2013–2017, Chilcotin plateau, British Columbia. Only items with OF > 2% were included.

Author Contributions

Writing – Original Draft: S.P. and W.P.M.; Writing – Review & Editing: S.P. and W.P.M.; Conceptualization: S.P. and W.P.M.; Investigation: S.P.; Methodology: S.P. and W.P.M.; Formal Analysis: S.P. and W.P.M.; Funding Acquisition: S.P. and W.P.M.

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Note

Conspecific nest attendance behaviour of Common Eider (*Somateria mollissima*) in response to Polar Bear (*Ursus maritimus*) foraging activity: error or intent?

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Abstract

Common Eider (*Somateria mollissima*) is a colonial nesting sea duck with extremely high nest attendance rates. Although individuals take few recess breaks away from their nest to feed or preen, previous research has shown that some female eiders in dense nesting assemblages engage in conspecific nest attendance, spending short amounts of time incubating nests of other females. However, to the best of our knowledge, most observations of these behaviours occur during regular recess events, as opposed to instances where females flush from their nest in response to a foraging predator. Using drone videography on East Bay Island, northern Hudson Bay, Nunavut, Canada, we observed conspecific nest attendance behaviours in 11 eiders that flushed in response to a foraging Polar Bear (*Ursus maritimus*). Of the 11 birds attending to other nests, only two predation events were observed at the focal bird's nest (i.e., two attenders' own nests were predated). Of the nine nests that were attended to, we also only observed two predation events. Motivations behind these behaviours are unclear, but conspecific nest attendance may serve as a type of distraction display, whereby activity at another female's nest leads the predator away from the focal bird's nest. However, given that, on East Bay Island, eiders are known to nest in proximity to kin, distraction displays at nests of related individuals would incur fitness costs. General confusion on nest location or the concealment of closely related eggs are more likely explanations for these behaviours.

Key words: Conspecific nest attendance; Common Eider; *Somateria mollissima*; Polar Bear; *Ursus maritimus*; incubation behaviour; distraction displays; drones

Common Eider (*Somateria mollissima*) is a large-bodied sea duck that typically nests in colonies on islands (Waltho and Coulson 2015). Eggs are incubated by females alone, which remain on their nest nearly constantly throughout the 21–24-day incubation period (Bolduc and Guillemette 2003; Bottitta *et al.* 2003). Eiders in Arctic populations fast throughout incubation, but may leave the nest occasionally to preen or drink water (Criscuolo *et al.* 2000); these recess events are typically short (median 401.5 s and 431.0 s before and after snow melt periods, respectively; Criscuolo *et al.* 2000) as unattended nests are vulnerable to predators such as Arctic Fox (*Vulpes lagopus*) and gulls (*Larus* spp.; Laurila 1989; Waltho and Coulson 2015). Apart from self-maintenance or rehydrating, behavioural activities away from the nest should be infrequent, as females are expected to reduce the time their eggs are exposed. However, Kristjansson and Jónsson (2015) report observations of females leaving their nests (recess events) to attend unoccupied nests of other females in the same colony. They report that in 10 out of 39 recess events in their study, focal females left their nest for an incubation recess and were observed to cover other unattended nests with insulating down feathers or even sit on a nest that did not belong to them. Similarly, during 31 of those 39 recess events, non-focal individuals attended the focal nest in the absence of the focal

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females. Although eiders may entirely usurp nests of conspecifics (Waldeck and Andersson 2006; Waldeck *et al.* 2011) or other species (Pratte *et al.* 2016), the phenomenon of temporarily attending to the nests of other eiders has not been rigorously examined (Waltho and Coulson 2015).

To the best of our knowledge, all the recess events reported in Kristjansson and Jónsson (2015) were true recess events, whereby females left their nest for an incubation break as opposed to flushing in response to a predator(s). Kay and Gilchrist (1998) report conspecific nest attendance by a single female eider during researcher activities at the East Bay Island, Nunavut, Canada, colony, but no other observations of these behaviours following predator-induced flushes have been reported in peer-reviewed literature. Waltho and Coulson (2015) report conspecific nest attendance in eiders during disturbance events, but they provide few details, which may reflect the logistic challenges associated with monitoring unmarked individual birds in dense nesting assemblages. Fortunately, the advent of drone technology (Chapman 2014) is providing unique visual perspectives on wildlife behaviour (e.g., Fortune *et al.* 2017; Jagielski *et al.* 2021b) and allows us to carefully parse out interactions between multiple individuals.

How individuals interact when living in large groups is of key interest to behavioural ecologists (Kopachena 1991). Eiders in brood rearing amalgamations are known to exploit social information and the vigilance of conspecifics (Bustnes 1993; Öst and Tierala 2011), but can also perform complex behaviours to avoid predation (McNair 1981; Kay and Gilchrist 1998). Eiders in several regions are facing increasing predation from Polar Bear (*Ursus maritimus*; Iverson *et al.* 2014; Prop *et al.* 2015; Barnas *et al.* 2020; Jagielski *et al.* 2021b), and little attention has been paid to the behavioural mechanisms by which eiders can avoid predation by bears (but see Dey *et al.* 2017). Understanding how the behaviours of individuals translate to population level effects can inform conservation practices (Bro-Jørgensen *et al.* 2019). Because eiders are a culturally and ecologically important species in the Arctic (Henri *et al.* 2018; Clyde *et al.* 2021), investigations into the behaviours of individuals are warranted.

Here, we describe observations of conspecific nest attendance by female eiders that flushed in response to Polar Bear foraging on East Bay Island (64°1′47.0″N, 81°47′16.7″W), in the Qaqsauqtuuq (East Bay) Migratory Bird Sanctuary, northern Hudson Bay, Nunavut, Canada. Eiders were observed between 10 and 20 July 2017 as a part of ongoing Polar Bear and eider behaviour monitoring using drone video from DJI Phantom 3 and 4 Professional quadcopters (Dà-Jiāng Innovations, Nanshan, Shenzhen, China). We reviewed video recorded at ~30 m above ground during Polar Bear foraging events. The use of drones is thought to reduce behavioural impacts on both Polar Bears (Barnas *et al.* 2018; Jagielski *et al.* 2022) and nesting eiders (Ellis-Felege *et al.* 2021) and, as such, we are confident that our method did not influence their behaviours. Additional details on the drone used and general methodology of video collection are in Jagielski *et al.* (2021b).

During the original review of video, we recorded flush responses from 193 birds, but noted conspecific nest attendance behaviours in 11 individuals (two birds attended a single nest in one of the 10 observations). In some cases, these interactions involved multiple individuals attending to the same nest, so we describe these behaviours from the perspective of the eider exhibiting the conspecific attendance behaviours. All field observations and eider flushes, summarized in Table 1 and described in detail in Appendix S1, are assumed to occur in response to a foraging Polar Bear (unless otherwise stated), because of the close proximity of the bear to focal nests (i.e., 3–10 m).

Although conspecific nest attendance in eiders was observed in only 11 individuals across a relatively short timespan, these observations contribute to the growing database of Arctic bird responses to foraging Polar Bears (Gaston and Elliott 2013; Iverson *et al.* 2014). Conspecific nest attendance following disturbance events (source of disturbance unclear) has been reported in eiders by Waltho and Coulson (2015). However, our observations are only the second record of such behaviours for the East Bay Island eider colony since the single instance reported by Kay and Gilchrist (1998) and the first involving multiple non-focal females attending to the same nest (Table 1; Appendix S1: observations 2, 3, and 5). Because the East Bay colony is well studied (see Love *et al.* 2010; Descamps *et al.* 2011; Hennin *et al.* 2016; Jean-Gagnon *et al.* 2018), we would expect more reporting of this phenomenon. But, it seems that conspecific nest attendance behaviours are either somewhat rare (although potentially common as we documented 10 instances within 10 days) or difficult to discern by observers, and/or are unreported in the literature. Although the paucity of observations prevents an understanding of the role of these behaviours in determining nest fate or fitness consequences, we can briefly hypothesize evolutionary origins and suggest future research needs.

Kristjansson and Jónsson (2015) proposed four possible explanations for the conspecific nest attendance behaviours they observed in eiders. First, individuals may get confused in dense colonies during disturbance events, lose awareness of their nest

TABLE 1. Summary of conspecific attendance observations involving nesting Common Eider (*Somateria mollissima*) and foraging Polar Bear (*Ursus maritimus*), East Bay Island, Nunavut, Canada captured using drone videos in July 2017. Each event involved a single bear.

Event, observation	Bird exhibiting conspecific nest attendance	Behaviours		Fate of nest
		Flushing	Conspecific nest attendance	
1,1	138	138 flushed from her nest by the bear	138 attended nest of 142 which had also been flushed by the bear and covered and sat on eggs in nest of 142 a couple of times, after 138 was chased off nest by 142 (see obs. 3)	Eggs in nest of 138 consumed by the bear
1,2	136	136 flushed from her nest by the bear in obs. 1	136 chased neighbour 135 off nest and sat on nest of 135 then departed	Neither nest visited by predators (bear or gulls)
1,3	142	142 flushed by bear in obs. 1	142 sat on nest of 135 after 136 departed in obs. 2	Neither nest visited by predators
1,4	148	148 and 145 flushed from their nests by bear eating eggs of 138 in obs. 1	148 visited nest of 145 and covered the eggs; did not return to her own nest	Neither nest visited by predators
1,5	Unknown 1 Unknown 2	141 flushed by approaching bear	Unknown 1 partially sat on nest of 141 then left, gull pecked at eggs, gull chased off by unknown 2 which then sat on nest of 141	Unable to assess damage to eggs or fate of nest
1,6	Unknown 3	152 flushed by approaching bear	Unknown 3 sat on nest of 152, then departed, 152 returned and sat on nest	Nest not visited by predators
2,7	126	126 flushed off her nest and walked behind bear while the bear consumed eggs of 124	126 performed broken wing display after bear began approaching her nest, redirecting the bear from the nest, scattering her ducklings, one of which was consumed by a gull, another of which fell into the unattended nest of 124 which 126 then sat on	No further predation by gulls or the bear
3,8	188	Both 188 and 189 flushed off their nests by a bear	188 sat on nest of 189, both then flushed again by approaching bear	Neither nest visited by predators
4,9	088	Both 088 and 086 flushed off their nests by a bear	088 sat on the nest of 086	Neither nest visited by predators
5,10	Unknown 4	While a bear consumed eggs from another nest, unknown 4 approached nest of 129 and removed 129	Both birds fought, unknown 4 left, 129 sat on her nest	Nest not visited by predators

Note: obs. = observation.

location, and submit to the strong visual stimulus to cover an unattended clutch of eggs (even those not their own). While other Arctic birds such as Common Murre (*Uria aalge*) and Thick-billed Murre (*Uria lomvia*) can recognize their own eggs (Gaston *et al.* 1993), high rates of conspecific nest parasitism in eider colonies (Waldeck and Andersson 2006; Hervey *et al.* 2019) suggest that they are poor at egg recognition. The combination of disturbance induced by a large predator and the inability to recognize their own nest suggests that general confusion is a highly likely explanation for conspecific nest attendance in eiders, but other explanations deserve consideration.

Second, sitting on unattended eggs may reduce heat loss of eider hens from their bare brood patch (although this is not satisfactory to explain the covering of eggs with insulating down feathers). Eiders do not feed during incubation, instead they exhibit a mass-loss incubation strategy (Moreno 1989; Criscuolo *et al.* 2000; Bolduc and Guillemette 2003). The restricted energy budget of eiders during incubation suggests that behaviours that retain heat should be favoured, but conspecific nest attendance bouts were short (e.g., 12 s) and likely did not provide ample heat transfer.

Third, the focal eider has a reproductive investment in other unattended nests because she has laid parasitic eggs in them (Hervey *et al.* 2019), and fourth, the focal eider is genetically related to the female of the unattended nest (McKinnon *et al.* 2006) and, therefore, gains direct fitness benefits from concealing the exposed eggs of relatives. Both of these hypotheses are plausible as high rates of conspecific nest parasitism (Waldeck and Andersson 2006; Hervey *et al.* 2019) and kin-grouping (McKinnon *et al.* 2006) occur in eider colonies. These hypotheses are intriguing and require further investigation. One caveat is that if eiders do nest close in proximity to relatives and simply attend nearby nests at random (as in the general confusion hypothesis), this may appear to be kin-based selection of conspecific nest attendance, when no such recognition of nests is actually required.

We examine a fifth possible explanation in more detail (originally postulated by Kay and Gilchrist 1998 as "nest betrayal behaviour") based on the conspecific nest attendance behaviours we observed in the context of predator foraging. Increased activity at bird nests in the presence of predators is hypothesized to attract predator attention (Skutch 1949; Martin *et al.* 2000) and, by attending other nests nearby, female eiders breeding in a dense colony may enhance their own nest survival by drawing bears to nests other than their own (Kay and Gilchrist 1998). Polar Bears rely heavily on olfactory senses to locate prey (Derocher 2012; Togunov *et al.* 2017), but recent work also suggests that bears may use visual cues to locate eider nests (Gormezano *et al.* 2017). On East Bay Island, Polar Bears located more eider nests when responding to the visual cues of flushing birds, although this strategy was not consistently used by all bears (Jagielski *et al.* 2021a). It is possible that the activity of a female eider near another nest could draw attention away from the focal bird's nest and direct the bear to consume eggs from another nest not their own. However, we observed only a single clear instance of a bear changing its presumed route to chase a distracting female eider (Table 1; Appendix S1: bird 126 in observation 7), which resulted in at least one of the distracting female's ducklings escaping predation. Although in observation 7 it is more likely that bird 126 was initially defending her duckling that fell into the nest of bird 124 rather than engaging in conspecific nest attendance, but given that she chose to remain on the nest, we felt it important to include. Of the 11 birds attending to other nests, only two predation events were observed at the focal bird's nest (i.e., two attenders' own nests were predated, bird 138 in observation 1 and bird 126 in observation 7). Of the nine nests that were attended to, we also only observed two predation events (bird 141 in observation 5, bird 124 in observation 7). As such, there is insufficient evidence to support the "nest betrayal" hypothesis, and there are several possible explanations for why this behavioural strategy is not observed at East Bay.

Eiders have been known to engage in "distraction displays" (McNair 1981; Kay and Gilchrist 1998), which are common in cryptic nesting birds, but less likely to evolve in colonial nesting species (Gochfeld 1984; Humphreys and Ruxton 2020). The rarity of these behaviours observed in eiders may reflect the negative fitness consequences of leading predators to nests of closely related individuals, as eiders often nest close to relatives (McKinnon *et al.* 2006; Hervey *et al.* 2019). At East Bay Island, eiders form kin-based social groups when arriving at the colony, during nest site selection, and when departing the colony (McKinnon *et al.* 2006). Because all conspecific nest attendance behaviours involving individuals with known nest locations occurred between neighbours less than 5 m apart (Appendix S1), true "nest betrayal" is not likely widespread at the East Bay Island colony as bears would be led to nearby nests. The conditions under which "nest betrayal" behavioural strategies could occur in a nesting colony of closely related individuals warrants future investigation.

Polar Bear foraging activity on eider nesting colonies has been reported more frequently in recent years, likely because of reductions in the extent of spring sea ice (Iverson *et al.* 2014; Prop *et al.* 2015; Barnas *et al.* 2020). At the landscape level, some predict that Polar Bear foraging will lead to increasingly dispersed nesting strategies as a means to avoid bear predation (Dey *et al.* 2017, 2018), but this has not yet been observed at large spatial scales (Dey *et al.* 2020). The behaviour of individual eiders in response to Polar Bears is less understood, and here we have shown that at least some birds may engage in conspecific nest attendance as a result. Future research should examine whether eiders performing conspecific nest attendance behaviours are more or less likely to lose their nest in the presence of foraging predators and how these behaviours impact nest success of neighbouring individuals.

The motivation behind these behaviours remains unknown, as are the potential fitness benefits, if any. Accurately estimating fitness consequences of these behaviours will require that birds of known relatedness are observed and demonstrate a change in predation risk for each nest (i.e., nest fate) as a result of these behaviours.

Author Contributions

Writing – Original Draft: C.A.B.S. and A.F.B.; Writing – Review & Editing: C.A.B.S., E.A.G., O.P.L., H.G.G., C.A.D.S., and A.F.B.; Conceptualization – C.A.B.S., E.A.G., C.A.D.S., and A.F.B.; Methodology – C.A.B.S., O.P.L., H.G.G., C.A.D.S., and A.F.B.; Funding Acquisition – O.P.L., H.G.G., and C.A.D.S.

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SUPPLEMENTARY MATERIALS:

Appendix S1. Detailed field observations of conspecific nest attendance behaviours of Common Eider (*Somateria mollissima*) in response to Polar Bear (*Ursus maritimus*) foraging activity, East Bay Island, Nunavut, Canada.

Figure S1. Screenshots from observation 7 drone footage of Common Eider (*Somateria mollissima*) flushing in response to a foraging Polar Bear (*Ursus maritimus*), East Bay Island, northern Hudson Bay, Nunavut, Canada.

Figure S2. Screenshots from observation 8 drone footage of Common Eider (*Somateria mollissima*) flushing in response to a foraging Polar Bear (*Ursus maritimus*), East Bay Island, northern Hudson Bay, Nunavut, Canada.

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Territorial scent-marking and proestrus in a recolonizing wild Gray Wolf (*Canis lupus*) population in central Wisconsin

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Abstract

Gray Wolf (*Canis lupus*) uses scent-marking to communicate breeding status, dominance, and territorial boundaries. Despite its importance for reproduction and pack dynamics, information on scent-marking and proestrus in wild wolf populations is limited to a handful of locations. We estimated the rate of territorial scent-marking and the probability of proestrus in a recolonizing Gray Wolf population near the species southern range extent in eastern North America. An analysis of 221 pack-winters of tracking data show that the incremental addition of one wolf pack increased marking rates by 3.4%, whereas increasing the number of wolves in a pack decreased marking rates by 12.1%. Scent-marking rates subsequently increased from 1.9 times/km during recolonization to 3.0 times/km once the population was saturated. We observed evidence of proestrus from 19 December to 14 March with the highest probability of proestrus occurring around 6 February, after peak marking rates around 26 January. Repeated observations of bloody urinations within individual packs suggest proestrus averages 27.9 days. Our study reveals the role of population growth on territorial behaviours and provides a foundation for studies exploring the role of geographic and temporal variation on territorial and reproductive behaviours in wolves.

Key words: Behaviour; Gray Wolf; *Canis lupus*; proestrus; raised-leg urinations; recolonization; reproduction; scent-marking; territory

Introduction

Communication has long been recognized as an important process in the development and maintenance of social bonds and conveying breeding status. Gray Wolf (*Canis lupus*) uses scent-marking to facilitate pair bonding, synchronize courtship and mating, identify breeders and dominance, and maintain spatial boundaries between neighbouring territorial packs (Mech and Peters 1977; Rothman and Mech 1979; Harrington and Asa 2003; Mech and Boitani 2003). In breeding pairs, males typically raised-leg urinate (RLU) and females flex-leg urinate (FLU), although these animals also use standing-urination (STU) and squat-urination (SQU) postures (Asa *et al.* 1985). Immature offspring and subdominant males and females normally urinate by standing and squatting, respectively (Peters and Mech 1975; Mech and Peters 1977; Rothman and Mech 1979; Asa *et al*. 1985, 1990). The scent-marks of subordinates and offspring are interpreted as generally eliminatory, whereas scent-marks of the breeding pair (RLUs, FLUs) are associated with territorial defense (hereafter, territorial scent-marks; Peters and Mech 1975; Mech and Peters 1977; Rothman and Mech 1979; Mech and Boitani 2003; Packard 2003; Mech and McIntyre 2022).

Territorial scent-marking appears to reflect perceived costs and benefits. Wolves tend to mark boundaries adjacent to other packs' territories more often than core areas, particularly where incursions have previously occurred (Peters and Mech 1975; Zub *et al*. 2003). In contrast, lone wolves, which may be more vulnerable than established packs, normally do not territorial scent-mark within saturated wolf populations (Peters and Mech 1975; Rothman and Mech 1979) but routinely territorial scent-mark in colonizing populations (Thiel 2000; Harrington and Asa 2003). Scratches associated with scent-marking are believed to express heightened assertiveness, possibly associated with breeding condition or territoriality (Peters and Mech 1975; Rothman and Mech 1979; Mech 2006).

Proestrus in mature female wolves is associated with bloody vaginal discharge and bloody urine can be used to identify whether a female wolf is in proestrus (Seal *et al*. 1979; Asa *et al*. 1985, 1990; Asa 1995; Packard 2003). Proestrus reportedly lasts 14–45 days with the onset and duration varying by individual (Young and Goldman 1944; Seal *et al*. 1987; Asa *et al*. 1990). In captive wolves, bloody discharge lasts between 15.7 ± 4.2 SD and 27 ± 6.5 SD days (Young and Goldman 1944; Seal *et al*. 1979, 1987; Asa *et al*. 1990; Esquivel *et al.* 1993 as cited in Alonso-Spilsbury *et al.* 2006), with proestrus extending from December to March (Asa *et al*. 1990). Schmidt *et al*. (2008) reported evidence of proestrus in wild Gray Wolves from mid-January to mid-March, peaking in February.

Information on scent-marking behaviour and proestrus in wild wolves is limited to a handful of locations (Peters and Mech 1975; Rothman and Mech 1979; Zub *et al.* 2003; Schmidt *et al*. 2008). Previous studies have evaluated spatial variation in territorial and reproductive behaviours in saturated populations; studying territorial scent-marking in a recolonizing population provides a unique opportunity to assess how population growth influences these same behaviours.

We studied scent-marking and proestrus over 20 years in a recolonizing wild Gray Wolf population near the southernmost range edge in eastern North America. We document the type and seasonal span of scent-markings and bloody urinations, and estimate the effect of population size, pack size, and day-of-year on territorial scent-marking behaviours and the probability of proestrus of wolves in the Central Forest Region (CFR) of west-central Wisconsin, USA. Our study reveals new insights into the relationship between canid population growth and territoriality, and provides a basis for future research assessing both geographic and temporal variation of territorial and reproductive behaviours in wolves.

Methods

The 7155 km^2 study area is situated on a glacial lakebed centred around 44.3733°N, 90.4974°W. This region consists of sandy soils that support numerous extensive marshes and bogs as well as upland forests of oak (*Quercus* spp.), pine (*Pinus* spp.), and aspen (*Populus* spp.). Wolves were extirpated from the area following European colonization and began recolonizing in the early 1990s (Thiel 1993). The wolf population initially increased from eight wolves in three packs in 1995 to 135 wolves in 32 packs in 2012, before stabilizing at about 100–150 wolves in 26–36 packs (Figure 1). Average road density in the CFR is 1.29 km/km^2, however, wolf packs have established territories with an average road density between 0.84 and 1.00 km/km^2 (Thiel *et al*. 2009; Simpson 2019). For a more detailed description of the study area, see Thiel *et al*. (2009) and Simpson (2019).

Data collection

Winter track surveys were conducted by trained staff and citizen volunteers following snowfall between the winters of 1994–1995 and 2017–2018 (Thiel *et al*. 2009; Wydeven *et al*. 2009; Thiel 2018). Each winter, trackers searched for wolf sign along plowed roads and trails by driving slowly within designated survey blocks. Data collected included date, distance driven, wolf pack identity, the number of wolves counted and lengths of wolf trails followed,

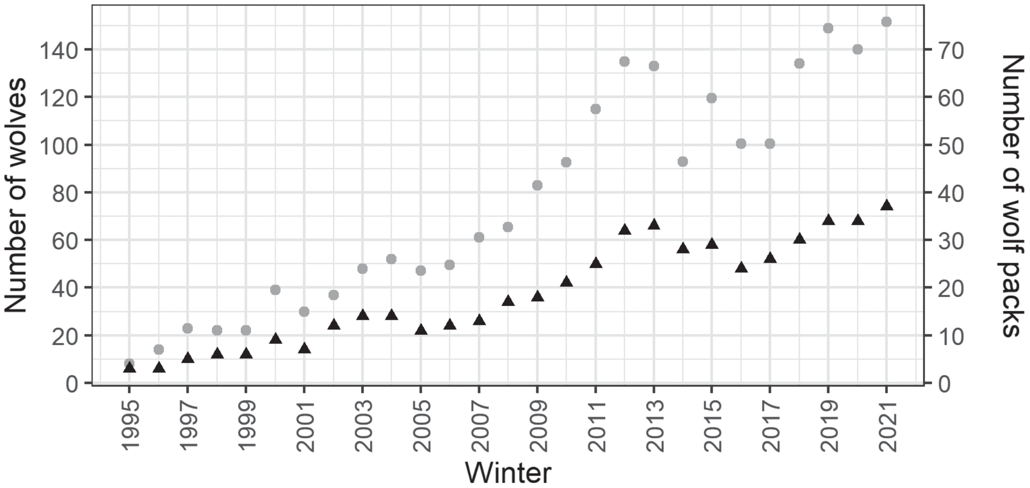

FIGURE 1. The number of Gray Wolf (*Canis lupus*) in the Central Forest Region, Wisconsin, USA based on data from the Wisconsin Department of Natural Resources. The number of packs is shown as black triangles and the number of wolves is shown as grey dots.

and the number and types of scent-marks encountered (Wydeven *et al*. 2009). Scent marks were identified by inspecting the position of wolf tracks relative to the urine. For example, urine is projected lateral to the direction of travel with one hind leg raised during RLU and projected down with one hind leg slightly raised during FLU. Neither hind leg is raised during SQU or STU, however, the hind legs are spread substantially wider than the body during the former but not the later (Asa *et al.* 1985). The presence of blood in the urine, evidence of a sexually mature female in proestrus (Peters and Mech 1975; Rothman and Mech 1979; Harrington and Asa 2003; Schmidt *et al*. 2008; Wydeven *et al*. 2009), was also recorded.

We summarized 20 years of winter-track survey data supplied by R.P.T. and three individuals who coordinated volunteers on behalf of the Wisconsin Department of Natural Resources. These records extend from November 1996 to February 1999, and from January 2002 to March 2018. Early winter data collection declined as the study progressed, so we restricted our study to data collected after 14 December. To compare our surveys to previous studies, we considered RLU, double raised-leg urinations (RLU^2), RLU with scratches, and RLU^2 with scratches as territorial scent-marks. Wisconsin winter-track surveys report FLUs as RLUs because the two scent marks are difficult to distinguish in some conditions, so our analyses include territorial scent-marks from both sexes. Bloody urine can occur in either territorial scent-marks or in eliminatory SQU, so we considered both as evidence of proestrus. Each encounter of a contiguous wolf trail segment was defined as an event in which the number of scent-marks was recorded by type. We assigned a tracking distance of 0.16 km in events where wolves merely crossed a road.

Statistical analyses

We estimated the rate of territorial scent-marks using a Poisson process model:

$$N_{it} \sim \text{Poisson}(\lambda_{it}) \cdot f_{it}$$

where N_{it} is the number of territorial scent-marking behaviours along path i on day t. The number of events is related to how far wolves were tracked so we included log(km) as an offset term (f_{it}) so that the estimated rate parameter log(λ_{it}) represents the average number of events/km of wolf-tracking effort. We also included a random intercept for survey block to account for correlated error structure that can arise from repeated measures of packs within an area. We evaluated seven models reflecting our expectation that territorial scent-marks could be related to the number of wolves in an event, the number of packs in the CFR, and day-of-year. Mid-winter pack sizes in the Upper Great Lakes region range from 2.7 to 5.5 wolves (Beyer *et al*. 2009; Erb and DonCarlos 2009; Thiel *et al*. 2009; Wydeven *et al*. 2009). Only 20 events (3%) recorded more than five wolves so we assigned all tracks ≥5 wolves a value of 5 to prevent overfitting. Statistical models were estimated by maximum likelihood methods using the "glmmTBM" package in R 4.0.5 (Brooks *et al*. 2017; R Core Team 2021). The most parsimonious model was identified using AIC (Akaike 1973).

Second, we tested evidence for a seasonal peak in proestrus using a binomial model:

$$S_{it} \sim \text{Binomial}(p_{it}).$$

We considered each individual urination an event, so the estimated parameter logit(p_{it}) represents the average probability that a territorial scent-mark or SQU contained blood. Urinations associated with the same animal are more likely to be similar to one another than we would expect at random, so we included a random intercept for survey block. We evaluated models reflecting no relationship, a linear relationship with time, a polynomial relationship with time, and the number of packs in the CFR. Statistical models were estimated using the beta-binomial distribution in "glmmTBM" (Brooks *et al*. 2017), which reduces to the binomial model when the number of trials per sample is one. We identified the most parsimonious model using AIC.

Results

Seventy-three volunteers drove 26 213 km over the 20-year period, resulting in 221 pack-winters of data. A total of 1301 territorial scent-marks were recorded along 642 km of wolf trails and accumulated 562 sample events (Table 1). Naïve winter marking rates averaged 2.3 marks/km (range 0–20). Due to monitoring protocols, all wolf trails were associated with

TABLE 1. Territorial scent-marks and squat urinations by type along 642 km of Gray Wolf (*Canis lupus*) tracks in the Central Forest Region, Wisconsin, USA.

	RLU	RLU^2	RLU with Scratch	RLU^2 with Scratch	SQU	Total
No blood	663	419	97	42	80	1301
Blood	49	30	1	3	7	90
Total	712	449	98	45	87	1391

Note: RLU = raised-leg and flexed-leg urinations, RLU^2 = double raised-leg and flexed-leg urinations, SQU = squat-urination.

at least one road and longer track segments often crossed multiple roads.

In winter, the average number of territorial scent-marks/km was related to the number of wolves in a pack, number of packs in the CFR, and day-of-year (Table 2). The most parsimonious model indicates that wolves were expected to mark an average of 2.4 times/km (range 0.9–4.6). The incremental addition of one wolf reduced territorial scent-marks/km by 12.1% ($P < 0.01$; Figure 2a) and the incremental addition of one wolf pack increased scent-marks/km by 3.4% ($P < 0.01$; Figure 2b; Table 3). We explored different sine waves and found that the average rate of territorial scent-marks in the most parsimonious model peaked around 26 January.

Volunteers recorded 90 bloody urinations in 66 sampling events (Table 1) between 19 December and 14 March (Figure 3). Repeated observations of bloody urinations in single winters were observed within six packs over seven winters. The length from onset to end averaged 27.9 ± 18.9 SD days ($n = 7$; range 8–58 days). Our data indicated that proestrus peaked around 6 February (Figure 4) and was unrelated to the number of packs (Tables 2 and 3). We observed seven

TABLE 2. Model selection for territorial scent-marking (TSM) rates and proestrus in Gray Wolf (*Canis lupus*), in the Central Forest Region, Wisconsin, USA. Covariates include the number of wolves in an event (wolf), number of packs in the study area (packs), and number of days since 1 December (days). Territorial scent-marking was modeled as a Poisson process, whereas proestrus was modeled as a binomial process. The number of variables (*K*), AIC, difference between AIC values (ΔAICc), and AIC weights (*w*) are provided for each model.

Model	Covariates	*K*	AIC	ΔAIC	*w*
TSM	wolf + packs + sine(day)	5	2513.8	0.0	0.94
	wolf + packs	4	2519.2	5.4	0.06
	packs + sine(day)	4	2533.2	19.4	0.00
	packs	3	2535.6	21.8	0.00
	wolf + sine(day)	4	2569.3	55.5	0.00
	wolf	3	2580.5	66.7	0.00
	sine(day)	3	2584.0	70.2	0.00
	null	2	2592.0	78.2	0.00
Proestrus	day + day^2	5	666.5	0.0	0.81
	sine(day)	4	670.0	3.5	0.14
	null	3	672.9	6.4	0.03
	packs	4	674.3	7.8	0.02

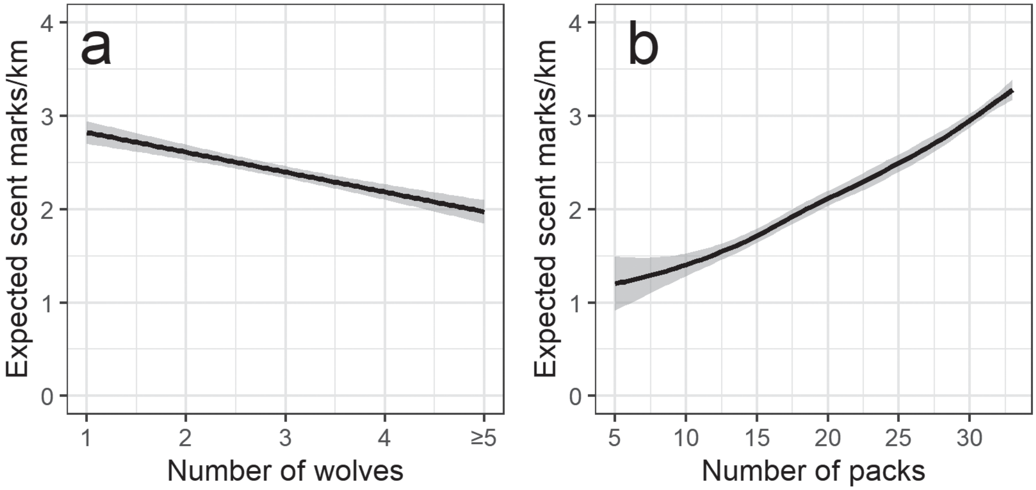

FIGURE 2. The mean rate of territorial scent marks/km by Gray Wolf (*Canis lupus*) from December to March in relation to a. pack size and b. number of packs in the study area. The estimated mean and 95% CI are shown in a black line and grey shading, respectively.

Table 3. Most supported mixed-effects models relating territorial scent-marking rates (TSM) to the number of Gray Wolves (*Canis lupus*) in a tracking event (wolf), the number of packs in the study area (packs), and relating the probability of proestrus to the number of days since 1 December (days). The estimated variance (σ) associated with the random intercept is shown for each model.

Model	Parameter	Estimate	SE	*z* value	*P* (>|z|)
TSM	Intercept	0.3725	0.1460	2.5507	0.011
	wolf	−0.1138	0.0247	−4.6104	< 0.001
	packs	0.0333	0.0044	7.6401	0.008
	sine(day)	0.0858	0.0321	2.6718	< 0.001
	σ	0.0694			
Proestrus	Intercept	−2.7339	0.1163	−23.5154	< 0.001
	scale(day)	8.8446	4.4992	1.9658	0.049
	scale(day)^2	−12.1534	4.9185	−2.4710	0.014
	σ	< 0.001			

SQU with evidence of proestrus (Table 1). The ratio of SQU to territorial scent-marks was similar where proestrus (8.4%) was evident and when it was not (6.4%). We saw no evidence that the rate of SQU/km increased with pack size ($P = 0.272$).

Discussion

Territorial scent-marking peaked in the third week of January, which is earlier than reported by Zub *et al.* (2003) and by Peters and Mech (1975) who reported peaks in late February at latitudes about 8° and 3° farther north than our study area, respectively. The number of territorial scent-marks increased during recolonization, with an average expected rate of 1.9 marks/km (range 0.9–3.6) during the recolonization phase and 3.0 marks/km (range 1.3–4.6) once saturated. These are similar to midwinter rates reported in Poland (1.2–3.0 marks/km; Zub *et al.* 2003; Bojarska *et al.* 2020), Minnesota (1.7–3.4 marks/km; Peters and Mech 1975), and Manitoba (1.2–1.7 marks/km; Paquet 1991). Scent-marking rates are often higher along roads (Rothman and Mech 1978; Stępniak *et al.* 2020) but volunteers did not collect detailed spatial information relating wolf trails to roads, so we could not reliably assess the role of roads on territorial behaviour.

We found that wolves increased scent-marking in response to population growth, independent of pack size. Previous studies indicate that wolves increase marking in potential conflict areas (Peters and Mech 1975; Zub *et al.* 2003). Territorial scent-marking and

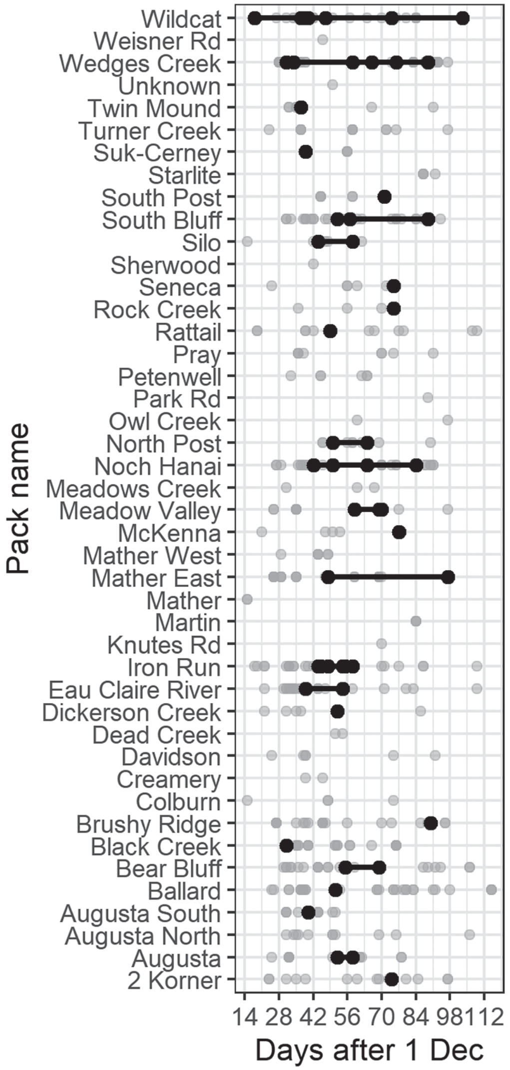

Figure 3. The occurrence of proestrus in territorial scent marking Gray Wolf (*Canis lupus*) from 14 December to 26 March by wolf pack. Black dots are scent markings with evidence of proestrus, black lines are the first and last date proestrus was observed in the same pack, and grey dots are sampling effort.

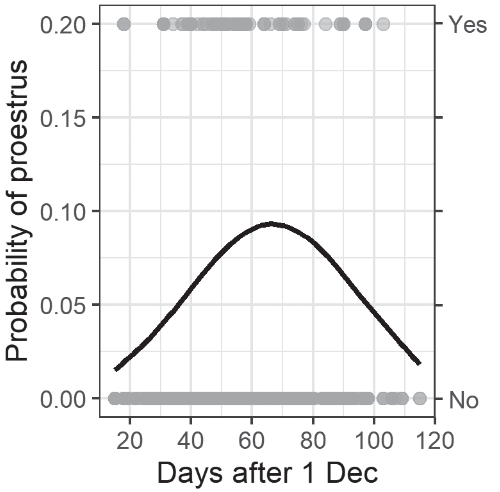

Figure 4. The mean probability of proestrus in Gray Wolf (*Canis lupus*) from 14 December to 26 March. The estimated mean is shown in a black line and the raw observations show whether individual scent-marks contained blood.

other olfactory cues might convey information on the size of wolf packs occupying territories or their willingness to defend a territory. This is important information to convey in maintaining competitive spaces because superior pack numbers, in addition to presence of males and older individuals, led by dominant individuals often sway outcomes in intra-pack aggressive encounters (Cassidy *et al*. 2015, 2017). Our study shows that wolf packs living in saturated landscapes invest more energy defending territories, whereas those that live in unsaturated landscapes can reallocate that energy to other pursuits. We speculate that the higher rates observed among newly forming pairs in a saturated wolf population arises from their need to be assertive because most pairs in such situations must usurp space from the interstitial areas between existing pack territories (Rothman and Mech 1979). Additional research would be required to assess the relationship between resource availability, pack formation, pack size, and scent marking.

Our findings are consistent with studies showing marking rates initially decline with increasing pack size (Peters and Mech 1975; Zub *et al*. 2003) and then increase as pack size exceeds five individuals (Peters and Mech 1975; Paquet 1991). We posit that the initial decline occurs because small packs need to mark assertively to usurp or maintain space while avoiding physical confrontation, whereas the subsequent increase may be related to pack composition. Territorial scent-marking is associated with dominant individuals (98%; Peterson *et al*. 2002) and small packs often consist of only two breeding adults and their pups. Because RLU first occurs during puberty, which typically occurs at 22 months old (Ranson and Beach 1985; Asa and Valdespino 1998), large packs may simply have more adults that are physiologically and behaviourally equipped to mark territory than smaller packs.

The observed season of bloody urinations (19 December to 14 March) compares favourably with those reported in Minnesota (4 January to 24 February; Rothman and Mech 1978) and Poland (12 January to 22 March; Schmidt *et al*. 2008). Proestrus in several central Wisconsin wolf packs spanned an average of 27.9 days and peaked in early February, which is consistent with observations in both captive and wild wolves (Seal *et al*. 1979, 1987; Asa *et al*. 1990; Esquivel *et al.* 1993 as cited in Alonso-Spilsbury *et al.* 2006). However, the mechanisms driving variability among individuals, neighbouring packs, and populations remain elusive. Reproductive phenology in wolves is positively correlated with lower latitudes, lower elevations, warmer summers, and warmer winters (Mech 2002; Joly *et al*. 2018; Mahoney *et al*. 2020), which are often associated with increased primary and secondary productivity. There is variable support for latitudinal gradients in ungulate reproduction across species and scales (Sigouin *et al*. 1997; Stoner *et al*. 2016; Neumann *et al*. 2020), indicating that geographic variation in wolf reproduction is not strongly linked to ungulate parturition. Wolves in western North America delayed denning after years with high primary productivity and high fall and winter precipitation but did not adjust denning dates over an 18-year period when start of the growing season advanced 14.2 days (Mahoney *et al.* 2020). That wolves fail to synchronize reproduction with spring onset suggests that breeding behaviour is highly conserved and that other processes or cues stimulate proestrus in female wolves (e.g., photoperiod or winter body condition). We speculate that reproductive phenology varies according to long-term patterns in resource availability and suggest that relating geographic and interannual measures of prey availability and body condition to proestrus, breeding, denning, and reproductive success may shed light on reproductive mechanisms in canids.

Author Contributions

Conceptualization: R.P.T.; Methodology: R.P.T. and P.D.D.; Investigation: R.P.T.; Formal Analysis: P.D.D.; Writing – Original Draft: R.P.T. and P.D.D.; Writing – Review & Editing: R.P.T. and P.D.D.

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Quantifying seeds egested by field-collected earthworms: a dynamic and overlooked pool in forest soil seed banks

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Abstract

Although awareness of the influence of earthworms on soil seed banks in Canadian forests is growing, there have been few direct field measurements. We used a novel pairing of field-collected earthworms from a central Great Lakes forest in Ontario with a laboratory seed egestion assay to obtain a snapshot of the number of seeds passing through earthworms compared with seeds found in the surrounding soil. We identified a pool of seeds egested by earthworms that accounted for 2.4% of all seeds found in the earthworms and the top 0–10 cm of soil. Individual earthworms contained 0–5 seeds. The large-bodied adult anecic non-native Dew Worm or Common Nightcrawler (*Lumbricus terrestris*) egested a disproportionate number of seeds for its abundance (50% of egested seeds from 17% of earthworms), but smaller earthworms were also an important source of egested seeds (the other 50%). This small-scale proof-of-concept study demonstrates a method of directly measuring earthworm–seed interactions in the field. It can also detect seeds egested by earthworms below ground that would otherwise be missed by other seed accounting methods and it highlights the importance of granivory by non-surface casting earthworms.

Key words: Granivory; seed dispersal; aboveground–belowground interaction; *Lumbricus terrestris*; novel method; forests

Introduction

Forest soil seed banks can be modified by earthworms that act as seed predators and dispersers by actively or passively ingesting seeds (Grant 1983; Thompson 1987; McCormick *et al.* 2013). Earthworms ingest seeds from the total available seed pool, destroying some through digestion and egesting others back into the soil below ground or at the soil surface after a relatively short gut transit, e.g., 8 h for Dew Worm/Common Nightcrawler (*Lumbricus terrestris*; Hartenstein and Amico 1983), a non-native species in Canada (Addison 2009). Many egested seeds remain viable and may be transported through the soil vertically (Willems and Huijsmans 1994; Zaller and Saxler 2007; Regnier *et al.* 2008) or horizontally (McTavish and Murphy 2021) and may experience increased or reduced germination (Ayanlaja *et al.* 2001; Clause *et al.* 2015).

Most studies of earthworm–seed interactions have been indirect or observational, with few direct measurements in the field, and key questions remain regarding the overall importance of these interactions in ecosystems (Cassin and Kotanen 2016; McTavish and Murphy 2020). Notably, we lack accurate measures of the pool of seeds that passes through earthworms under field conditions. Because of logistic challenges, most manipulative experiments occur in the laboratory—with a few exceptions, such as Cassin and Kotanen (2016) and McTavish and Murphy (2020)—and most rely on indirect measures, such as associations between earthworm density and seed bank or vegetation composition (Nuzzo *et al.* 2015), seed removal (Cassin and Kotanen 2016), or quantification of seeds in surface casts, which are produced by only some species (Willems and Huijsmans 1994; Decaëns *et al.* 2003). No studies have attempted to directly quantify the pool of seeds actively passing through earthworms in the field.

The purpose of our study was to examine earthworms as a transient/ephemeral belowground seed pool, evaluate the overall importance of earthworm granivory, and enhance the accounting of the total forest soil seed bank. We used a novel pairing of live earthworm collection from the field with an immediate earthworm seed egestion assay in the laboratory to obtain an instantaneous snapshot of the seeds passing through earthworms and compared this to the density of seeds found in the surrounding soil. This proof-of-concept study occurred at a central Great Lakes temperate forest field site in Ontario, Canada.

Methods

Sampling occurred at the University of Toronto's Koffler Scientific Reserve at Joker's Hill, Newmarket, Ontario, Canada (44°02′10.0″N, 79°32′11.9″W). The study area consisted of mature, secondary growth forest dominated by Sugar Maple (*Acer saccharum* Marshall), American Beech (*Fagus grandifolia* Ehrhart), Eastern Hemlock (*Tsuga canadensis* (L.) Carrière), and Red Oak (*Quercus rubra* L.). The understorey was not characterized at the time of this study (which took place during the late fall); however, taxa known from the study area include Brown Knapweed (*Centaurea jacea* L.), plume thistles (*Cirsium* Miller), pepperweed (*Lepidium* L.), Butter-and-Eggs (*Linaria vulgaris* Miller), Bouncing-bet (*Saponaria officinalis* L.), White Trillium (*Trillium grandiflorum* (Michau) Salisbury), and Common Mullein (*Verbascum thapsus* L.; M.J.M. and A.R. unpubl. data). Soils are sandy loam, grey-brown podzols overlaying morainal sand (Cassin and Kotanen 2016). The study area was a 60 m × 30 m block between two walking trails with 24 quadrats (30 cm × 30 cm) placed randomly throughout.

In late October 2019, earthworms were extracted from the soil in each plot by searching and clearing the surface leaf litter and pouring 3 L of mustard solution (10 g mustard powder [Bulk Barn Food Limited, Aurora, Ontario, Canada] per litre water) on the plot over 12 min to extract earthworms (Lawrence and Bowers 2002; Hale 2013). To rapidly collect gut contents, all earthworms were immediately placed in portable, aerated, plastic containers (14 cm × 9 cm × 5 cm; Dollar Tree Canada, Mississauga, Ontario, Canada) lined with moistened viscose cloth (Figure 1). All earthworms from a plot were placed in a single container, with the exception of adult *L. terrestris*, which were placed in a separate container for each plot as they could be reliably distinguished from other earthworm species (thus, up to one container for adult *L. terrestris* and one for other earthworms per plot). Containers were placed in a large plastic bin with the lid closed to create dark conditions known to be more amenable to earthworm activity (M.J.M. pers. obs.). After field collection, the bins were returned to the laboratory (~21°C) and left on a bench for 24 h.

After 24 h, earthworms were removed and rinsed with water over the containers to remove any seeds and then euthanized in isopropyl alcohol, fixed in 10% formalin, and stored in isopropyl alcohol. After fixation, earthworms were identified (no vouchers were collected) to genus and species where possible using Reynolds (1977) and Hale (2013), assigned to functional groups including litter-dwelling epigeics, mineral soil-burrowing endogeics, and vertically burrowing anecics (*sensu* Bouché 1977, but see Bottinelli *et al.* 2020 for continuing discussion of these functional groups), air dried for 24 h, and weighed. The viscose cloths from the containers were rinsed with water over a 300-µm sieve and air dried to collect egested seeds. After 24 h in the containers, no seeds were expected to remain within the earthworms; all seeds should have been egested.

Figure 1. The earthworm egestion collection unit containing an adult *Lumbricus terrestris*. The portable containers (14 cm × 9 cm × 5 cm) were an economical and efficient means of immediately segregating large numbers of live earthworms in the field to collect gut contents. Photo: M. McTavish.

At each plot, the soil seed bank was sampled after the earthworms were collected using a 5-cm diameter soil corer at the four corners and mid-point of each edge of the quadrat ($n = 8$ soil samples/plot). Because searching for seeds is time-consuming, only the top 0–10 cm of soil (expected to contain the greatest proportion of the soil seed bank) was retained for analysis. Although detailed mapping of the depth distribution of seeds was not available for our study area, similar research suggests that burial of surface-deposited seeds is minimal in the absence of earthworms and that many earthworm-buried seeds can be found in the top 1–10 cm (Willems and Huijsmans 1994; Regnier *et al.* 2008; Cassin and Kotanen 2016; McTavish and Murphy 2021). The eight subsamples from each plot were aggregated, mixed, and sieved (1.70 mm) to remove larger debris. Seeds were extracted using a seed flotation assay described in Malone (1967) and a 300-µm sieve.

Seeds from the earthworm egestion collection units and the seed flotation assay were counted by systematically sorting each sample using a microscope at 10× to 40× magnification. Seeds were distinguished from other inorganic and organic soil features by cutting into ambiguous samples with a scalpel to check for distinctive organic matter (e.g., seed coat, endosperm). Seeds could not be reliably identified to genus or species morphologically but were between 300 µm and 1.70 mm in size as a result of the collection process. A subset of the soil samples was also subjected to a 3-month cold stratification at 5°C and potted in a greenhouse in an emergence assay; this was intended as an alternative method for quantifying the seed bank and to identify species, but it was abandoned because of a failure of the greenhouse facilities during the course of the experiment.

Soil seed density (in the top 0–10 cm) was calculated per plot by dividing the sum of seeds found across eight subsamples by the total surface area of those eight soil cores. The density of seeds found in earthworms per plot was calculated by dividing the total number of seeds egested by earthworms in a plot by the plot area. Total seed density was calculated as the sum of the soil and earthworm seed densities. Paired *t*-tests were used to compare soil seed density and earthworm seed density. Because individual egestion could not be directly measured from groups of earthworms in a container, total egestion was pooled across all earthworms in a container (either adult *L. terrestris* or other earthworms) and calculated as an average individual egestion per earthworm. Paired *t*-tests were used to compare the abundance of total egested seeds per plot between adult *L. terrestris* and other earthworms. Because not all plots contained both adult *L. terrestris* and other earthworm taxa, we could not calculate individual earthworm egestion for each plot and, therefore, did not have fully paired data. We instead used Welch's test (Welch's unequal variances *t*-test) for heteroscedastic data (Welch 1951) to compare individual egestion by adult *L. terrestris* and all other earthworms. Correlations between earthworm density, earthworm air-dried biomass, average individual earthworm seed egestion numbers, and soil seed density were assessed using the Pearson correlation in cases when the data demonstrated bivariate normality or the Spearman correlation for data lacking bivariate normality. Test assumptions were checked using the Anderson-Darling test for normality and Levene's test for equal variance. All tests were carried out in R version 3.6.1 (R Core Team 2019) at $\alpha = 0.05$. Values are mean ± SD.

Results

The earthworm community across the 24 plots consisted of four species: epigeic *Dendrobaena octaedra* (Savigny 1826), endogeic *Aporrectodea turgida* (Eisen 1873; synonym *Aporrectodea caliginosa* (Savigny 1826, in part)) and *Aporrectodea tuberculata* (Eisen 1874), and anecic *L. terrestris*. Because no other species were recorded in the plots, juvenile *Aporrectodea* spp. and *Lumbricus* sp. were presumed to be either *A. turgida*/*A. tuberculata* or *L. terrestris*, respectively, and functionally classified as endogeic and anecic. Total earthworm density and dry biomass for the 24 quadrats were 125 ± 63/m^2 and 12.6 ± 8.0 g/m^2, respectively, which are typical of North American forests (Addison 2009; Sackett *et al.* 2013). The community was dominated by endogeic *Aporrectodea* spp. in density and by anecic *L. terrestris* in biomass (Figure 2).

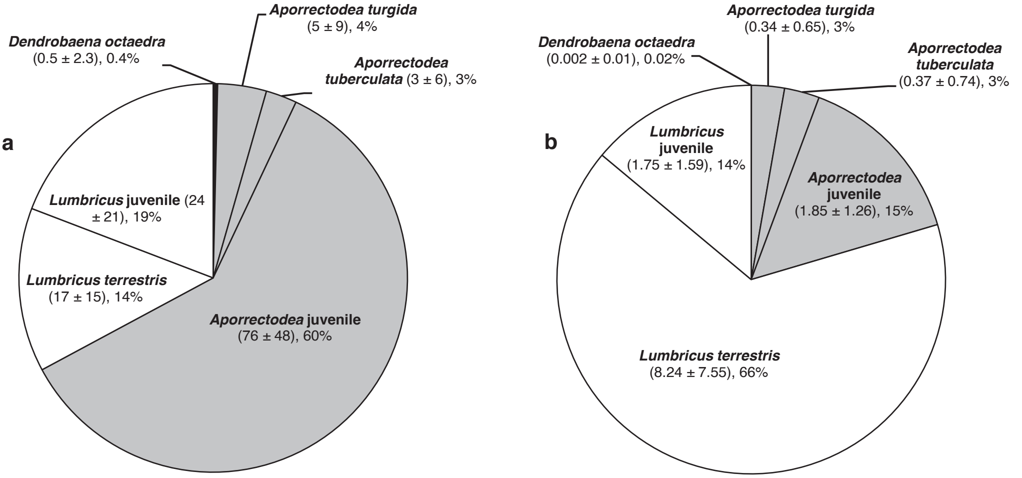

Figure 2. a. Density (mean *n*/m^2 ± SD and % of total) and b. dry biomass (mean g/m^2 ± SD) of earthworm communities from 24 plots in a central Great Lakes forest, Ontario, Canada, October 2019. Shaded area shows earthworm functional group including epigeic (black for *D. octaedra*, not visible in b), endogeic (grey), and anecic (white).

Seeds were collected from 37 adult *L. terrestris* and 234 other earthworms. Total recovered seed density was 2125 ± 827/m^2 from the top 0–10 cm of soil, 46 ± 36/m^2 from earthworms, and 2171 ± 828/m^2 in total. Per plot, significantly more of the recovered seeds were found in the soil (97.6 ± 2.0%) than in earthworms (i.e., seeds in earthworms at the time of collection that were egested afterwards; 2.4 ± 2.0%; paired $t_{23} = 12.29$, $P < 0.001$). The egested seed pool was split evenly between earthworm species groups with no statistically significant difference found between the number of seeds collected from adult *L. terrestris* and other earthworms (paired $t_{23} = 0.33$, $P = 0.75$).

Individual earthworms egested an average of 0.4 ± 0.5 seeds/earthworm (range 0–5). However, individual adult *L. terrestris* egested a significantly higher mean number of seeds per earthworm (1.62 ± 0.35) than other species (0.35 ± 0.58; Welch's test, $F_{1,19.68} = 11.67$, $P = 0.003$; $n = 17$ adult *L. terrestris* containers, $n = 24$ other earthworm containers). Therefore, the contribution of adult *L. terrestris* to the egested seed pool (~50%) was disproportionately high for their density (17% of earthworms) and more proportionate to their biomass (66% of earthworms by weight). There was a positive correlation between earthworm density and earthworm biomass but no other statistically significant correlations were found between the other variables (Table 1).

Discussion

Ours is the first study to directly quantify seeds actively passing through earthworms in the field. A small previously unrecognized portion of the forest soil seed bank is found in earthworms (2.4% of collected seeds per plot, 46 ± 36 seeds/m^2). This portion consists of seeds that have been removed from the total pool of available seeds via ingestion minus those lost to digestion. Assuming that the seeds we collected in the laboratory would normally have been egested back into the soil several hours after ingestion (Hartenstein and Amico 1983), they would have returned to the soil seed pool. Thus, over time, an increasing portion of the seed bank would be composed of seeds egested by earthworms. Earthworms may also re-ingest seeds previously egested by themselves or other earthworms, although there is evidence that they will preferentially avoid these previously egested seeds (McTavish and Murphy 2019).

Many of the egested seeds we collected would not normally have been counted, except for those that might have been deposited in and quantified from aboveground casts (e.g., Decaëns *et al.* 2003). Although measuring seed densities from surface casts remains useful to assess the impact of earthworms on seedbank dynamics, it does not capture the transient pool of seeds found within earthworms and does not account for seeds egested below ground. Large-bodied anecic earthworms such as *L. terrestris* are often considered the primary contributors to seed predation because of their size (Asshoff *et al.* 2010). Although we did find that *L. terrestris* egested more seeds per individual than smaller earthworms, the latter occurred at higher densities overall and egested just as many seeds in total. The influence of mineral soil-dwelling endogeic earthworms may be even greater than observed because of the tendency of mustard extraction to marginally under-sample these taxa (Lawrence and Bowers 2002). Given the predominantly belowground feeding behaviour of many of the earthworms that egested seeds, these findings also reinforce the relatively unique ability of earthworms to access seeds both below and above ground (Thompson 1987).

Our findings also contribute to better understanding of the overall ecological importance of earthworm–seed interactions. Individual earthworms contained an average of 0.4 ± 0.5 seeds (range 0–5) when they were collected. Although this may seem small, the cumulative number of seeds that may pass through earthworm communities with densities of up to several hundred individuals/m^2 (Addison 2009; Sackett *et al.* 2013) could be considerable, particularly as we found no relation between earthworm density and the number of seeds per earthworm (Table 1). In addition, given the rapid transit time of seeds moving through earthworms (in the order of several hours; Hartenstein

Table 1. Correlation between earthworm density, earthworm biomass, seeds per earthworm, and density of plant seeds in soil from 24 quadrats in a central Great Lakes forest, Ontario, Canada. Cells contain the correlation coefficient and corresponding P values (in bold if significant at α = 0.05).

	Earthworm density, no./m^2	Earthworm biomass, g/m^2	No. seeds/earthworm
Earthworm biomass, g/m^2	**0.58** **(P = 0.003)**	—	—
No. seeds/earthworm	−0.13* (P = 0.55)	0.22* (P = 0.22)	—
Soil seeds, no./m^2	0.09 (P = 0.67)	0.14* (P = 0.51)	0.02* (P = 0.91)

*Correlations for variables lacking bivariate normality were calculated using Spearman's correlation.

and Amico 1983), a large number of seeds could be ingested and egested over a year. Notably, our instantaneous measure of 46 earthworm seeds/m^2 was only slightly smaller than the annual estimate of 60–100 germinable seeds/m^2 found in earthworm casts in a Dutch grassland (Willems and Huijsmans 1994), again suggesting how studies of only surface-egested seeds might underestimate the pool of seeds egested by all earthworm taxa throughout the soil profile.

It is important to note that this proof-of-concept study focussed on one sampling effort in a single forest and was intended to see if seeds egested by field-collected earthworms could be quantified. It was not designed to provide a full accounting of the soil seed bank *per se*, although we hope that this approach may be used in such future studies. Given our assumption that most unburied and earthworm-buried seed would be found in the top 10 cm of soil (Willems and Huijsmans 1994; Regnier *et al.* 2008; Cassin and Kotanen 2016; McTavish and Murphy 2021) and to simplify the laborious seed extraction process, we did not sample the deeper soil profile. In addition, although we initially attempted to sample earthworm casts for seeds, wet field conditions and degraded casts collected later in the fall made it difficult to reliably distinguish between casts and surface soil. Overall, we expect that these limitations may have omitted seeds deeply buried by earthworms (Regnier *et al*. 2008; McTavish and Murphy 2021) and deposited in casts (Willems and Huijsmans 1994), thereby producing an underestimate of the size of the earthworm seed pool and the contributions of deep-burrowing, surface-casting *L. terrestris*.

It is also unknown whether bringing the earthworms into the laboratory may have altered rates of seed digestion/egestion compared with field conditions; although temperature can affect processes, such as soil consumption (Curry and Schmidt 2007), we do not think the conditions compromised the egestion estimates. Conditions in the field would naturally fluctuate over time, and earthworm seed egestion has already been observed to be unaffected by other variables such as seed density and previous seed egestion (McTavish and Murphy 2019). We recommend that future studies attempt a more complete seed bank accounting including identification of the seed species present (e.g., from the vegetation present on site or a seed emergence assay), viability testing of recovered seeds, and analysis of a deeper soil profile and surface earthworm casts sampled across multiple locations and time points.

Conclusions

The results of our study show the dynamic nature of the soil seed bank and the often-unseen biotic interactions that help shape it (Chambers and MacMahon 1994). Specifically, our study identifies a previously overlooked pool of soil seeds found within earthworms in small but potentially ecologically significant numbers. Although field studies of earthworm–seed interactions are scarce, our findings are consistent with emerging evidence that the primary ecological significance of these interactions is not strictly associated with the magnitude of seed removal (Cassin and Kotanen 2016; McTavish and Murphy 2020), but rather with more subtle processes such as seed burial (Zaller and Saxler 2007) and spatial aggregation (Milcu *et al.* 2006; McTavish and Murphy 2021). We therefore encourage further consideration of this small but potentially ecologically significant pool of seeds in the soil seed bank that are egested by earthworms and propose the adoption of methods to study this interaction at a larger scale and in a broader range of habitats.

Author Contributions

Writing – Original Draft: M.J.M.; Writing – Review & Editing: M.J.M., A.R., R.S.B., and S.M.S.; Conceptualization: M.J.M. and A.R.; Investigation: M.J.M. and A.R.; Methodology: M.J.M. and A.R.; Formal Analysis: M.J.M. and A.R.; Funding Acquisition: R.S.B. and S.M.S.

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Range expansion of Fisher (*Pekania pennanti*) in Nova Scotia

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Abstract

Fisher (*Pekania pennanti*) is a medium-sized mesocarnivore that typically occupies mature hardwood and softwood forest where its preferred prey is abundant. In Nova Scotia, Fisher populations are reported as restricted to the mainland; they have been absent from Cape Breton Island for the past 50–80 years. A record of a Fisher on Cape Breton Island in February 2002 prompted us to collate and analyze other records of Cape Breton Island sightings of the species from that date to May 2021. Based on reported sightings, we conclude that Fisher has extended its range from mainland Nova Scotia, apparently crossing the Strait of Canso, and that a breeding population now exists on Cape Breton Island and is expanding. We also comment on possible negative interactions between this expanding Fisher population and the provincially Endangered American Marten (*Martes americana*) population on the island.

Key words: Fisher; *Pekania pennanti*; range expansion; American Marten; *Martes americana*; extirpation; trail cameras; snow tracking; ice bridge; causeway; Maritime Canada

Introduction

In the northeastern United States and mainland Canada, Fisher (*Pekania pennanti*) prefers mature conifer, hardwood, and mixed-wood forests where medium-sized mammalian prey, such as Snowshoe Hare (*Lepus americanus*), Red Squirrel (*Tamias hudsonicus*), and Porcupine (*Erethizon dorsatum*), are abundant (Buskirk and Powell 1994; Powell and Zielinski 1994). Fisher is a mesocarnivore with an estimated historical range in eastern Canada before ca. 1600 that included mainland Nova Scotia and adjacent Cape Breton Island (CBI; Gibilisco 1994).

Cape Breton Island has been separated from mainland Nova Scotia since 8000–6000 years before present (BP), following glacio-isostatic, eustatic, and hydro-isostatic processes associated with the retreat of the Laurentide Ice Sheet ~12 000 years BP (Shaw *et al*. 2002, 2006). The island's landmass slopes upward from the south to the north from sea level to a maximum elevation of 535 m on the northern plateau. Higher elevations are dominated by heathlands, stunted Balsam Fir (*Abies balsamea* (L.) Miller), spruce (*Picea* spp. A. Dietrich), tree and shrub swamps, and expansive bogs. Mid-elevations are extensively vegetated with shade tolerant Yellow Birch (*Betula alleghaniensis* Britton), Sugar Maple (*Acer saccharum* Marshall), and American Beech (*Fagus grandifolia* Ehrhart) while low-lying elevations have shade tolerant hardwoods in addition to Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh), White Spruce (*Picea glauca* (Moench) Voss), White Pine (*Pinus strobus* L.), Balsam Fir, Red Maple (*Acer rubrum* L.), and White Ash (*Fraxinus americana* L.; all from Neily *et al*. 2017). The Canso Causeway, completed in 1955, joins CBI to the mainland across the point of narrowest width (~1 km) of the Strait of Canso. Power and Gilhen (2018: 9) described the causeway as a "busy thoroughfare" bounded by industrial lands. Its construction has impeded currents, thereby facilitating development of an ice bridge across the strait in winter (Power *et al*. 2015).

The historical presence of Fisher on both the mainland of Nova Scotia and CBI is confirmed by the Fisher pelts sent annually to the European market between 1783 and 1853 (Gwyn 2003) with pelts specifically from CBI listed (Gwyn 2003: 74). However, by the mid-19th century, Gilpin (1867: 10) felt that the Fisher, always uncommon in Nova Scotia, was "rapidly becoming extinct in our province" and harvested animals were primarily sourced from Cumberland County in the northeast of the mainland adjacent to the New Brunswick border. Smith (1940) noted the lack of reports of Fishers since 1922 and Rand (1944) concluded the species was extirpated from the province. Fisher declines and extirpations elsewhere in North America have been attributed to over-trapping and habitat loss caused by logging (Powell and Zielinski 1994; Strickland 1994) and long-term climate warming (Krohn 2012).

Reintroductions, augmentations, improved regulatory practices, and increased forest cover have facilitated the recovery of Fisher across much of its former range in eastern North America (Gibilisco 1994; Powell and Zielinski 1994; Proulx *et al.* 2004; Powell *et al.* 2012). Efforts have been made to re-establish the species within its former range, e.g., on mainland Nova Scotia where reintroduction programs occurred in 1947–1948 (Bensen 1959; sourced from ranch stock) and 1963–1966 (Dodds and Martell 1971; sourced from wild-caught Maine stock), with one translocation program occurring in 1993–1995 (Potter 2002; sourced from local stock). However, there have been no re-introductions of Fisher into CBI (M.S. O'Brien pers. comm. 10 December 2021).

Potter (2002) described the distribution of Fisher in Nova Scotia using harvest locations from 1981 to 1999. During that period, the species was largely confined to two geographically separate populations in eastern (Cumberland, Colchester, Pictou, and Antigonish) and western (Queens, Annapolis, and Digby) counties of mainland Nova Scotia. The eastern mainland population was reported to extend from the New Brunswick–Nova Scotia border region to the Strait of Canso, with no records from CBI. The first suggestion of re-establishment of Fisher on CBI occurred on 10 February 2002 when an adult male was incidentally caught in a legally set Eastern Coyote (*Canis latrans* var.) snare; this Fisher is now a taxidermy mount residing at the Nova Scotia Department of Natural Resources and Renewables (NSDNRR) office in Whycocomagh, Nova Scotia. To better understand recent Fisher re-establishment and expansion on CBI, we report records of Fishers on CBI from that first capture in 2002 to May 2021. This is the first report of Fishers on CBI since extirpation of the species on the Island 50–80 years ago.

Methods

Geo-referenced occurrences for Fishers were obtained from the Biodiversity Investigation Reporting (BIR) system of the NSDNRR for 1999–2021. Since 1999, this has been the principal data-entry and reporting system used internally by the NSDNRR to capture and manage wildlife occurrences reported by staff and the public. Records for Fishers on CBI were extracted from the BIR system up to 20 May 2021 and combined with additional species sighting records on file with regional NSDNRR biologists. Fisher occurrence records were also consolidated from NSDNRR staff-conducted predator and prey snow-track surveys employing a road-intercept approach between January and March along 23 transects each 5 km long totalling 1030 km (2005–2020) and 225 transects each a minimum 1 km long totalling 244 km (2013–2015) distant from a road edge among natural and actively managed forest stands. Finally, images from motion-triggered trail cameras (multiple brands) baited with American Beaver (*Castor canadensis*) carcasses at 277 sites established by NSDNRR between 2012 and 2020 in Inverness and Victoria Counties were reviewed for the presence of Fishers. All Fisher locations were converted to an ArcMap shapefile (ArcGIS Desktop, release 10.8.1; Esri, Redlands, California, USA) and spatially joined with elevation data and binned into 100-m classes.

Results and Discussion

The review of available data sources provided 131 occurrence records for Fishers on CBI (Figure 1). Among these, 77% were documented by photographic evidence (*n* = 66; Figure 2), dead or caught in snares (18), tracks (14), and three were sightings by NSDNRR staff. The remaining 23% were sightings reported by the public and determined to be valid following investigation by NSDNRR staff based on description of the animal and situation in which it occurred.

Although there are few records of Fishers in and north of Cape Breton Highlands National Park (Figure 1a), the abundance of records south of the park boundary likely reflects the relatively higher survey effort in that area. With only two records of Fishers on the eastern side of CBI, in Cape Breton and Richmond Counties, Fisher re-establishment and expansion appears to have largely occurred in Inverness and Victoria Counties at this time.

Although the distribution of all records by elevation suggests a preponderance of Fisher occurrence between sea level and 100 m (Figure 3), many of these sightings were reported by private citizens to NSDNRR staff and documented in the BIR. The relatively recent return of Fishers to CBI and the novelty

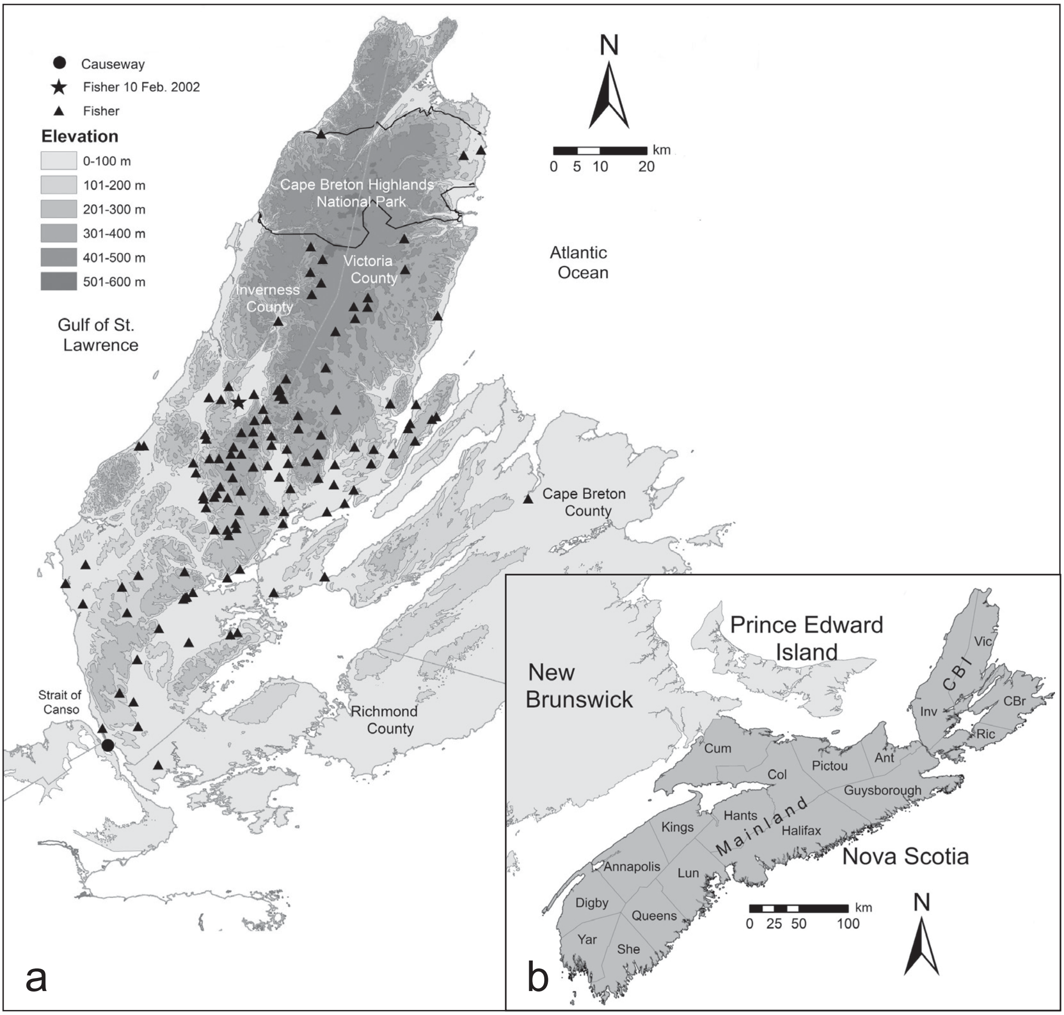

FIGURE 1. a. The distribution of Fisher (*Pekania pennanti*) occurrence records since 2002 on Cape Breton Island, Nova Scotia, Canada. b. County map for mainland Nova Scotia and Cape Breton Island (CBI) relative to New Brunswick and Prince Edward Island: Antigonish (Ant), Cape Breton (CBr), Colchester (Col), Cumberland (Cum), Inverness (Inv), Lunenburg (Lun), Richmond (Ric), Shelburne (She), Victoria (Vic), and Yarmouth (Yar).

of sighting the animal may stimulate reporting by residents, who reside predominately at lower elevations.

Fisher re-establishment on CBI likely occurred via juveniles/subadults dispersing from natal areas on the mainland to seek unoccupied territories. The February 2002 record of a Fisher on CBI, at 46.3°N, 61.03°W (Figure 1a), is ~80 km north of the Canso causeway between mainland Nova Scotia and CBI. The Strait of Canso is 1 km wide at its narrowest point and periodically freezes north of the causeway. This would facilitate immigration to CBI following population expansion on the mainland from aforementioned earlier releases (Potter 2002). The narrowing of this strait is considered by Scott and Hebda (2004) as the probable route of invasion of several other mesocarnivores onto CBI including Bobcat (*Lynx rufus*) and Eastern Coyote. Instances of long-distance (i.e., 30–60 km) juvenile dispersal by Fishers from natal areas have been noted by others (e.g., Leonard 1980; Arthur *et al*. 1993; Aubry *et al*. 2004), supporting juvenile dispersal as a possible source of Fisher re-establishment on CBI. This implies that the Fisher captured as an adult may have been present before 2002 and only detected that year. Also, the male captured in February 2002 could have had an established home territory, suggesting the species was present in low numbers on CBI before 2002. Regardless, Fishers have re-established and expanded from sea level

FIGURE 2. Fisher (*Pekania pennanti*) captured on a Nova Scotia Department of Natural Resources and Renewables (NSDNRR) trail camera on 1 April 2018 (0713) at 46.18°N, 60.85°W, 301–350 m above sea level. Photo: NSDNRR.

to >400 m elevation across Inverness and Victoria Counties on the western side of CBI.

The re-establishment of Fisher on CBI has implications for another small CBI meso-carnivore. American Marten (*Martes americana*) was released on CBI during an augmentation program (2007–2011) to restore the provincially Endangered local population of this species (Nova Scotia American Marten Recovery Team 2006). Re-establishment or expansion of Fisher, a competitor and predator of marten, has been implicated in declines in marten populations (Krohn *et al*. 1997; Fisher *et al*. 2013; Manlick *et al*. 2017; Suffice *et al*. 2017, 2020). Competition among predators can affect species recovery efforts (Stoskopf 2012; Hamel *et al.* 2013) and could compromise the ability of American Marten to re-establish a sustainable breeding population on CBI. The impacts of the re-establishment and expansion of a CBI Fisher population on American Marten on CBI warrants investigation.

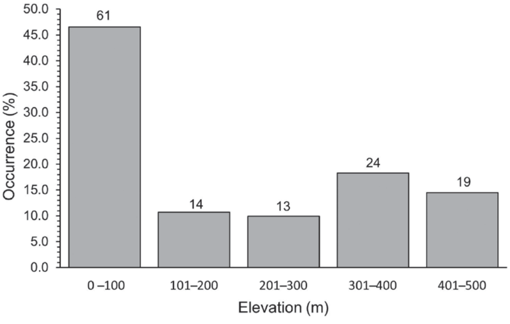

FIGURE 3. The occurrence of 131 Fisher (*Pekantia pennanti*) observations by elevation since 2002 on Cape Breton Island, Nova Scotia, Canada. The number of observations per elevation category is shown above the bar.

The Strait of Canso may be an important filter for several species, especially those in which populations are expanding in Nova Scotia in response to climate change. Populations of temperate–boreal mammals, such as Fisher, American Marten, and Moose (*Alces americanus*) are predicted to shift northward as temperature and snow conditions change (Murray *et al*. 2006; Krohn 2012; Lawler *et al*. 2012; Weiskopf *et al*. 2019). Historically, the ability of these species to cross the Strait of Canso to CBI was restricted by the lack of a causeway and no winter ice formation. Moose and American Marten, which had both been almost extirpated from CBI by the early 1900s and 1980s respectively, were re-established by human reintroduction and augmentation programs (Benson and Dodds 1977; Nova Scotia American Marten Recovery Team 2006). For other species, including Fisher, the periodic formation of an ice corridor after the causeway was built in 1955 appears to have facilitated immigration to the island. However, such an ephemeral wildlife corridor may become more sporadic as ice formation is predicted to decrease along coastal areas of the Maritimes in a warming climate (Mudryk *et al*. 2018).

Author Contributions

Writing – Original Draft: G.R.M.; Writing – Review & Editing: G.R.M., L.I.D., G.H.W., and G.J.F.; Conceptualization: G.R.M., L.I.D., and G.J.F.; Investigation: G.R.M., L.I.D., and G.H.W.; Formal Analysis: G.R.M.; Funding Acquisition: G.R.M. and L.I.D.

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Note

Salmon Shark (*Lamna ditropis*) scratching behaviour using floating anthropogenic debris

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Abstract

Observations of animal behaviour in the open ocean are relatively rare. However, while conducting surveys in the Northeast Pacific in the summers of 2019 and 2021, we encountered two Salmon Shark (*Lamna ditropis*) using floating anthropogenic debris to scratch their bodies. We captured the activity with aerial (drone) and underwater cameras. We document and describe this novel behaviour as high energy, high impact, repetitive, fast, and long lasting (e.g., every ~15 s for >20 minutes). We explore these observations in light of traditional ecological knowledge and scientific literature.

Key words: Shark; animal behaviour; scratching; Salmon Shark; *Lamna ditropis*; parasites; marine pollution; changing ocean; traditional ecological knowledge; drone

Sharks are keystone species found throughout the world's oceans, from coastal waters to the high seas. Nearly 30 oceanic species are known (Compagno 2008), but open ocean observations are relatively rare as humans visit these vast areas infrequently. Salmon Shark (*Lamna ditropis*) is a common oceanic and coastal species found in the subarctic and temperate waters of the North Pacific (McFarlane and King 2020). These sharks segregate by size and sex, undergo lengthy seasonal migrations, and follow schools of salmon around the Pacific basin; as members of the endothermic Lamnidae family, they have high metabolism and elevated body temperatures, which enable them to swim relatively fast (Goldman and Musick 2008; Manishin *et al.* 2019; McFarlane and King 2020). In short, they have evolved to be efficient long-distance swimmers in the open ocean. Satellite tagging and tracking technology have enabled the mapping of their large-scale movement offshore (Weng *et al.* 2008; Block *et al.* 2011; Coffey *et al.* 2017; Garcia *et al.* 2021), but little information exists regarding their fine-scale activities and behaviours. Here we describe two encounters with Salmon Sharks hundreds of kilometres offshore from the traditional territories of the Nuu-chah-nulth and Kwakwaka'wakw Nations, what is now known as northern Vancouver Island, British Columbia, Canada (Figure 1, Table 1).

In 2019 and 2021, scientists from the Nuu-Chah-Nulth Tribal Council, Council of the Haida Nation, Fisheries and Oceans Canada (DFO), and partners were conducting deep-sea research in the proposed Tang.ɢ̱wan-ḥačxʷiqak-Tsig̱is Marine Protected Area (MPA). In 2019, we were in the small auxiliary vessel deploying scientific equipment when we intercepted a barnacle-encrusted anthropogenic log (cut flat at both ends) drifting toward a deployed C-PROOF Glider (an autonomous oceanographic profiling instrument;

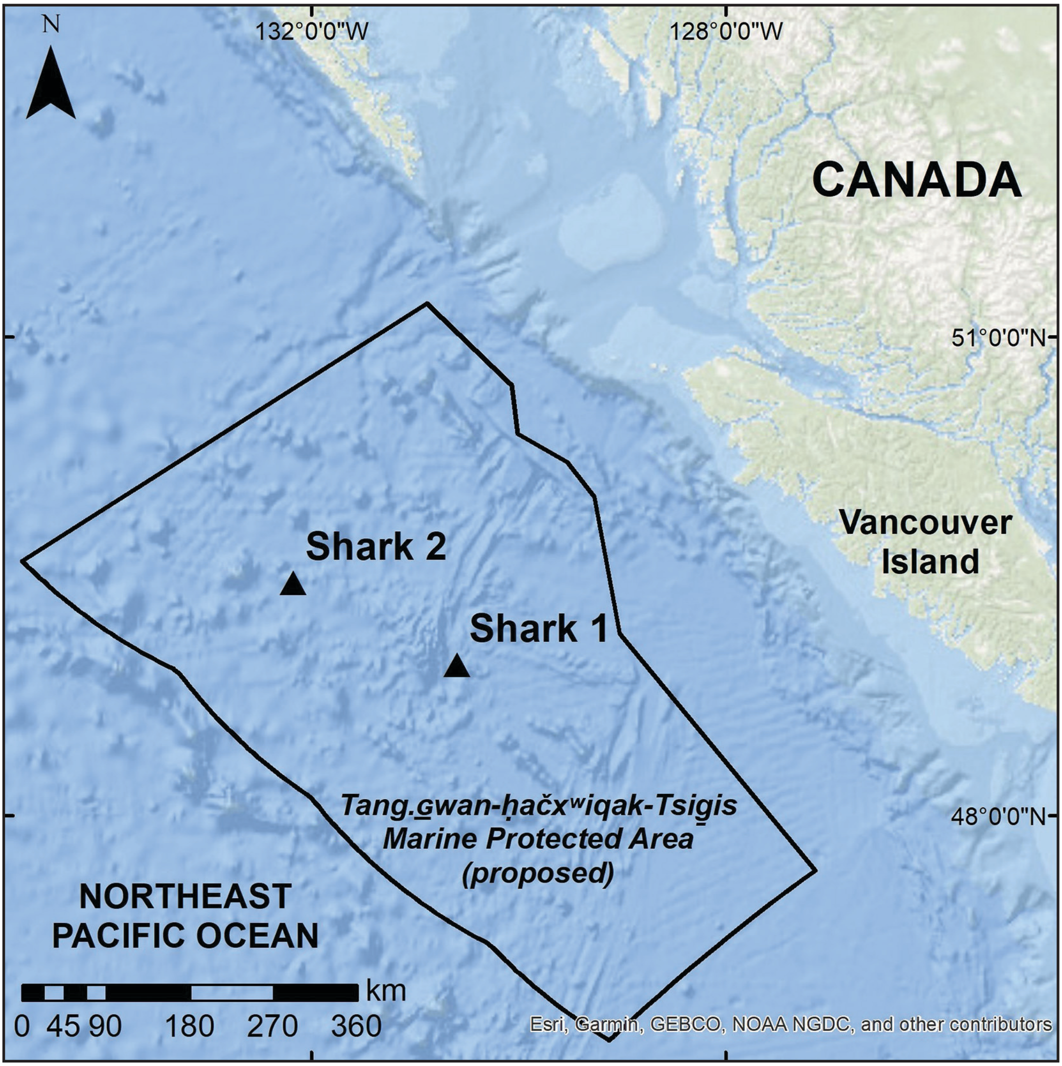

FIGURE 1. Locations of Salmon Shark (*Lamna ditropis*) observations in the proposed Tang.ɢ̱wan-ḥačxʷiqak-Tsig̱is Marine Protected Area, offshore from the traditional territories of the Nuu-chah-nulth and Kwakwaka’wakw Nations, of what is now known as Vancouver Island, British Columbia, Canada.

University of Victoria 2022). To avoid damage to the scientific equipment, we used rope to secure the log and tow it out of the vicinity. A shark appeared immediately after the log was released and began exhibiting a scratching behaviour (Figure 2a,b, Figure 3). The team in an auxiliary vessel filmed the interaction above and below water and radioed to launch a drone from the Canadian Coast Guard Ship *John P. Tully* to capture aerial footage. The behaviour was ongoing when the log and shark drifted out of sight. In 2021, we came across another Salmon Shark already engaged in scratching, this time on a square piece of fibreglass (Figure 2c). Again, the team launched a drone from the *John P. Tully* to capture aerial footage of the interaction. Unfortunately, high winds and poor sea state limited the duration of the drone flight and prevented ship-based photography.

The 2019 and 2021 photos and videos were annotated to assess the nature and frequency of the scratching behaviour, count parasites, and measure lengths. VLC media player 3.0.8 Vetrinari (VideoLAN Organization, Paris, France) was used for video playback, ImageJ 1.53m (https://imagej.nih.gov/ij/download.html) was used for reviewing photos, and scaling was based on the known dimensions of the auxiliary vessel. In addition to describing and discussing

TABLE 1. Summary of Salmon Shark (*Lamna ditropis*) scratching behaviour using floating anthropogenic debris in the open ocean of the Northeast Pacific.

	Shark 1, male 1.9 m	Shark 2
Date and time	19 July 2019	25 June 2021
Location	East of Explorer Seamount	Above UN 13 Seamount
Coordinates (lat., long.)	49°00′39.5362″N, 130°36′54.9091″W	49°29′47.1942″N, 132°11′01.1501″W
Distance offshore	250 km	300 km
Footage and camera(s)	From boat and GoPro HERO7* Aerial: DJI Mavic 2 Zoom drone*	Aerial: DJI Mavic 2 Pro drone*
Duration of observation	29 min	20 min
Duration of documentation	GoPro: 26 min, drone: 14 min (11 min overlap)	12 min
Imagery	GoPro: 9 videos totalling 9 min 43 s (mp4, 1920 × 1440) Drone: 14 videos totalling 4 min 49 s (mp4, 2688 × 1512) and 153 stills (20 JPGs and 133 DNGs)	Drone: 13 videos (mp4, 3840 × 2160) and 45 stills (jpeg, 5472 × 3648)
Anthropogenic debris	2-m barnacle-encrusted log	Square of fibreglass, size undetermined
No. of scratching events	48 (GoPro: 10, drone: 24, both: 14)	41
Average frequency (s between events)	16.7 s (avg. for GoPro: 17.3 s; avg. for drone: 15.7 s)	11.4 s

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our findings below, we provide summary information (Table 1), details on our image-based observations (Table S1), example photos (Figure 2), a science field note drawing of the 2019 observation (Figure 3), and example video clips in Video S1 with a shorter sequence at DFO (2019).

The Salmon Shark observed in 2019 was a large male, approximately 1.9 m in length, with visible parasitic copepods (Figure 2b, Video S1; DFO 2019). We filmed 48 repetitive scratching events in 26 min of usable footage i.e. total duration of stop and start recording. The shark followed the log at the surface and hit it with such force that the animal would sometimes breach as it slid across the 2 m length of the log (Figure 2a), crushing and dislodging attached barnacles (Video S1). The shark often contacted the ends of the log, which had the largest clumps of gooseneck barnacles. After making contact, the shark would immediately circle back and repeat the behaviour. On average, scratching occurred every 16.7 s (range 14.5–20.0 s). The shark scratched its ventral, dorsal, and lateral sides and fins (32%, 32%, 24% of the 48 interactions, respectively, and 12% undetermined) and often scratched the same body part repeatedly. Despite forceful slides against the encrusting barnacles, we observed no visible change in the number of large parasites on the dorsal and pectoral fins of the shark (12 copepods) and no visible injuries were sustained (no cuts or blood).

In 2021, unfortunately, we could not resolve the length, sex, or parasites of the shark, the debris-encrusting taxa on the fibreglass, or the size of the fibreglass, because of the constraints associated with use of aerial cameras; however, measuring relative size and distance was still possible. In 2021, the Salmon Shark's behaviour was similar to that in the 2019 observations, with one notable difference: this shark scratched almost exclusively by rolling under the fibreglass with its pelvic fins up (Figure 2c, Video S1). This difference in behaviour could be a response to the differences in debris (i.e., the piece of fibreglass was thin, smaller than the shark, and lay flat on the surface, whereas the log was round, larger than the shark, and protruded above the surface). We captured 41 scratching events in 12 min of usable footage. On average, a scratch occurred every 11.4 s (range 10.6–12.5 s). The shark scratched its ventral side and fins predominately (83% of the 41 interactions, 7% dorsal, and 10% undetermined). The shark stayed close to the fibreglass, circling back when it reached a distance of 3.3 times its body length on average.

In summary, the scratching behaviour of these Salmon Sharks is high energy (partly breaching at times), high impact (dislodging fouling animals on the debris), repetitive (once every ~15 s), fast (short turnaround distance), and long lasting (at least 20 min but could be much longer). This behaviour is very conspicuous, easily noticed in 2019 despite our low-lying perspective, and again in 2021 despite the large swell and choppy conditions. That said, we reviewed local Nuu-chah-nulth traditional ecological knowledge and the scientific literature and found little to no

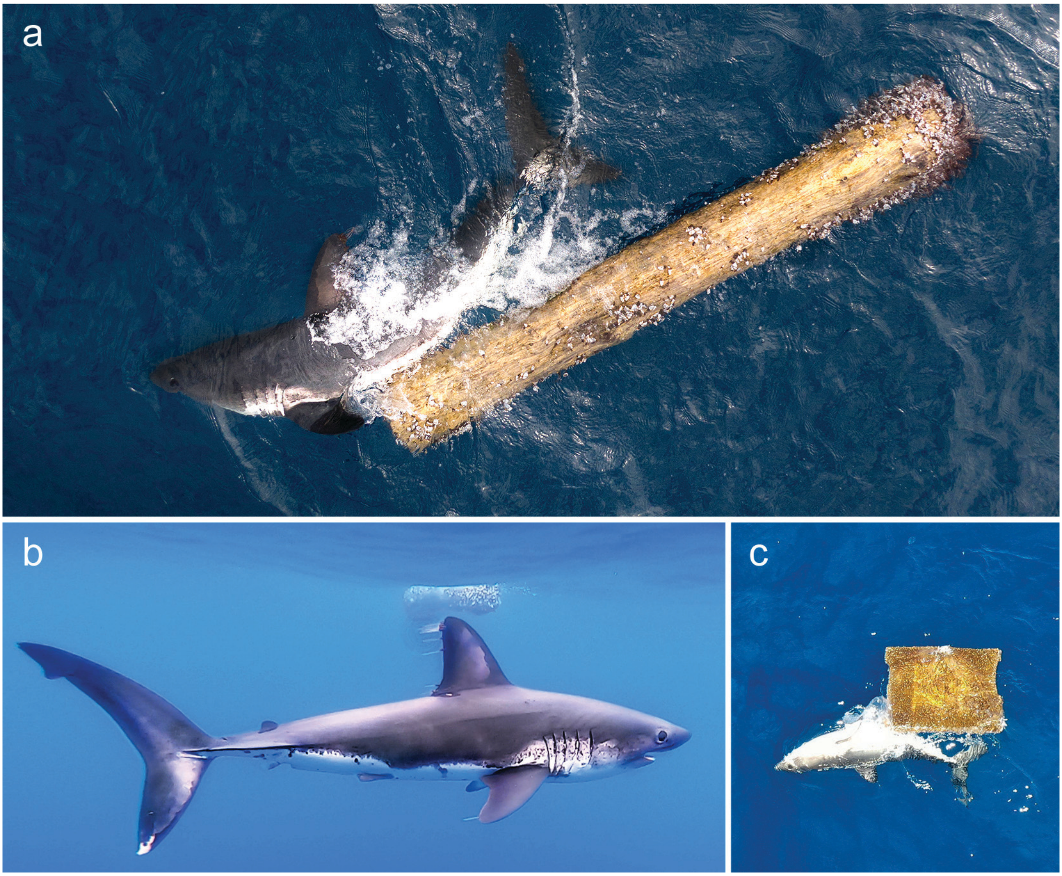

FIGURE 2. Salmon Shark (*Lamna ditropis*) scratching behaviour using floating anthropogenic debris in the open ocean of the Northeast Pacific in 2019 (a,b) and 2021 (c), captured using drones and an underwater camera. a. Shark using a barnacle-encrusted log. b. Parasitic copepods on the shark's fins. c. Shark using a square of fibreglass. Photos: a. Shelton Du Preez. b, c. Cherisse Du Preez.

pre-existing documentation of this scratching behaviour in Salmon Sharks. We did learn of another Salmon Shark sighting in the coastal waters of Monterey Bay, California, USA, where an individual shark was scratching against a log (K. Cummings pers. comm. 1 May 2021), and we found a single mention in the literature of another shark species, Blue Shark (*Prionace glauca*), scratching with anthropogenic debris (a floating fish box; Lyne and Quigley 2013). However, sharks scratching along natural substrates appears to be more common and has been documented for Bonnethead Shark (*Sphyrna tiburo*; Myrberg and Gruber 1974), Blacktip Shark (*Carcharhinus limbatus*; Ritter 2011), Caribbean Reef Shark (*Carcharhinus perezi*; Ritter 2011), and Grey Nurse Shark (*Carcharias taurus*; Smith *et al*. 2015). Sharks even use other sharks as scratching substrates (Williams *et al.* 2022).

Our novel documentation of Salmon Shark scratching along anthropogenic debris in the open ocean raises potential future research questions. Could oceanic sharks have evolved this scratching behaviour on naturally adrift trees and now be shifting to floating anthropogenic debris? Do encrusting fauna and olfaction contribute to sharks' ability to locate debris? What are the associated costs and benefits of the scratching behaviour?

We surmise that scratching an itch is the most likely benefit and explanation of our observed Salmon Shark behaviour, because we saw no evidence of feeding and no conspicuous conspecifics or other species in the area; so, the behaviour is not likely signalling. Itch sensation and scratching behaviours are primary responses to ectoparasite loads, as documented in primates (Duboscq *et al.* 2016). Williams *et al.* (2022) compiled observations of 47 incidents of fish scratching against sharks; this work contains numerous citations about scratching behaviour in aquatic environments and speculates why fish and sharks

FIGURE 3. A field note drawing in the style of Nuu-chah-nulth traditional art by expedition member and co-author Hawilh-Wayanis (Joshua Watts) illustrating the 2019 shark encounter. A human figure is depicted aboard a vessel witnessing the Salmon Shark (*Lamna ditropis*) scratching behaviour. The rounded or arched shark represents the frequent circling of the animal back to the log. The shark's silhouette includes many faces depicting the visible parasitic copepods. The use of a canoe silhouette honours the Nuu-chah-nulth Peoples' long history as oceanic explorers and fishers. Such Indigenous traditional art is a highly successful way of knowing and sharing ecological knowledge and natural science. Drawing: Hawilh-Wayanis (Joshua Watts).

may scratch. Sharks are highly parasitized animals (Ciara and Healy 2004) and sharks infested with ectoparasites may suffer a variety of health consequences, including anemia and debilitating skin disease (summarized in Oliver *et al.* 2011). We were able to see obvious ectoparasitic copepods in the 2019 footage (Figure 2b, Video S1). Although none of the visible parasites were dislodged, parasite removal may only be a bonus of scratching. The primary driver is likely the ability to respond to the itch sensation with debris during a long, open ocean journey.

When anthropogenic debris includes lines, sharp objects, or fishing gear, scratching behaviour could have a high associated cost, putting Salmon Sharks at risk of injury, entanglement, and even mortality (Parton *et al.* 2019). Floating anthropogenic debris is one of the most pervasive problems plaguing global oceans (Sheavly and Register 2007). Winds and surface currents carry debris across the ocean, concentrating it in massive gyres and along shorelines (Luna-Jorquera *et al*. 2019). Although area-based management, such as the proposed Tang.ɢ̱wan-ḥačxʷiqak-Tsig̱is MPA, can relieve stressors related to human activities, reducing floating anthropogenic debris requires global actions (Luna-Jorquera *et al.* 2019). The recent and rapid accumulation of debris in the Northeast Pacific Ocean is a source of alarm, particularly for Indigenous coastal communities whose traditional ecological knowledge provides historical context (SSTOA and WTA 2020). The region's debris includes adrift logs from the timber industry (e.g., our 2019 observation), derelict fishing gear, vessels, and mooring buoys (Gonor *et al*. 1988; SSTOA and WTA 2020). Debris impacts wildlife behaviour and fitness and can affect individuals, populations, and species (SCBD 2012). The Secretariat of the Convention on Biological Diversity has reported adverse impacts of debris for more than 663 marine species (SCBD 2012). Some impacts are well studied, particularly those on marine mammals, sea turtles, and sea birds (e.g., entanglement and ingestion, SCBD 2012); however, an ocean full of interactions is yet to be investigated.

In the last decade, drones and underwater cameras have become accessible and affordable, offering new opportunities for documenting and studying animal behaviours and fine-scale activities (e.g., Butcher *et al.* 2021; Schad and Fisher 2022). Drone technology, in particular, has proven extremely valuable for capturing wild shark behaviour, sometimes for the first time (Butcher *et al.* 2021), as in our case. Although the main objective of our 2019 and 2021 expeditions was to study the deep sea, we were able to respond quickly to opportunistic animal encounters at the surface because we had these camera systems and trained operators. As such, our overall Tang.ɢ̱wan-ḥačxʷiqak-Tsig̱is MPA research program has benefited from monitoring pelagic animals in areas that are difficult to access, sharing footage in support of open science (similar to Giersberg and Meijboom 2022), supporting citizen science (e.g., DFO 2022), and science outreach and communication (e.g., DFO 2019). Additional advantages include minimal influence on the animals from the presence of an observer and footage that could be archived and reviewed for multiple objectives (Butcher *et al.* 2021; Giersberg and Meijboom 2022). For example, by resolving the sex of the 2019 shark, we collected rare information regarding the open ocean distribution of male Salmon Sharks (Garcia *et al.* 2021). Research endeavours in unfrequented areas should consider incorporating drone and underwater camera operations to enhance opportunities to photo-document data-deficient species (Schofield *et al.* 2019; Butcher *et al.* 2021; Schad and Fisher 2022), such as marine mammals, sea turtles, and, of course, sharks.

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Author Contributions

Writing – Original Draft: C.D., H.N.G., and L.C.; Writing – Review & Editing: C.D., H.N.G., H.-W., L.C., S.D., and T.N.; Visualization: C.D., H.-W., and S.D.; Conceptualization: C.D., H.N.G., H.-W., L.C., S.D., and T.N.; Investigation: C.D., H.N.G., H.-W., L.C., S.D., and T.N.; Methodology: C.D., H.-W., S.D., and T.N.; Formal Analysis: C.D.; Funding Acquisition: C.D. and T.N.

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SUPPLEMENTARY MATERIALS:

Table S1. Image-based records of Salmon Shark (*Lamna ditropis*) scratching events.

Video S1. Natural history footage of Salmon Shark (*Lamna ditropis*) scratching behaviour.

The Canadian Field-Naturalist

Erratum

A synopsis of lycophytes in Manitoba, Canada: their status, distribution, abundance, and habitats

Staniforth, R.J., and D.F. Brunton. 2022. A synopsis of lycophytes in Manitoba, Canada: their status, distribution, abundance, and habitats. Canadian Field-Naturalist 136(2): 107–121. https://doi.org/10.22621/cfn.v136i2.2669

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Brunton, D.F. 2022. Erratum: a synopsis of lycophytes in Manitoba, Canada: their status, distribution, abundance, and habitats. Canadian Field-Naturalist 136(3): 281–283. https://doi.org/10.22621/cfn.v136i3.3137

The second half of couplet 7 in the key should be to couplet 12, not 11.

Key to Lycophytes of Manitoba

The following key includes all lycophyte taxa confirmed from Manitoba. It is based on the keys in Staniforth (2012) as modified by subsequent literature (e.g., Gilman and Testo 2015; Testo *et al.* 2016; Palmer 2018; Grigoryan *et al.* 2020) and personal experience of D.F.B. Each taxon is individually addressed in the Annotated Checklist.

1. Terrestrial, creeping; with above-ground or subterranean rhizomes (horizontal stems); upright shoots covered by numerous small, evergreen leaves **4**
– Submerged aquatic; globose corm topped by a crown of long, quill-like leaves .... (Isoetaceae) **2**

2. Individuals larger than typical plants of the population; megaspores polymorphic, often lens-shaped (aborted); densely congested ornamentation pattern includes both spines and muri (ridges) .... ***Isoetes* ×*hickeyi***
– Plants uniform in size within the population; megaspores uniformly globose (viable); ornamentation either exclusively echinate or with muri **3**

3. Leaves light green; moderately to strongly reflexed; megaspores small (450–525 µm), ornamentation uniformly, densely echinate (spiny); no equatorial band .... ***Isoetes echinospora***
– Leaves dark green to green-brown; straight to slightly recurved; megaspores large (650–800 µm), broken reticulate pattern ornamentation of thin-walled muri; prominent equatorial band of densely distributed papillae (minute tubercles) .... ***Isoetes macrospora***

4. Sporangia in the axils of specialized leaves (sporophylls) clustered into strobili (cones) at shoot summit; no gemmae (vegetative buds) **5**
– Sporangia in the axils of ordinary stem leaves and not arranged in strobili; gemmae conspicuous on shoots .... (*Huperzia*) **17**

5. Plants tall (>4 cm), resemble large moss plants or miniature coniferous trees; strobili cylindrical, megaspores small (<100 µm) **6**
– Plants short (<4 cm), resemble small (often matted) moss plants; strobili typically four-sided, megaspores large (>300 µm) .... (Selaginellaceae) **20**

6. Plants annual, small; stem prostrate and creeping; strobili "bushy" with green leaves; spores rugulate .... ***Lycopodiella inundata***

– Plants perennial, robust; sprawling or erect; stem upright or low arching, strobili narrow with appressed scales, on thin, erect stems; spores reticulate **7**

7. Leafy shoots (branches) narrow (2–6 mm), flat; leaves 4–5 ranked along stem .... (*Diphasiastrum*) **8**
– Leafy shoots wide (5–12 mm), round; leaves many-ranked along stem **12**

8. Horizontal stems on or near soil surface (often hidden under litter); peduncles with 1–2 strobili **9**
– Horizontal stems deeply buried in soil; peduncles with 2–4 strobili **10**

9. Solitary strobilus sessile; abaxial (underside) leaves arched, trowel-shaped, slightly shorter than other branch leaves .... ***Diphasiastrum alpinum***
– 1–2 strobili peduncled; abaxial leaves appressed, narrowly deltoid, much shorter than other branch leaves .... ***Diaphasiastrum complanatum***

10. Plants short (<10 cm); strobili sessile or stalked <1 cm; leaves divergent, ascending, separate or partially overlapping .... ***Diphasiastrum sitchense***
– Plants short (10–15 cm tall); strobili long stalked (2–10 cm); leaves strongly appressed, overlapping ... **11**

11. Branches narrow (<2 mm), round to square in cross-section; strongly ascending (“popped-umbrella” form); leaves glaucous blue-green colour .... ***Diphasiastrum tristachyum***
– Branches wide (>2 mm), flat; sprawling arrangement; leaves glossy dark-green colour .... ***Diphasiastrum ×zeilleri***

12. Strobili long stalked; leaves densely arranged about stem in groups of 6–10, softly hair-tipped (not prickly) .... (*Lycopodium*) **13**
– Strobili sessile; leaves loosely arranged about stem in groups of 3–5, acute to spine-tipped (prickly) **14**

13. Peduncles typically with solitary strobilus; stems sparsely branched, ascending to erect; leaves 3–5 mm long, appressed .... ***Lycopodium lagopus***
– Peduncles typically with 1–5 strobili; stems frequently branched, sprawling; leaves 4–6 mm long, divergent .... ***Lycopodium clavatum***

14. Leaves about the stem in groupings of 4–5; leafy rhizome superficial .... (*Spinulum*) **15**
– Leaves about the stem in groupings of 3; naked rhizome subterranean .... (*Dendrolycopodium*) **16**

15. Strobili 1.5–4.5 cm long; leaves toothed, 5–10 mm long; those immediately above annual constriction widest at or near mid-length .... ***Spinulum annotinum***
– Strobili <1.7 cm long; leaves entire, 3–6 mm long; those immediately above annual constriction widest at or near base .... ***Spinulum canadense***

16. Leaves along stem strongly appressed (stem smooth); single rank (row) of leaves on abaxial side of branches .... ***Dendrolycopodium hickeyi***
– Leaves along stem strongly divergent (stem prickly); double rank (rows) of leaves on abaxial side of branches .... ***Dendrolycopodium dendroideum***

17. Leaves wide (1.5–2.0 mm), toothed, parallel-sided or widest above middle, dark green; always shiny; annual constrictions on stem conspicuous **18**
– Leaves narrow (1.0–1.25 mm) entire, widest near base; yellow-green to green; dull to somewhat shiny; annual constrictions on stem inconspicuous **19**

18. Leaves coarsely toothed, widest above middle; spore regular in shape (viable) .... ***Huperzia lucidula***
– Leaves entire or with few teeth, parallel sided; spores misshaped (aborted) .... ***Huperzia ×buttersii***

19. Gemmae arranged in single whorl at apex of annual growth segment .... ***Huperzia selago***
– Gemmae scattered along stem or arranged in several whorls at apex of annual growth segment .... ***Huperzia continentalis***

20. Delicate, mat-forming; leaves divergent, flat, narrow, acute-tipped and with numerous coarse marginal cilia .... ***Selaginella selaginoides***
– Dense tufted clumps; leaves strongly appressed, oblong, bristle-tipped, with few fine marginal cilia **21**

21. Leaf tip bristles 1.25–2.0 mm long; dense clumps appearing “frosty”; upper leaves longer than lower .... ***Selaginella densa***
– Leaf tip bristles 0.5–1.0 mm long, loosely arranged to dense clumps green; upper and lower leaves

approximately equal in length .... ***Selaginella rupestris***

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The Canadian Field-Naturalist

A tribute to George William Argus, 1929–2022

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The genus *Salix*, the willows, is widely acknowledged by amateur naturalists and professional botanists alike to be among the most perplexing and challenging genera of flowering plants. There are about 400 species and numerous subspecific kinds of willows worldwide, with about 62 species native to Canada. To attempt an understanding of this complex and diverse group requires patience, intelligence, a clear head, a willingness to work in the field from the Arctic to the subtropics, humility, and a healthy sense of humour. George W. Argus, one of the foremost experts on willows of the world for over 60 years, was such a person, and he left us on 21 October 2022.

George loved the outdoors, camping, collecting plants, and climbing mountains. He successfully climbed Mount McKinley, now Mount Denali, in April 1954 when he was 25 (Figure 1) and was nearly killed by a fall on the descent (Egan 2004; Belyaeva and Chamberlain 2014). It therefore may come as a surprise that he grew up in the most urban of settings, the Flatbush area of Brooklyn in New York City. He was born on 14 April 1929, and spent his childhood living in a Brownstone rowhouse above the German bakery that his father owned and operated, developing street smarts to avoid the toughies in the neighbourhood, and rooting for the Brooklyn Dodgers (before they moved to Los Angeles).

George was an enthusiastic student and originally wanted to be an engineer, attending Valparaiso University in northern Indiana for two years. He had a strong desire for adventure and decided to explore Alaska with a buddy while still a student at Valparaiso. With no particular plan in mind, he borrowed some money from his father, bought a truck, and drove north in 1949 (by himself; his friend decided not to go). Once there, he took a job as a labourer on the Alaska Railroad cutting brush and maintaining the roadbed. He then found work as a lineman's assistant in the gold mines of central Alaska, doing some paleontology on the side and developing an interest in geology and botany. The rugged beauty and adventure of Alaska appealed to George more than engineering in Indiana, so he switched to a biology and geology program at the University of Alaska Fairbanks, completing his undergraduate degree in 1952. It was in Fairbanks that he developed his interest in botany and systematics. It was also in Alaska that he developed an interest in Mary Smirnoff, a California girl whom he met at the university. The two were married

Figure 1. George Argus in 1954 at the time when he and his party climbed to the summit of Mount McKinley. Photo: Mary Argus.

in 1955, after he recovered from the fall he suffered on Mount McKinley.

After graduating, George applied for a Master's degree program at the University of Wyoming. His advisor, Dr. John F. Reed, was documenting the flora of Wyoming and casually suggested that George take up a study of the willows of Wyoming as a thesis project. As Mary told us (pers. comm. 29 November 2022), "George wasn't afraid to try anything or to take on any challenge", so the daunting task of tackling this difficult genus was readily accepted. George completed the study in 1957, which led to his first publication on the genus (Argus 1957). Hugh Raup, Director of the Harvard Forest at Harvard University, was well known for his ground-breaking studies of the vegetation of northwestern North America and had published a major treatment of *Salix* of the Hudson Bay and Labrador region (Raup 1943), so George decided to continue his doctoral studies with him, earning a Ph.D. degree in 1961 (Argus 1962).

With his strong interest in Alaskan botany and geology, George made an appropriate addition to the Institute of Northern Studies at the University of Saskatchewan in 1963. The institute had been founded only a few years before (1960) to foster multidisciplinary studies that focus on northern Saskatchewan and other parts of northern North America. Although George was active in the institute, his home base was the Department of Plant Ecology in the College of Agriculture and Bioresources. He remained on the faculty at the university for eight years teaching botany and ecology and serving as Curator of the W.P. Fraser Herbarium. He then spent a year at the University of Oregon as the curator of their plant collection, but the job was not what he hoped it would be, and so he again sought a job back in Canada. Fortunately, there was a position open at the Forest Ecology Institute of the Canadian Forest Service in Ottawa. The institute was headed by Dr. Jag S. Maini, whom George had met while in Saskatoon. George got the job and so his family traded the west coast for eastern Canada. There, he continued his botanical work at the forestry lab on Anderson Road from 1970 until 1972.

In 1972, a position for a Research Botanist became available at the National Museum of Natural Sciences (now the Canadian Museum of Nature [CMN]), and George was clearly the most qualified applicant. He served as a Research Scientist in the CMN's Botany Division from 1972 until his retirement in 1995 in various capacities including Head of the Vascular Plants Section (1984–1991; Figures 2 and 3).

The conservation of rare or endangered plants in Canada was the focus of George's work at the Forestry Service and it continued to be a high priority at the CMN. The Rare Plants of Canada project, which grew out of this interest, was innovative and thorough, resulting in a series of CMN publications from 1982 until 1995. The project involved a number of collaborators at the CMN, but also specialists in the flora of a particular province or territory. Among his coauthors were David White, Kathleen Pryer, Cheryl McJannet, Paul and Cathy Keddy, Sylvia Edlund, Jacques Cayouette, and Robert V. Maher. In keeping with his interest in rare vascular plants, George was the Canadian representative on the Convention on International Trade in Endangered Species (CITES) for 22 years. He also served for several years as Chair of the Subcommittee on Plants for COSEWIC (Committee on the Status of Endangered Wildlife in Canada).

George continued his taxonomic studies of *Salix* throughout this time, describing new species and discussing problematic groups, as well as publishing regional treatments. The first of George's major *Salix* floras dealt with Alaska and Yukon, begun while he was still in Saskatoon and published as one of the first of the CMN's "Publications in Botany" (Argus 1973a). Other regional willow treatments included Alberta, British Columbia, northern Quebec, Missouri, California, Colorado, and the southeastern United States. His vast knowledge of North American willows was put to good use when he authored a 140-page monograph on *Salix* for the Flora of North America (Argus 2010a). All these floristic and taxonomic treatments involved field work and thorough studies of herbarium specimens. As a result of collecting material for these projects, as well as documenting his many field experiments in the hybridization of willows, George has made the National Herbarium of Canada at the Canadian Museum of Nature (CAN) one of the world's most important centres of study for the genus *Salix.*

George's knowledge of plants was by no means limited to the willows. Soon after George came to the CMN he became involved in Hugh Raup's on-going studies of the flora of northern Canada begun in the 1930s. They collaborated in a study of the ecology, evolution, and endemism of the flowering plants living in the sand dunes around Lake Athabasca requiring several seasons of field work in Alberta (Raup and Argus 1982).

George had an interest in the computerization of herbarium data since his days at the University of Saskatchewan. There, he worked with lichenologist John Sheard of the Department of Biology, College of Arts and Sciences, on capturing herbarium data using the computer techniques being used at that time (Argus and Sheard 1972). In 1984, his attention turned to the use of computers in creating botanical descriptions and identification keys after hearing a lecture given by Dr. Susan Aiken on the subject. Dr. Aiken,

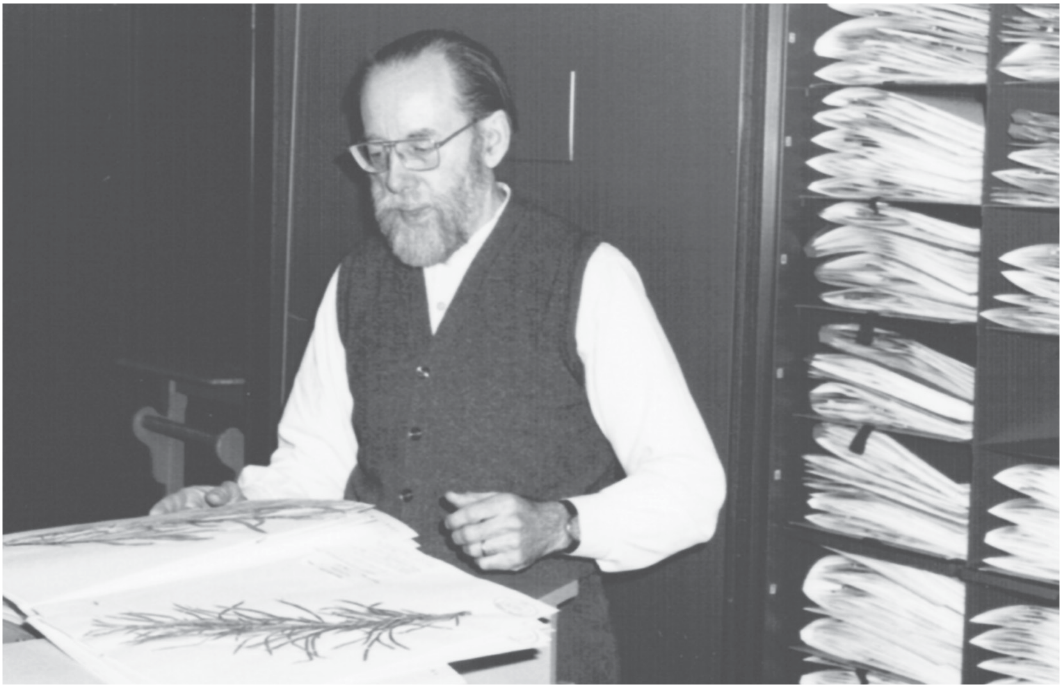

FIGURE 2. George Argus at work in the 1980s in the willows section of the National Herbarium of Canada, Canadian Museum of Nature, Ottawa, Ontario, Canada. Photo: E. Haber.

who had just joined the CMN's Botany Division, had been working with the characterization and identification of grass genera using the new DELTA (DEscription Language for TAxonomy) programs developed in Australia by Mike Dallwitz and Les Watson. With both Aiken and Argus using DELTA in their work, Dallwitz became a frequent visitor at the CMN to fine-tune the INTKEY (INTeractive KEY) and DELTA programs as they applied to preparing descriptions and keys to willows and Arctic plants. George and Susan became the local DELTA experts and helped other botanists at the CMN interested in applying these useful tools to their own groups, including I.M.B. for lichens. Over the years, George gave numerous willow identification workshops using DELTA (Figure 4).

George was an enthusiastic and excellent field botanist, collecting plants throughout North America and even in Siberia with his colleague, Dr. Alexei Skvortsov. George, together with I.M.B., E.H., and phycologist Paul Hamilton, had a memorable CMN excursion in 1977 to four remote, subalpine localities in the mountains of northeastern British Columbia: Wokkpash Lake, Fairy Lake, Robb Lake, and Fern Lake (Figure 5). George was in top form, instructing us all on how to negotiate extremely steep scree slopes with a walking pole (on the up-hill side to keep you vertical). He was also quite adept and resourceful at stream crossings even with his willow-basket backpack laden with plants (Figure 6). He showed us how to collect willows, and the advantages and pleasures of adding some rum to your tea before crawling into your sleeping bag (Figure 7).

FIGURE 3. Botanists at the Botany Division of the Canadian Museum of Nature, Ottawa, in April 1986. The occasion celebrated the acquisition of the 500 000th specimen (not a willow) in the National Herbarium of Canada (CAN). From left to right: Erich Haber, Susan Aiken, George Argus (Head, Vascular Plant Section), Michel Poulin, Bob Ireland, and Ernie Brodo. Photo: E. Haber.

George Argus had many friends and admirers in Ottawa, throughout North America, and abroad. His

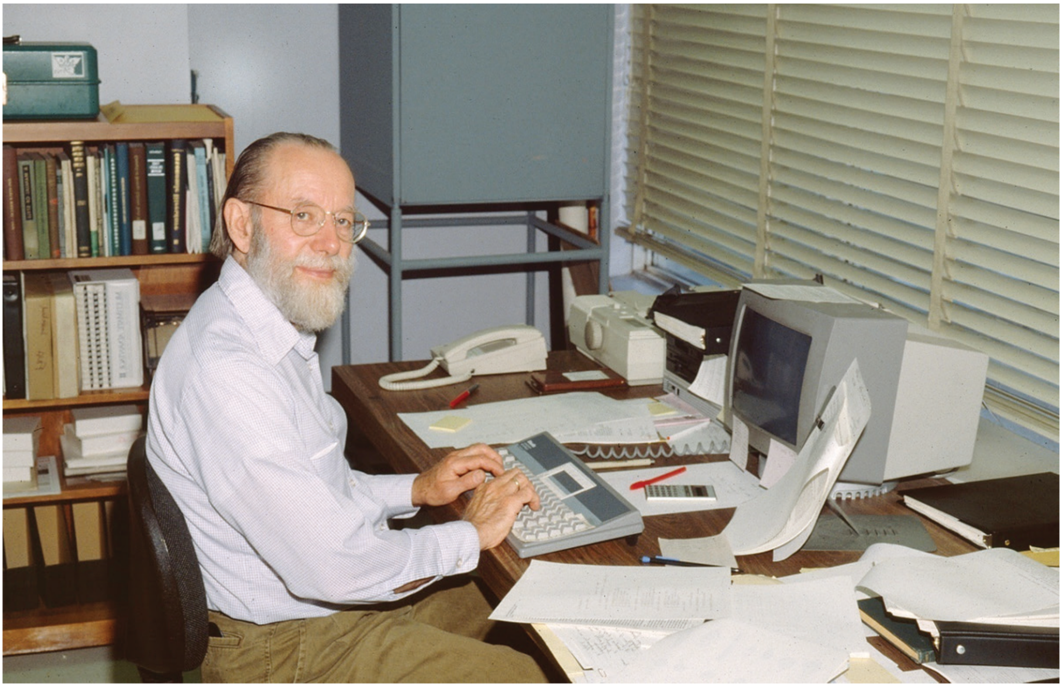

FIGURE 4. George Argus at his computer at the Botany Division in 1992 entering willow data used in the DELTA system identification programs. Photo: E. Haber.

FIGURE 5. Lunch break at 1607 m beside a small alpine lake to the west and above the Wokkpash Lake campsite, northeastern British Columbia (22 July 1977). From the left: George Argus, Paul Hamilton, and Ernie Brodo. Photo: E. Haber.

keen intellect and knowledge made him a valuable member of the CMN's Botany Division, and his wit, humility, and caring nature made him a cherished friend. George had a noticeable stammer when speaking, but that never prevented him from becoming an excellent, effective lecturer and teacher … or singer. He was a devoted member of the North Grenville Concert Choir. He relished being outdoors, whether walking around his small farm in Burritts Rapids or on a trail in Alaska. He enjoyed canoeing and kayaking, making pottery, playing the banjo, and especially traditional country dancing, actively participating in the Country Dance and Song Society and 12th Night Society of Ottawa. He even sewed his own costumes … by hand! At various times, together with his wife, Mary, he raised chickens and kept bees and, of course, had a marvelous vegetable garden. He did not like television (and didn't own one) and avoided computers as much as he could, other than using them for the DELTA work. Smart phones? No thank you.

During a visit to the herbarium at Harvard with E.H., George decided to take in an introductory talk on Transcendental Meditation given by the internationally renowned yoga guru, Maharishi Mahesh Yogi. On returning to Ottawa, George enrolled in such a course and practiced meditation for many years. He also participated in Tai Chi lessons during botany coffee breaks. This was taught to a number of us by I.M.B.'s lab assistant, Pak Yau Wong, who practiced Tai Chi every morning before his start of the day.

In the course of his professional career, George was awarded many scholarships, grants, and fellowships. He also received several major honours for professional contributions in science and conservation. George's systematic work on willows was recognized when he received the Gleason Award of the New York Botanical Garden "for an outstanding recent publication in plant systematics" for his monograph, The genus *Salix* in the southeastern United States (Argus 1986a). Three other awards reflect George's contributions to the conservation of rare and endangered plants. In 1983, he, together with David J. White, received the Conservation Award of the Federation of Ontario Naturalists. It was "awarded to individuals within the public service in recognition of a valuable contribution to and support for environmental issues". This was with respect to the Atlas of the Rare Vascular Plants of Ontario. The George Lawson Medal from the Canadian Botanical Association was awarded for an outstanding scientific achievement with respect to the Rare and Endangered Plants Program at the CMN in 1991. In 2008, he received the Goldie Award from the Field Botanists of Ontario, again for his role in the Rare and Endangered Plants Program.

FIGURE 6. George Argus with his traditional willow backpack fording a mountain stream. He used this backpack to carry the day's collections of plants stored in plastic bags. Photo was taken at one of the four sites the field party explored in northeastern British Columbia in 1977. Photo: E. Haber.

When in 1995 the Botany Division moved from its quarters in Ottawa to new facilities across the Ottawa River in Aylmer, Quebec, 30 minutes farther by car from his farm in Burritt's Rapids, George thought it would be a good time to retire (Figure 8). Some unfinished projects and studies nevertheless brought George to the herbarium in Aylmer from time to time, but after several years, even these visits became less and less frequent. The last few years of George's life were spent quietly, first in a retirement home with Mary and finally in long term care facilities.

Figure 7. A quiet moment in camp at the end of a long day in 1977 along the south shore of Fern Lake at 1371 m, in north-eastern British Columbia. Dinner was often followed by a good cup of tea re-enforced with a soothing touch of rum (note bottle on table). From left: George Argus, Erich Haber, and Paul Hamilton. Photo: E. Haber.

George and Mary Argus were married for over 60 years and had five children: Michael, Eric, John, Martin, and Rebecca. Michael tragically died in an accident in 1986. George also had a younger brother, Roland, and sister, Joan.

With the death of George Argus, the world has lost more than one of its greatest experts of willow taxonomy; it has lost a great human being.

Acknowledgements

In writing this tribute, we made frequent use of George's detailed *curriculum vitae*, prepared in 2012, as well as a well-written and informative biography written by Irina Belyaeva and Keith Chamberlain in celebration of George's 85th birthday (Belyaeva and Chamberlain 2014). Mary Argus was immensely helpful in providing details of George's early life in Alaska, and for checking the drafts for accuracy. Susan Aiken generously provided us with the story behind the adoption of DELTA by botanists at the Canadian Museum of Nature, and John Sheard checked and improved our comments on the Saskatoon days. We also acknowledge the help of Stephen Haber in scanning text and photographs and solving other digital problems.

Figure 8. George Argus at his retirement party in 1995, held at the Brodo's residence in Ottawa, attended by family, friends, and professional colleagues. Photo: E. Haber.

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The Canadian Field-Naturalist

Book Reviews

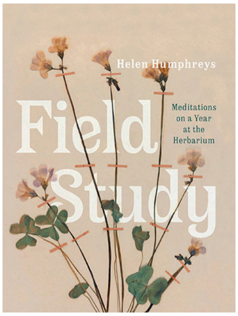
Book Review Editor's Note: *The Canadian Field-Naturalist* is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those 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.

BOTANY

Field Study: Meditations on a Year at the Herbarium

By Helen Humphreys. 2021. ECW Press. 232 pages, 32.95 CAD, Hardcover, 17.99 CAD, E-book.



Field Study is a very charming little book. Its small size and attractive cover image of a herbarium specimen evoke its theme, and the inclusion of herbarium sheet reproductions (in the form of high-quality scans), specimen labels, and plant illustrations maintains this theme throughout the book. Humphreys is a poet and novelist, and *Field Study* chronicles her one-year study of the Fowler Herbarium collection held by the Department of Biology at Queen's University Biological Station (QUBS) in Elgin, Ontario.

Book sections are organized into the four seasons of the year, and the author's comments on the passage of time flow organically throughout the book. Chapters are predominantly labelled for the plant groups that Humphreys discusses (e.g., Ferns, Pines, Grasses) as she moves through the herbarium collection. Peppered with philosophical musings and reflections from the author, most of the writing comprises short biographies (ranging from a few sentences to a few pages) of collectors who contributed to the herbarium and information about the specimens they collected. Humphreys's deep appreciation and fondness for the Fowler Herbarium and its contents are palpable, and reading this book feels a bit like looking over her shoulder as she explores the collection and the lives of the people who made it possible.

This is an easy, quick read with many full-page herbarium sheet reproductions and illustrations. Many of these herbarium sheets are sourced from the Fowler Herbarium, but several others are from the collections of Emily Dickinson and Henry David Thoreau. Superscript is used sparingly in the text to link to extra information—such as references and definitions—compiled in a Notes section at the back of the book. I appreciate that Humphreys comments on the settler-colonial history of plant collecting in several instances, highlighting the traditional Indigenous knowledge that is missing from the otherwise detailed historical botanical record stewarded by herbaria.

Whether you will enjoy this book is a question of personal interest. Although I enjoyed *Field Study*, I cannot exactly say that I would recommend it. Despite the inclusion of some plant facts and miscellany, the bulk of this book is dedicated to brief plant collector biographies that just do not appeal to me as much as other topics related to herbaria. If you are curious about the plant collectors of days gone by and wish to be steeped in a herbarium for a short while, you could do much worse than spending time with this attractive little book.

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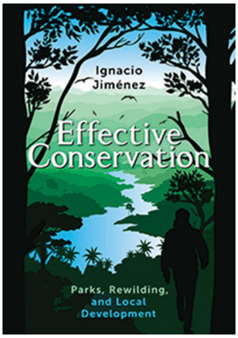
CONSERVATION AND CLIMATE CHANGE

Effective Conservation: Parks, Rewilding, and Local Development

By Ignacio Jiménez. 2022. Island Press. 280 pages and 39 illustrations, 45.00 USD, Paper. Also available as an E-book. First published in Spanish, 2018.



The author of *Effective Conservation*, Ignacio Jiménez, has an extensive background in conservation. In 2005, he began working with The Conservation Land Trust (CLT) Argentina, a project initiated by the co-founder of The North Face and Esprit, Douglas Tompkins. Tompkins had purchased and preserved 810 000 ha (more than 2 million acres) of property in Chile and Argentina in the early 1990s, establishing a series of parks. At CLT Argentina, Jiménez worked on endangered species recovery in the Iberá wetlands, a region of northern Argentina included in the new parks, and he coordinated one of the largest species reintroduction programs in the Americas. He directed the Iberá rewilding program until 2018.

In *Effective Conservation*, Jiménez promotes a style of conservation that could be described as a business management approach to ecological conservation and wildlife rescue. The book is intended as a user-friendly manual with the kinds of highlighted sidebars and explanatory charts that you might find in a textbook. There is extensive supplementary material—30% more—available to readers online (but not reviewed here). The print version focusses on strategic management (with core chapters on method, promotion, planning, operationalizing, conflict management, and evaluation and renewal) and is both comprehensive and clear. Some of this material may strike the reader as self-evident or overly utilitarian, but Jiménez sees his advocacy as a race against time and pushback against older "conservative" ideas about conservation.

Throughout, what will particularly interest field-naturalists, are very brief descriptions of efforts to restore endangered species and the longer outlines of back-from-the-brink case histories. These include the reintroduction of Black-footed Ferret in the United States (p. 85), Spain's Lesser Kestrel (p. 90), Mauritius Kestrel (p. 116), Andean Condor (pp. 92, 116), Costa Rica's manatees (p. 95 and the subject of the author's Master's thesis), Golden-crowned Sifaka in Madagascar (p. 96), Bonelli's Eagle in Spain (p. 100), Hooded Grebe in southern Argentina (p. 103), Iberian Lynx (p. 117), White Rhino in South Africa (p. 116), and Brazilian Jaguars (p. 131). He also looks at the problem of Eurasian Griffon Vulture collisions with wind turbines (pp. 98–99).

There is very little reference to climate change, considering the book's theme, although the subject looms in the background. For example, Jiménez agrees that,

> On a planetary scale, climate change does have the capacity to trigger the destruction of not only small populations but also even of abundant species and whole ecosystems and complete groups of species. (p. 88)

While that is an unequivocal position found in *Effective Conservation*, concern about climate change from anthropogenic sources seems understated.

Full Nature Conservation

The goal of conservation, the book argues, is to at a minimum slow down any threatening extinction-level crisis. This moral obligation "to put a brake on the current drift toward environmental decline" (from all causes; p. 130) will require concerted breaches of the status quo through human intervention, rewilding, and a "Full Nature" (pp. 13–31) or "institutional ecology" approach (p. 436; Child *et al.* 2012).

The Full Nature approach, Jiménez explains, incorporates a feedback cycle that includes national parks, local development, wildlife ecosystems, and restorative economies. It requires simultaneous actions to address ecological and human community health to fulfil the goal of global wilderness recovery. It may include tools such as community poverty alleviation, job creation through eco-tourism (a major theme throughout the book), and controlled recreational camping and hunting. It also responds to extermination-level hunting frenzies, cattle importation that is destructive of the livelihoods of local communities, and mining company excesses (that can be replaced by more sustainable nature tourism, such as where this has occurred in post-Apartheid South Africa [pp. 1–3]).

Successful outcomes of a Full Nature approach must therefore: establish better natural ecosystems, not utopias; tie-in local social processes (employment, decision-making); engage interdisciplinary organizations and teams (not only biological expertise); coordinate the policy processes affecting both natural and human ecosystems; and effectively communicate to the public. A tall order.

One of *Effective Conservation*'s goals is to reframe the debate away from the reductionist false dichotomy of humans versus nature. Jiménez wants us to understand conservation as an alternative type of production, but also as a more enticing counterargument to those who insist that "a tree should not get in the way of development" (pp. 14–16). This entirely pragmatic argument is necessary, Jiménez says, because in the standoff between people, wildlife, economy, and environment, people and economy always win.

Understanding the policy process as central means learning the skills of message promotion and marketing, activism and mobilization, boycotts and petitions, legal action, diplomacy, and bridging the urban-rural-Indigenous divides. This language is not typically in the biological lexicon. The route to successful conservation is complex, Jiménez argues, and therefore merely conserving biodiversity or promoting sustainable development are goals that are too vague, and likely to only deliver an "occasional pyrrhic victory" (p. 92).

The Science and the Politics

The Canadian Field-Naturalist authors and readers may be disappointed to learn that Jiménez doubts the impact of scientific papers (p. 95). Their value is not denied entirely, but other vehicles (perhaps distantly backed by research) with wider public appeal (for example, comic books and popular publications) are touted as having greater currency among the public and decision-makers.

A scientific paper, unread by most, he argues, is still important because it can be referred to as peer-reviewed, credible evidence. But scientists are often underappreciated because they are seen as early guidance rather than as tools for measurement and evaluation (p. 101). After a problem is clearly defined in a potential conservation or rewilding project, the fallback is on "robust research in population or landscape ecology" (p. 92). But ahead of this, a decision must be made as to "whether or not a species or habitat is of any particular importance to society in general" (p. 92).

This kind of language may rankle readers, but it's central to the book's thesis that some projects are too complicated and costly to be worthwhile while others are worth pursuing despite the price tag (examples include the release of Andean Condors and the restoration of Mauritius Kestrels). The goal of the science is not just to generate documentation; it is to ensure that those "put in charge of drafting the conservation plans" are also the experts in the field for the species-at-risk (p. 111). However, the experts on a particular species may know nothing about managing a public conservation project, which is essentially a political process that must manage conflicts between conservationists and vested interests (e.g., mining, dam-building, ranching, plantations, and hunting).

Jiménez believes that 90% of conservation is about working with people. Those focussed and trained primarily in the biological sciences may fail at generating "change on the ground" (p. 220). By making conservation relevant to the wider population, he believes "we will be able to avoid—or at least, mitigate—the great Sixth Mass Extinction" (p. 232). This entails assuaging the concerns of wary "conservative" conservation professionals and activists who retain an "aversion to perverting the purity of natural ecosystems with management actions" (p. 244).

Objections to Reintroduction

As becomes clear to the reader, *Effective Conservation* has a particular bone to pick with a segment of the conservation community who at heart believe that nature will resolve existential threats without human intervention. Jiménez vehemently disagrees. He also challenges the idea that reintroduced species are inherently harmful to existing resident species. In his view,

> [f]ew cases exist of natural areas (be they public, private, or communally owned) that ever manage to maintain or even restore their natural populations without any [human] intervention. (p.144)

This explains his emphasis on establishing national parks.

Natural restoration, writes Jiménez, is "only possible in certain highly remote regions, untainted by human contact" (p. 144). The exception he offers here—remoteness—may be key, and a place where many field-naturalists and Full Nature conservation advocates meet in significant agreement.

Important points are made throughout this important book, all of which are worth thinking about right now. Many may ring true enough that they will deserve implementation.

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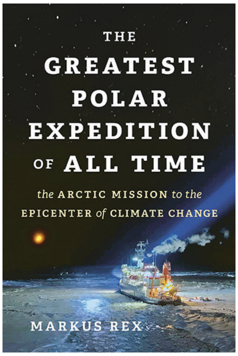
The Greatest Polar Expedition of All Time: the Arctic Mission to the Epicenter of Climate Change

By Markus Rex. Translated by Sarah Pybus. 2022. Greystone Books. 296 pages, 34.95 CAD, Hardcover.



The Arctic is warming at twice the rate of the global average and has been described as the epicentre of global climate change. The multi-year sea ice that once covered the Arctic Ocean throughout the year has nearly all melted. It's been replaced by ice that, each year, forms in the autumn and winter and melts in the spring and summer. Current climate modelling forecasts that by 2050 the Arctic Ocean will be entirely free of sea ice during the summer months. These changes have far-reaching implications, because ice at the planet's poles moderates climate across the globe. Despite the clear importance of Arctic sea ice to global climate, obtaining *in situ* measurements in the Arctic to validate models is quite difficult and expensive due to its remoteness and harsh climate.

The MOSAiC (Multidisciplinary drifting Observatory for the Study of Arctic Climate) expedition set out to bring together a large team of scientists to study one full year of the Arctic sea ice cycle. This included experts on the atmosphere, sea ice, oceanography, and ecosystem. *The Greatest Polar Expedition of All Time* is written by the chief scientist of MOSAiC, Markus Rex, and provides a detailed account of the expedition. In autumn 2019, the MOSAiC team sailed the icebreaking German research vessel (RV) *Polarstern* close to the North Pole, where they allowed it to get stuck in an ice floe. It remained locked in the ice until the spring. During this time, researchers made an unprecedented number of scientific measurements of the atmosphere, sea ice, ocean, and ecosystem around that ice floe. After breaking free of the ice in the spring, the *Polarstern* continued to the North Pole during the summer of 2020, where researchers finished obtaining measurements and completed their observations of the annual cycle of Arctic sea ice.

The MOSAiC expedition was a largely successful mission, but it also had many logistical hurdles to overcome. First and foremost, keeping a ship frozen in an ice floe in the middle of the Arctic Ocean throughout the winter required support from multiple organizations, people, and vessels. The team of researchers and support staff on the *Polarstern* rotated every few months, which required other icebreakers to break through the ice to reach the *Polarstern*. Being surrounded by sea ice and dealing with some of the coldest temperatures on Earth were significant challenges. The team also had to worry about Polar Bear encounters. To keep scientists and crew safe, there were systems in place around the ship for detecting the bears, as well as dedicated Polar Bear guards. Last, but certainly not least, the COVID-19 pandemic started in the middle of the MOSAiC expedition. The *Polarstern* was already locked into the ice when the pandemic was announced, which complicated all subsequent operations. Some countries that had previously promised support completely withdrew support, and all procedures for resupplying the expedition and changing out crew became far more complicated. Despite these significant challenges, MOSAiC was still successful in its mission.

The Greatest Polar Expedition of All Time was a really interesting book. I am biased, of course, because I read it while in the Canadian Arctic during the winter conducting my own fieldwork. However, for any field scientist, particularly an Arctic scientist, this book will not disappoint. It is written like a journal or diary, with entries for different days of the expedition. It starts off with near-daily entries that take place during the early phases of the expedition when the *Polarstern* was making its initial voyage into the Arctic Ocean to find the perfect ice floe to get stuck in. The ice floe needed to be large enough to support the ship and all of its research operations, and also needed to be older, thick ice that could hold the ship in place. The entries then get a bit farther apart, especially those written after the start of 2020 when Rex was no longer on board the *Polarstern* and was instead managing logistics remotely from Germany. Journal entries become more regular again after Rex comes back on board the *Polarstern* for the last two legs of the expedition. The book is also filled with other information about climate science and the importance of the mission, which should make it an interesting read for a general science audience who may not be familiar with Arctic fieldwork or climate science. Overall, I highly recommend this book.

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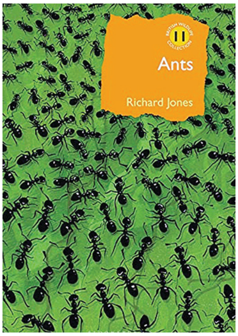
Entomology

Ants: the Ultimate Social Insects. British Wildlife Collection (Book 11)

By Richard Jones. 2022. Bloomsbury Wildlife. 368 pages, 330 colour photos and black and white illustrations, 61.00 CAD, Hardcover. Also available as an E-book.



Late in his book, Richard Jones reveals that he has been studying ants for 45 years, almost three-quarters of his time on earth. Over the years, his knowledge has grown and his enthusiasm—and sense of humour—remains undiminished. *Ants* is part of Bloomsbury's British Wildlife Collection, and although its focus is on the ants of Britain and Ireland, the book's 10 chapters contain information and observations from around the world, providing value for ant-lovers everywhere. Jones covers a good deal of territory, and the book is an amalgam of many parts. The first nine chapters fall into three sets, as discussed below. All are enhanced through the excellent use of illustrations, including many colour photographs of ants and other arthropods; reproductions from historical, scientific, artistic, and cultural sources; and line drawings of physical characters. Occasional text boxes and tables highlight additional information and data complementing the main text.

The first two chapters in the introductory set of chapters each begin with a question. Chapter 1, What's so Special about Ants?, explores why these tiny insects deserve our interest and attention. Jones begins his response with the unpromising observation that "ants are the epitome of insignificance" (p. 11). But it's size he's noting here—ants "are so very, very small" (p. 11)—and physical size matters less than "sheer numbers and sophisticated coordinated behaviour", which form their "real superpower" (p. 11). Their size, adaptability, capacity for variable social organization, and presence world-wide make ants unique among insects in the number of opportunities they provide for studies of evolution, ecology, and interrelationships with humans and other animals. Chapter 2, What is an Ant?, covers the obligatory discussion of ant morphology and taxonomy. It sounds rather dry, but Jones maintains the reader's interest through vivid description and anecdotes. The chapter concludes with What is not an Ant?, a fascinating section on ant mimics that includes other hymenopterans, as well as several hemipteran (true bug) nymphs, ant-flies, beetles, spiders, and a rather surprising caterpillar. Chapter 3 lists and describes 73 species (I counted) of ants living in Britain and Ireland, organized by family, some 50 of which are native. Jones manages to avoid being overly technical, often including historical references and cultural anecdotes in his descriptions.

The next set of three chapters explores ant evolution, an ant's daily behaviours, and the development of colonies. These topics are the heart of the book. Ant fossils are hard to come by and difficult to relate to other hymenopterans, which as a group are difficult to relate to other insect orders. As a result, much of the scientific discussion on ant evolution is speculative, focussing on the many challenges rather than the scant, hard-to-come-by conclusions. Indeed, Jones notes, "the origins of the Hymenoptera are a source of constant bafflement" (p. 119). A good deal more is known about ant behaviour and colony systems. Jones gets into the sophisticated chemistry through which ants sense their world, communicate about it, and organize themselves for defence, both individually and through collective warfare. When he discusses life in the colony, he goes well beyond the physical aspects of colony formation to explore the organization of ants in their highly variable nests. Ant societies include queen(s), nurses, workers, pirates and 'slave-makers' (a process known as dulosis), guards, and warriors. This high degree of social organization presents problems for evolutionary theory, however. The thorniest issue is the apparent altruism of the non-reproductive worker ants. The colliding theories, based in biology and mathematics, that attempt to explain this anomaly are as technical as things get in the book. Yet Jones manages to steer a clear path while lightening his review of each theory with humour and interesting examples from field research.

The final set of three chapters examines interactions between ants and humans, ants and other arthropods, and the enormous impact of ants on the physical landscape. Jones's wide-ranging approach to the first of these chapters includes a discussion of historical and cultural perceptions of ants, from ancient times to the present-day, culled from parables, the *Bible*, and the arts, including literature and movies. In the next chapter, the interactions among ants and "[p]arasites, squatters, thieves and other interlopers" (p. 254) are fascinating, myriad, and complex. Jones follows a system that organizes these interactions into five categories—Synechthran (hostile persecuted lodger), Synoekete (indifferently tolerated lodger), Symphile (true guest), Parasite, and Trophobiont—that were established in the late 19th century and are "still useful today" (p. 256). The final topic of how ants have changed the landscape shows that while some colonies are small with limited local impact, others may reach staggering sizes. These giant colonies shift immense amounts of soil that, in some cases, results in patterns on the land observable from space (p. 278). The discussion here graphically illustrates the book's major theme that very small and very numerous is a formula for "massive effect" (p. 277). Not only is the landscape affected—ecological impacts are important, too, and a wrap-up note looks at the potential effects of climate change on ants. Understanding these effects, Jones says, little known as yet, can assist in a broader understanding of climate change's impacts on all life in our interconnected world.

Chapter 10, How to Study Ants, provides excellent and detailed information for citizen scientists on finding, observing, photographing, collecting/preserving, and communicating their data and observations to the myrmecological community. Modern entomology increasingly involves specialized work in the laboratory, leaving a gap in live observations from the field. At about 12 500 species worldwide, ants are the least speciose group in the Hymenoptera, yet their secretive lives and great numbers make them challenging to study. Jones is generous in his valuation and encouragement of citizen scientists at every level—he eschews the term 'amateur' (p. 301)—to share their stories and accounts of the ants they see.

An Appendix contains a key, tied to Chapter 3, to the worker caste of British ants; most couplets contain a drawing of the character involved. A welcome Glossary and extensive Bibliography round out the book. The illustrations and photography come from a wide range of historical and modern-day sources, the writing is lively and accessible—the sole exceptions being occasional British slang terms (I had to look up 'twee'!)—and the inevitable technical aspects (haplodiploidy, for example) are lucidly presented. The book is a fine addition to the libraries of myrmecophiles at any level, and especially those engaged in field observations and citizen science.

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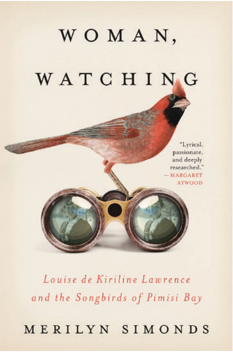
ORNITHOLOGY

Woman, Watching: Louise de Kiriline Lawrence and the Songbirds of Pimisi Bay

By Merilyn Simonds. 2022. ECW Press. 416 pages and 49 black and white figures, 28.95 CAD, Paper, 19.99 CAD, E-book.



The insatiable curiosity of Louise de Kiriline Lawrence allowed her to make significant contributions to the study of songbirds breeding in the boreal forest of northern Ontario. The title of this biography—*Woman, Watching*—is an apt description of Lawrence's approach to five decades of fieldwork in the woods outside her home at Pimisi Bay. But this is also the story of a woman trying to make her way in the world, on her own terms. In 18 chapters, Merilyn Simonds leads us from Lawrence's earliest years in Sweden to her time in Canada, where she became a prominent self-taught amateur ornithologist and the first Canadian woman elected as a member of the American Ornithologists' Union (AOU).

Lawrence was born in Sweden in 1894, the daughter of Danish nobility on her mother's side and landed Swedish gentry on her father's side. It was her father who taught her to love nature, which she explored on their estate overlooking a fjord on the Baltic Sea, 300 km south of Stockholm. Her family often hosted scientific visitors who had a profound influence on Lawrence. When she was 17 years old her father died; the family estate faltered and was sold.

Finding herself in reduced circumstances at the start of World War I, Lawrence trained as a nurse, which was unusual for a debutante but a very patriotic act. The following decade of her life could be the script for a movie (think *Doctor Zhivago*): nursing an injured White Army Russian soldier whom she falls in love with and marries; fleeing from the Bolsheviks with her new husband by sleigh and on foot; getting captured by the Red Army; supporting her imprisoned husband, Gleb, until his disappearance; working with starving Russians as a nurse with a humanitarian relief organization while searching for three years for Gleb, to no avail. In 1927, when she had finally accepted Gleb's death, Lawrence decided to emigrate to Canada—she had been captivated by descriptions of it from a wounded Canadian airman.

With little money, Lawrence took a job with the Canadian Red Cross, working as a nurse at remote outposts and hospitals in northern Ontario. She took to the remote and harsh conditions with enthusiasm, often travelling with her own dogsled team to reach patients at home. This quiet existence changed in the spring of 1934 when Lawrence took on the task of keeping the famous Dionne quintuplets alive. But after a year, with the Quints flourishing, Lawrence wanted to get back to the land she had bought on Pimisi Bay, a widening of the Mattawa River before it flows into the Ottawa River. In 1939 she married Leonard Lawrence, a local handyman whom she had hired a few years earlier to work on projects she couldn't take on alone: furnishing the cabin; raising and selling poultry and eggs; and running a mink farm. Although each came from different backgrounds, they had a deep and abiding love. Four months after they were married, at the start of World War II, Len enlisted in the army. He was away for five years.

Lawrence had a steady income from Len's army paycheque, which meant she could now devote her time to writing and observing the birds around her. A friend had loaned her a copy of Percy A. Taverner's *Birds of Canada* (National Museum of Canada, 1934); a few weeks later she wrote Taverner about some of her observations, not expecting a reply. But Taverner, chief ornithologist for the National Museum of Canada (now the Canadian Museum of Nature), responded and encouraged her to capture and band birds so that she could record detailed observations of individuals. Thus began her voluminous correspondence with a who's who of ornithology: Doris and Murray Speirs, Jim Baillie, W. Earl Godfrey, Margaret Morse Nice, Eugene Odum, and Alexander Skutch. Godfrey was particularly interested in the distribution of bird species, especially in the understudied boreal forest where Lawrence lived, and told her, "'[y]ou have the opportunity, ability, patience, and enthusiasm, a combination that is hard to beat'" (p. 172).

Over the subsequent decades, Lawrence was a prolific writer of long-form nonfiction, creative nonfiction, personal essays and poems, environmental essays, narrative natural history articles, comparative life history studies of birds, and short, narrowly-focussed scientific studies, as well as a memoir. Simonds located 90 articles, which are listed in the Bibliography, along with seven books and eight anthologies in which Lawrence's work was reprinted. Lawrence also wrote over 500 reviews and abstracts of Swedish and French ornithological books and articles for North American journals. She published many articles in this journal as well. (In 1981, Lawrence was elected an Honorary Member of the Ottawa Field-Naturalists' Club, the organization that publishes *The Canadian Field-Naturalist*.)

Simonds first met Lawrence in 1980 when she moved to North Bay. In 1989 she wrote an article about Lawrence for *Harrowsmith* magazine, but it was three decades before she began serious research for this book. Lawrence died in 1992, so Simonds recreated her life by reading through all of her books and articles, unpublished manuscripts, and numerous letters (Lawrence kept up a weekly correspondence with her mother for 40 years), from which she pulled copious quotes to help the reader "hear" Lawrence's voice. I found Chapter 11 (The Eyes of the Heart) very interesting because it introduced other, earlier trailblazing women ornithologists, some of whom I had not heard of previously. And in a world of increasingly high-tech, narrowly-focussed studies it was refreshing to read about the general life histories of different species.

I will leave the last word to Lawrence: "[b]ecause you see a bird, you do not know it" (p. 350).

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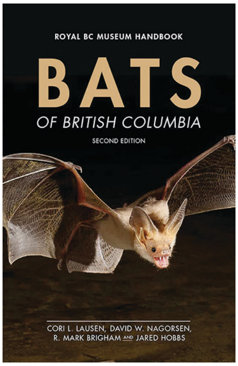
ZOOLOGY

Bats of British Columbia. Second Edition

By Cori L. Lausen, David W. Nagorsen, R. Mark Brigham, and Jared Hobbs. 2022. Royal BC Museum. 384 pages, 34.95 CAD, Paper.



Go ahead, judge this book by its cover; it has a very cool nocturnal (of course) shot of a flying bat, mouth agape, presumably emitting one of its calls or about to capture an insect. The teeth are awesome, the blood vessels of the wings stand out, and those ears! I want to credit the photographer, I want to tell you what kind of bat it is, but I can't; there is no information on either. This is just one of the very few (very, very few) minor annoyances in this otherwise fantastic book.

The second edition of *Bats of British Columbia* greatly expands on the first (published in 1993); the page count alone has doubled. The photographs are typically great (not just good) quality, which is surprising given the nocturnal settings of the vast majority of these shots. Technological advances since the first edition was published have allowed amateur naturalists to contribute to the second edition. These advances include photography equipment that now lets the untrained take the kinds of photos once regarded as only attainable by professionals. Where visual contact is not possible for species-level identification, amateurs now also have access to small, lightweight sound-recording equipment that plugs into their cell phones.

Like many other books of its kind, *Bats of British Columbia* starts with introductory material about the 18 different species of bats found in the province. These 18 species include three accidentals (e.g., Brazilian Free-tailed Bat) and 15 natives (e.g., Hoary and Pallid Bats). The scope of the introduction is broad, from anatomy and echolocation to roosting sites and threats (including, thankfully, a mention of free-roaming cats, which take a toll not just on birds, but bats as well). A very detailed, photographically-enhanced chapter on in-hand identification ends with a similarly photographically-enhanced key. And on the topic of keys, the section on acoustics terminates with a key, and there is a key to skulls in one of the appendices. There is also a glossary.

The remainder of the book is made up of species accounts. At about 10 pages each, they are quite thorough. Included in each account are detailed photographs, sonograms, a table of measurements, and text covering much of the species' biology. A distribution map is included that plots the different record types (voucher, acoustic, visual) amalgamated for this book, and it shows known and suspected ranges for each species. In the text accompanying the map, reference is often made to communities in British Columbia. However, these aren't marked on the map, so they are rather meaningless to the reader unless an atlas is opened alongside it. This, I believe, is one of the book's very few shortcomings.

Over 300 works were used to compile *Bats of British Columbia*, and there are 22 pages of references for anyone who wants to find out more information on the subject matter. Overall, *Bats of British Columbia* is an awesome resource for both dedicated bat enthusiasts and broad-scope naturalists. I suspect it will become the standard by which similar books are measured.

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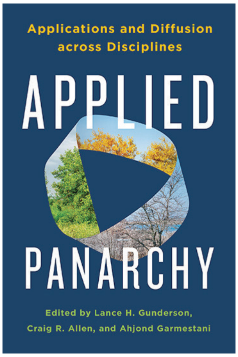
OTHER

Applied Panarchy: Applications and Diffusion across Disciplines

Edited by Lance H. Gunderson, Craig R. Allen, and Ahjond Garmestani. 2022. Island Press. 344 pages and 34 illustrations, 49.00 USD, Paper. Also available as an E-book.



The concept of panarchy is rooted in the original and creative theories of C.S. Holling, a Canadian scientist whose name and work may be familiar to you. Holling moved ecological theory away from traditionally simple, linear climax models to more complex "non-linear, cyclical, ecosystem dynamics" (p. xiii). Building on Holling's models of natural systems, panarchy takes the next step towards "coupled, multiscale, socio-ecological systems that generate abrupt, episodic and non-linear system changes [a.k.a. panarchies]" (p. 13). Interestingly, the word panarchy was created "by combining *Pan*, the mischievous Greek god of nature who scattered discord and chaos in mythology, with the Greek word *arkos*, 'rules'" (p. xi), suggesting that even chaos must follow the rules of science.

In simple terms, panarchy is kind of a 'theory of everything', with the COVID-19 pandemic being the perfect example that fits very nicely into the complex definition noted above. First, it is a coupled human-natural environmental event (i.e., socio-ecological system). It began with a small-scale event when the COVID-19 virus jumped species (likely bats to civets to humans). Then, as viral variants travelled across the globe, this led to an impact that was abrupt, multiscale, episodic, and non-linear—the global pandemic we know all too well. Climate change is another example of panarchy. It has coupled, multiscale, socio-ecological systems leading to abrupt, episodic, and non-linear system changes.

I work in international development, and I had hoped that *Applied Panarchy* would offer practical, useable, real-time models to help guide *Homo sapiens* out of the socio-ecological disaster we have created for ourselves. My hope quickly vanished as I became bogged down in dense descriptions laced with terminology and Möbius strip diagrams labelled with Greek symbols of rho, alpha, kappa, and omega in reference to the four phases observed in socio-ecological systems: exploitation, reorganization, conservation, and release, respectively. While the book devotes over 100 pages to Applications of Panarchy Theory (Part 2, Chapters 2 to 7), each of the six chapters in this section focusses more on theory than application, reiterating the non-linear, multiscale, coupled nature of the socio-ecological world we live in. Actual applications are sorely lacking, although there are some ideas worth noting. One such example is "coerced panarchy" in Chapter 4, where societal changes that reduce greenhouse gas emissions have the capacity to "coerce" the complex system of climate change away from catastrophe. Chapter 6, An Engineering Perspective on Managing for Resilience and Panarchy, recommends nature-based solutions as a resilience management strategy. Nature-based solutions are currently promoted by Global Affairs Canada, Canada's international development agency, which provides funding to development initiatives that conserve, restore, and sustainably use biodiversity and ecosystems to enhance human livelihood security.

Ultimately, *Applied Panarchy* is a book written by theoretical scientists for theoretical scientists working in this field. It is well-written, presents many complex graphs and diagrams, and the work is well-referenced. While it is useful to understand the evolving science of panarchy theory, the book provides little practical advice on how to address the chaos driving non-linear, multiscale, and often abrupt changes associated with climate change, which is testing the resilience of all species (including humans) and their ecosystems globally.

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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

Cave Biodiversity: Speciation and Diversity of Subterranean Fauna. Edited by J. Judson Wynne. 2022. Johns Hopkins University Press. 352 pages, 16 colour photos, 18 black and white photos, and 29 black and white illustrations, 95.00 USD, Hardcover. Also available as an E-book.

The Trials of Life: a Natural History of Animal Behaviour. Third Edition. By David Attenborough. 2023. HarperCollins. 288 pages, 34.99 CAD, Hardcover, 24.99 CAD, Paper. Also available as an E-book.

BOTANY

American Wildflowers: a Literary Field Guide. Edited by Susan Barba. Illustrations by Leanne Shapton. 2022. Abrams. 340 pages and 80 colour illustrations, 37.95 CAD, Hardcover, 30.99 CAD, E-book.

The Botany of Beer: an Illustrated Guide to more than 500 Plants used in Brewing. By Giuseppe Caruso. Translated by Kosmos, Reggio Emilia. 2022. Columbia University Press. 640 pages, 34.95 USD, Hardcover. Also available as an E-book.

***À la Découverte des Mousses et Autres Bryophytes du Québec.** Pour Société québécoise de bryologie. 2022. **Éditions** NaturAT. 227 pages, 39.00 CAD, livre de poche.

***Flora's Fieldworkers: Women and Botany in Nineteenth-Century Canada.** Edited by Ann Shteir. Afterword by Suzanne Zeller. 2022. McGill-Queen's University Press. 488 pages and 87 photos, 70.00 CAD, Hardcover. Also available as an E-book.

In the Name of Plants: from Attenborough to Washington, the People behind Plant Names. By Sandra Knapp. 2022. University of Chicago Press. 192 pages and 100 colour plates, 25.00 USD, Hardcover. Also available as an E-book.

Plant Words: 250 Terms for Plant Lovers. By Royal Botanic Gardens Kew. 2022. Welbeck Publishing. 208 pages, 19.99 CAD, Hardcover. Also available as an E-book.

***Pressed Plants: Making a Herbarium.** By Linda P.J. Lipsen. Illustrations by Derek Tan. 2023. Royal BC Museum. Distributed by University of Toronto Press. 96 pages, 19.95 CAD, Paper, 11.99 CAD, E-book.

Seaweeds of the World: a Guide to Every Order. By John Bothwell. 2023. Princeton University Press. 240 pages, 249 colour illustrations, 17 black and white illustrations, and 77 maps, 29.95 USD, Hardcover. Also available as an E-book.

Trees: from Root to Leaf. By Paul Smith. 2022. University of Chicago Press. 320 pages and 500 colour plates, 49.95 USD, Hardcover.

†White Pine: the Natural and Human History of a Foundational American Tree. By John Pastor. 2023. Island Press. 276 pages, 30.00 USD, Paper. Also available as an E-book.

CONSERVATION AND CLIMATE CHANGE

Canada and Climate Change. Canadian Essentials Series No. 2. By William Leiss. 2022. McGill-Queen's University Press. 200 pages, 24.95 CAD, Hardcover. Also available as an E-book.

The Climate Book: the Facts and the Solutions. By Greta Thunberg. 2023. Penguin Random House. 464 pages, 41.00 CAD, Hardcover, 18.99 CAD, E-book.

Climate Change: What Everyone Needs to Know. Third Edition. By Joseph Romm. 2022. Oxford University Press. 348 pages, 74.00 CAD, Hardcover, 18.95 CAD, Paper. Also available as an E-book.

The Future is Now: Solving the Climate Crisis with Today's Technologies. By Bob McDonald. 2022. Penguin Random House. 304 pages, 32.95 CAD, Hardcover, 15.99 CAD, E-book.

Greenhouse Planet: How Rising CO_2 Changes Plants and Life as We Know It. By Lewis H. Ziska. 2022. Columbia University Press. 240 pages, 25.00 USD, Hardcover. Also available as an E-book.

Imminent Domains: Reckoning with the Anthropocene. Essais Series Number 14. By Alessandra Naccarato. 2022. Book*hug Press. 240 pages, 23.00 CAD, Paper, 14.99 CAD, E-book.

Masters of the Lost Land: the Untold Story of the Amazon and the Violent Fight for the World's Last Frontier. By Heriberto Araujo. 2023. HarperCollins. 432 pages, 36.99 CAD, Hardcover, 18.99 CAD, E-book.

The Petroleum Papers: Inside the Far-Right Conspiracy to Cover Up Climate Change. By Geoff Dembicki. 2022. Greystone Books. 256 pages, 34.95 CAD, Hardcover, 27.99 CAD, E-book.

The Rescue Effect: the Key to Saving Life on Earth. By Michael Mehta Webster. 2022. Timber Press. 296 pages, 28.00 USD, Hardcover. Also available as an E-book.

The Sacred Balance: Rediscovering our Place in Nature. 25th Anniversary Edition. By David Suzuki. Foreword by Robin Wall Kimmerer. Afterword by Bill McKibben. 2022. Greystone Books. 336 pages, 24.95 CAD, Paper.

Science for a Green New Deal: Connecting Climate, Economics, and Social Justice. By Eric A. Davidson. 2022. Johns Hopkins University Press. 264 pages, 27.95 USD, Hardcover. Also available as an E-book.

Wildlife Management and Conservation: Contemporary Principles and Practices. Second Edition. Edited by Paul R. Krausman and James W. Cain III. 2022. Johns Hopkins University Press. 472 pages, 99.95 USD, Hardcover. Also available as an E-book.

ECOLOGY

Ancient Woods, Trees and Forests: Ecology, History and Management. Edited by Alper H. Çolak, Simay Kirca, and Ian Rotherham. 2022. Pelagic Publishing. 488 pages, 49.99 GBP, Hardcover.

The Darkness Manifesto: on Light Pollution, Night Ecology, and the Ancient Rhythms that Sustain Life. By Johan Eklöf. Translated by Elizabeth DeNoma. 2023. Scribner. 272 pages, 35.00 CAD, Hardcover, 17.99 CAD, E-book.

The Ecology Book. Big Ideas Series. By DK. 2022. DK. 352 pages, 25.99 CAD, Paper.

†**Ecology of a Changed World.** By Trevor Price. 2022. Oxford University Press. 352 pages and 134 images, 79.95 CAD, Hardcover. Also available as an E-book.

ENTOMOLOGY

Essential Entomology. Second Edition. By George C. McGavin and Leonidas-Romanos Davranoglou. Illustrations by Richard Lewington. 2023. Oxford University Press. 336 pages, 90.00 CAD, Hardcover, 45.00 CAD, Paper. Also available as an E-book.

Extinct and Endangered: Insects in Peril. By American Museum of Natural History. Photography by Levon Bliss. 2022. Abrams. 144 pages and 80 colour photos, 42.99 USD, Hardcover, 16.99 USD, E-book.

Stick and Leaf-Insects of the World. By Paul D. Brock and Thies H. Büscher. 2022. NAP Editions. 611 pages, 85.00 EUR, Hardcover.

HERPETOLOGY

The Origin and Early Evolutionary History of Snakes. Edited by David J. Gower and Hussam Zaher. 2022. Cambridge University Press. 488 pages, 120.95 CAD, Hardcover. Also available as an E-book.

Salamanders and Newts of the World. Third Edition. By Jean Raffaëlli. 2022. Penclen Edition. 1100 pages, 4000+ colour photos and illustrations, and 154 colour maps, 120.00 GBP, Hardcover.

ORNITHOLOGY

101 Curious Tales of East African Birds: a Brief Introduction to Tropical Ornithology. By Colin Beale. 2022. Pelagic Publishing. 224 pages, 20.00 GBP, Paper.

Conversations with Birds. By Priyanka Kumar. 2022. Milkweed Editions. 296 pages, 28.00 USD, Hardcover, 10.99 USD, E-book.

A History of Oregon Ornithology: from Territorial Days to the Rise of Birding. By Alan L. Contreras, Vjera E. Thompson, and Nolan M. Clements. 2022. Oregon State University Press. 296 pages and 52 black and white illustrations, 34.95 USD, Paper.

The Meaning of Geese: a Thousand Miles in Search of Home. By Nick Acheson. 2023. Chelsea Green. 240 pages, 20.00 GBP, Hardcover.

Ornithographies. By Xavi Bou. 2022. Lynx Edicions. 190 pages, 55.00 EUR, Hardcover.

Passions for Birds: Science, Sentiment, and Sport. By Sean Nixon. 2022. McGill-Queen's University Press. 328 pages, 49.95 CAD, Hardcover. Also available as an E-book.

The Peregrine Falcon. By Richard Sale and Steve Watson. 2022. Snowfinch Publishing. 526 pages, 49.99 GBP, Hardcover.

Robin. By Helen F. Wilson. 2022. University of Chicago Press. 224 pages, 60 colour plates, and 45 halftones, 19.95 USD, Paper. Also available as an E-book.

Shrikes of the World. Second Edition. Helm Identification Guide Series. By Norbert Lefranc. Illustrations by Tim Worfolk. 2023. Helm. 336 pages, 108.00 CAD, Hardcover. Also available as an E-book.

Slow Birding: the Art and Science of Enjoying the Birds in Your Own Backyard. By Joan E. Strassmann. 2022. Penguin Random House. 352 pages, 37.00 CAD, Hardcover, 16.99 CAD, E-book.

Zoology

***The Alpha Female Wolf: the Fierce Legacy of Yellowstone's 06.** By Rick McIntyre. Foreward by Jane Goodall. 2022. Greystone Books. 280 pages, 34.95 CAD, Hardcover, 24.95 CAD, Paper. Also available as an E-book.

The Ecological Buffalo: on the Trail of a Keystone Species. By Wes Olson. Photography by Johane Janelle. 2022. University of Regina Press. 304 pages, 39.95 CAD, Paper.

The Golden Mole: and Other Living Treasure. By Katherine Rundell. Illustrations by Talya Baldwin. 2022. Faber & Faber. 196 pages, 14.99 GBP, Hardcover. Also available as an E-book.

How to Speak Whale: a Voyage into the Future of Animal Communication. By Tom Mustill. 2022. Grand Central Publishing. 304 pages, 37.00 CAD, Hardcover, 19.99 CAD, E-book.

Pacific Salmon Field Guide. By Sean Godwin and Martin Krkosek. Illustrations by Joseph R. Tomelleri. Photography by Tavish Campbell. 2022. Lone Pine Publishing. 160 pages, 24.95 CAD, Paper.

Sexual Segregation in Ungulates: Ecology, Behavior, and Conservation. By R. Terry Bowyer. 2022. Johns Hopkins University Press. 200 pages, 74.99 USD, Hardcover. Also available as an E-book.

Shark: Why We Need to Save the World's Most Misunderstood Predator. By Paul de Gelder. 2023. HarperCollins. 240 pages, 26.99 USD, Hardcover, 12.99 USD, E-book.

A World in a Shell: Snail Stories for a Time of Extinctions. By Thom van Dooren. 2022. MIT Press. 288 pages and 16 colour plates, 39.95 CAD, Hardcover, 31.99 CAD, E-book.

Other

Alone in the Great Unknown: One Woman's Remarkable Adventures in the Northwestern Wilderness. By Caroll Simpson. 2022. Harbour Publishing. 256 pages, 26.95 CAD, Paper. Also available as an E-book.

Animal as Machine: the Quest to Understand How Animals Work and Adapt. By Michel Anctil. 2022. McGill-Queen's University Press. 344 pages, 49.95 CAD, Hardcover. Also available as an E-book.

Antarcticness: Inspirations and Imaginaries. Edited by Ilan Kelman. 2022. University of Chicago Press. 336 pages and 100 colour plates, 75.00 USD, Hardcover, 45.00 USD, Paper.

The Best American Science and Nature Writing 2022. Edited by Ayana Elizabeth Johnson and Jaime Green. 2022. HarperCollins. 336 pages, 21.99 CAD, Paper, 11.99 CAD, E-book.

Curious Devices and Mighty Machines: Exploring Science Museums. By Samuel J.M.M. Alberti. 2022. University of Chicago Press. 256 pages and 99 halftones, 27.50 USD, Hardcover. Also available as an E-book.

Darwin's Love of Life: a Singular Case of Biophilia. By Kay Harel. 2022. Columbia University Press. 192 pages, 26.00 USD, Hardcover. Also available as an E-book.

Deer Man: Seven Years of Living in the Wild. By Geoffroy Delorme. Translated by Shaun Whiteside. 2022. Greystone Books. 240 pages, 32.95 CAD, Hardcover. Also available as an E-book.

The Huxleys: an Intimate History of Evolution. By Alison Bashford. 2022. University of Chicago Press. 576 pages, 30.00 USD, Hardcover. Also available as an E-book.

The Mycocultural Revolution: Transforming our World with Mushrooms, Lichens, and Other Fungi. By Peter McCoy. Foreword by Robert Rogers. 2022. Microcosm Publishing. 192 pages, 24.50 CAD, Hardcover. Also available as an E-book.

Nature's Wild Ideas: How the Natural World is Inspiring Scientific Innovation. By Kristy Hamilton. 2022. Greystone Books. 288 pages, 32.95 CAD, Hardcover, 26.99 CAD, E-book.

A Poison Like No Other: How Microplastics Corrupted our Planet and our Bodies. By Matt Simon. 2022. Island Press. 252 pages, 30.00 USD, Hardcover, 12.99 USD, E-book.

Silent Spring Revolution: John F. Kennedy, Rachel Carson, Lyndon Johnson, Richard Nixon, and the Great Environmental Awakening. 2022. HarperCollins. 896 pages, 50.00 CAD, Hardcover, 24.99 CAD, E-book.

***The Sounds of Life: How Digital Technology is Bringing Us Closer to the Worlds of Animals and Plants.** By Karen Bakker. 2022. Princeton University Press. 368 pages, 33.00 USD, Hardcover. Also available as an E-book.

Weather Permitting: Twenty-Five Years of Ice Storms, Hurricanes, Wildfires, and Extreme Climate Change in Canada. By Chris St. Clair. 2022. Simon & Schuster. 256 pages, 24.99 CAD, Paper, 13.99 CAD, E-book.

Wild Miami: Explore the Amazing Nature in and Around South Florida. By T.J. Morrell, Shannon Jones, Brian Diaz, and Fernando Bretos. 2023. Timber Press. 376 pages, 32.99 CAD, Paper.

***Wild New World: the Epic Story of Animals and People in America.** By Dan Flores. 2022. W.W. Norton. 448 pages, 40.00 CAD, Hardcover, 30.99 CAD, E-book.

Wild Visions: Wilderness as Image and Idea. By Ben A. Minteer, Mark Klett, and Stephen J. Pyne. 2022. Yale University Press. 284 pages, 67 colour illustrations, and 55 black and white illustrations, 40.00 USD, Hardcover.

The Canadian Field-Naturalist

News and Comment

Compiled by Amanda E. Martin

Upcoming Meetings and Workshops

Midwest Fish & Wildlife Conference

The 83rd Midwest Fish & Wildlife Conference, hosted by the Kansas Department of Wildlife & Parks, to be held 12–15 February 2023 at the Sheraton Overland Park Hotel and Overland Park Convention Center, Overland Park, Kansas. Registration is currently open. More information is available at https://www.midwestfw.org/.

Annual Society for Range Management Meeting

The 76th annual meeting of the Society for Range Management to be held 12–16 February 2023 as a hybrid event, with online content and an in-person meeting at the Boise Centre and The Grove Hotel, Boise, Idaho. Registration is currently open. More information is available at https://rangelands.org/annual-meeting-2023/.

Forests Ontario Annual Conference

Forests Ontario's 9th Annual Conference to be held 16–17 February 2023 as a hybrid event, with online content and an in-person meeting at the Nottawasaga Inn Resort & Conference Centre, Alliston, Ontario. The theme of the conference is: 'Growing a Healthy Tomorrow–For Communities, For Earth, For Life'. Registration is currently open. More information is available at https://forestsontario.ca/en/event/annual-conference.

Wetland Science Conference

The 28th annual Wetland Science Conference to be held 21–23 February 2023 at the Holiday Inn Hotel & Convention Center, Stevens Point, Wisconsin. The theme of the conference is: 'Wetlands: Central to Wisconsin'. Registration is currently open. More information is available at https://www.eventleaf.com/e/WSC2023.

Society of Canadian Aquatic Sciences Montréal

Society of Canadian Aquatic Sciences Montréal to be held 22–25 February 2023 at Le Centre Sheraton Montreal Hotel, Montréal, Quebec. Registration is currently open. More information is available at https://www.scas-scsa.ca/CONFERENCE.

Alberta Chapter of The Wildlife Society Conference

The conference of the Alberta Chapter of The Wildlife Society to be held 10–12 March 2023 in Calgary, Alberta. The theme of the conference is: 'Where the Wild Things Meet'. Registration is currently open. More information is available at https://www.actws.ca/conference/.

Entomological Society of America, Southeastern Branch Meeting

The Southeastern Branch Meeting of the Entomological Society of America to be held 12–15 March 2023 at the Little Rock Marriott, Little Rock, Arkansas. The theme of the conference is: 'Building upon a Tradition of Innovation, Collaboration, and Adaptation'. Registration is currently open. More information is available at https://www.entsoc.org/membership/branches/southeastern/meeting.

Entomological Society of America, Eastern Branch Meeting

The Eastern Branch Meeting of the Entomological Society of America to be held 18–20 March 2023 at the Graduate Providence, Providence, Rhode Island. The theme of the conference is: ‘Casting a Wider Net: Entomology for Everyone’. Registration is currently open. More information is available at https://www.entsoc.org/membership/branches/eastern/meeting.

IALE-North America Annual Meeting

The International Association for Landscape Ecology - North American Regional Chapter (IALE-North America) Annual Meeting to be held 19–23 March 2023 at the Convention Center, Riverside, California. The theme of the conference is: ‘Equity, Inclusion, and Landscapes of Change’. Registration is currently open. More information is available at https://www.ialena.org/annual-meeting.html.

Eastern Bird Banding Association Centennial Meeting

The 100th anniversary meeting of the Eastern Bird Banding Association, hosted by the Willistown Conservation Trust, to be held 24–26 March 2023 at the Rushton Conservation Center, Newtown Square, Pennsylvania. Registration is currently open. More information is available at https://ebba2023.org/.

Entomological Society of America, Pacific Branch Meeting

The Pacific Branch Meeting of the Entomological Society of America to be held 2–5 April 2023 at the Motif Seattle, Seattle, Washington. Registration is currently open. More information is available at https://www.entsoc.org/membership/branches/pacific/meeting.

Northeast Natural History Conference

The Northeast Natural History Conference to be held 21–23 April 2023 at the Doubletree by Hilton, Burlington, Vermont. Registration is currently open. More information is available at https://www.eaglehill.us/NENHC_2023/NENHC2023.shtml.

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