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COVER: Plain Pocketbook (*Lampsilis cardium*, left), Deertoe (*Truncilla truncata*, upper right), and Threehorn Wartyback (*Obliquaria reflexa*) were three species, among others, that were historically collected in southern Ontario for the button industry at the onset of the 20th century. While this commercial harvest ended by the mid-1940s, its effects may still be lingering on some of these long-lived animal populations. See the article by Hayes Morris and Morris (pp. 205–216). Photos: Fisheries and Oceans Canada..

The Canadian Field-Naturalist

The history of commercial freshwater mussel harvest in southern Ontario: a short-lived fishery with long-lasting consequences

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Abstract

Freshwater mussels (Bivalvia: Unionidae) have long been an important aquatic resource for humans, and North America's Indigenous nations have harvested them for over 10 000 years. European exploitation began in the latter half of the 19th century, initially focussing on the collection of pearls and later shifting to the manufacture of buttons at the onset of the 20th century. By 1911, Canadian pearl button factories operated in Windsor, Berlin (now Kitchener), and Trenton, Ontario, and, by 1921, Ontario shell was being exported to factories in the United States. The Canadian harvest did not last long and ended by the mid-1940s as resources dwindled because of overexploitation, pollution, and industrial shifts to other raw materials for buttons (e.g., plastics). Annual river-specific harvest ranged from ~ 66 to 110 tonnes with a maximum of 291 tonnes (~1.1–4.4 million animals) collected at Dunnville on the lower Grand River in 1915. Although detailed collection information is lacking, species such as Mucket (*Actinonaias ligamentina*), Threeridge (*Amblema plicata*), and Round Pigtoe (*Pleurobema sintoxia*, now listed federally as Endangered) were targetted, while Purple Wartyback (*Cyclonaias tuberculata*, also now Endangered) was discarded (i.e., killed). Commercial harvests typically targetted adults, because they provided the desired quantity and type of material, resulting in death. Recent studies have shown that this type of directed mortality can have the greatest impact on the long-term persistence of these populations and, although the specific impacts of the historical harvest cannot be determined, it is likely that these harvests contributed to the current state of imperilment of this fauna.

Key words: Bivalvia; Unionidae; history; button industry; Grand River; Thames River

Introduction

Freshwater bivalves are among the most imperilled taxa worldwide with 40% of species considered to be at-risk (Lopes-Lima *et al.* 2018). Within this group, the freshwater mussels in the order Unionida have experienced important large-scale declines and are now considered the most at-risk with more than two thirds of North America's ~300 species considered to be at serious risk of extinction (Williams *et al.* 1993; Lopes-Lima *et al.* 2018). Bogan (1993) identified 19 extinctions within the North American freshwater mussel fauna. Causes of these declines have been well studied and they can be attributed to broad-scale habitat destruction from historical land-use practices and resource extraction, pollution from industrial sources such as pulp and paper mills, instream flow modifications from dams and impoundments, loss of host fishes, invasive species (e.g., dreissenid mussels), and overexploitation for buttons and pearls (Bogan 1993; Haag 2019).

Efforts are underway across North America to stop these declines and to recover populations of many freshwater mussels. In Canada, 20 species (36%) have been assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as Extirpated to Special Concern. Almost all are now the beneficiary of a federal recovery strategy (for Extirpated, Endangered, or Threatened species) or a management plan (for Special Concern species) under the Canadian *Species at Risk Act* (*SARA*) with a goal of protecting and recovering species where possible (SARA 2002). During the first 15 years under *SARA*, meaningful progress has been made on many recovery actions for freshwater mussels particularly in areas relating to understanding population ecology and habitat needs; however, less progress has been made on understanding and mitigating threats (Drake *et al.* 2021). Because freshwater mussels can be very long-lived with life-spans exceeding 100 years in some cases (Haag and Rypel 2011), it is important to assess not only current threats but also, where possible, historical threats. Commercial harvest for the production of buttons and/or the collection of pearls (Figure 1) is one threat that no longer occurs but whose impact undoubtedly remains imprinted on the current faunal composition.

Freshwater mussels (Bivalvia: Unionidae) have long been an important aquatic resource, having been harvested by North America's Indigenous nations for over 10 000 years (Haag 2012). Examination of middens and other archaeological sites suggests that, while mussels were used primarily for food, shells were also used for other purposes including tools (e.g., spoons, dippers, and scrapers), fishing lures, and less often for decoration (Haag 2012). The collection, use, and trade of freshwater pearls was a common practice amongst many Indigenous communities as well. While we recognize the longstanding traditional uses of freshwater mussels by North America's Indigenous nations, we focus on commercial uses by European settlers of Turtle Island (North America).

Methods

We examined historical newspapers, permits, and first-person accounts to assess the potential impacts of one historical threat, the shell button industry, on freshwater mussels in southern Ontario. Achieving an understanding of the scope, scale, and specific composition of Ontario's historical commercial mussel harvest will assist recovery practitioners in assessing the potential impact of past exploitation on the modern assemblage.

Results and Discussion

Early North American button manufacturers

Southern Ontario's freshwater mussel shell harvest was closely tied to the American button industry, which was centred in Muscatine, Iowa, beginning in the late 19th century. By 1898, there were more than a dozen factories employing an estimated 1500 people operating in Muscatine, where a single factory produced more than 4 million buttons for the 1897 holiday season (Haag 2012). Between 1908 and the 1920s, the industry used an annual average of 44 000 to 66 000 tonnes of shell annually, reaching a peak around 1912 (Neves 1999; Knopp 2012). This industry quickly outcompeted the exploitation of mussels for pearls, which could be worth more but were rare (Haag 2012). In the United States (US), Johann Boepple is identified as being largely responsible for the start of the commercial industry in the 1890s (Thiel and Fritz 1993); however, there are references to the utility of mussel shell in button making as early as 1802 (Haag 2012). By 1912, 196 factories across 20 states were active in the industry (Coker 1919). Many US mussel beds were commercially exhausted as early as 1899 (Smith 1899), before the Ontario industry was in full operation. This decline of US shell resources may have spurred interest in the availability of Canadian shell to supplement the expanding industry.

The Ontario harvest begins

The Ontario shell button industry traces its origins to around 1866, when Pioneer Button Works, owned by Emil Vogelsang and H.S. Huber, operated

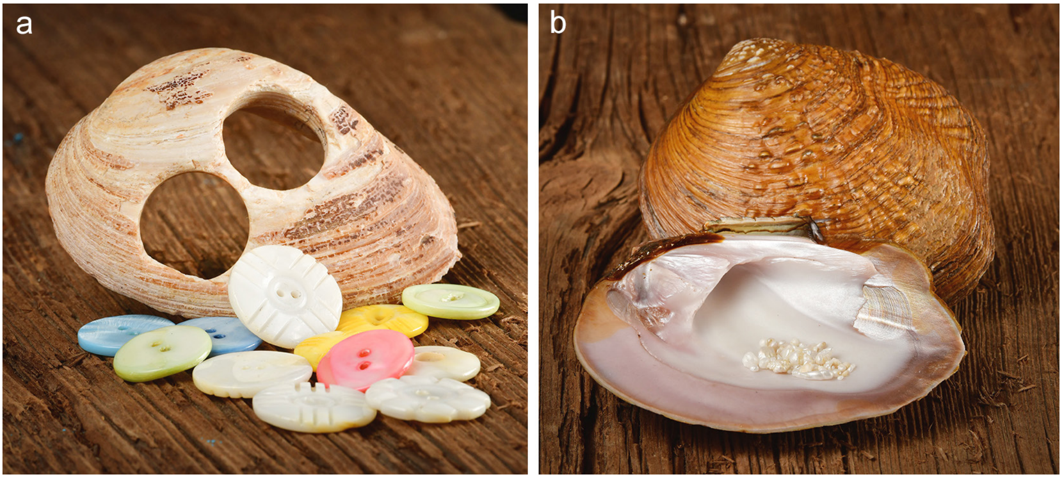

FIGURE 1. a. Freshwater mussel shell collected from southern Ontario showing evidence of drilling to produce shell buttons, along with a collection of buttons produced from freshwater mussels from the Mississippi River in Muscatine, Iowa, USA. b. Purple Wartyback (*Cyclonaias tuberculata*) showing freshwater pearls collected from southern Ontario specimens of multiple species. Photos: Todd J. Morris.

in Berlin (now Kitchener), Ontario (Kitchener Waterloo Record 1979). At this time, button manufacturers were familiar with making buttons from a variety of natural materials such as wood, vegetable ivory (tagua nuts), and bone, and recent activities in the US sparked an interest in the use of shell material. In 1871, Pioneer Button Works became known as the Shantz Button Manufacturing Company and went on to operate as Dominion Button Works from 1912 until its closure in 1964. Under this name, it would become a major player in the Canadian pearl button industry, acquiring shell from local suppliers on the Grand and Thames rivers (Kitchener Waterloo Record 1979). Other shell button companies were soon created in Ontario, with the Windsor Pearl Button Company opening in 1908 (Evening Record 1908), the Elmira Button Factory in 1909 (Elmira Signet 1909), and the Canadian Pearl Button Company in 1911 (Trenton Courier 1911a). The opening of commercial harvest of mussels in Ontario occurred at roughly the same time as these factories were beginning to operate, with Arthur Ullyot beginning to fish for mussels in the lower Grand River from Port Maitland through Dunnville and into the Feeder Canal around 1910 (Ullyot 1917). Detweiler (1918) discusses the extent of and methods used in the Grand River harvest between 1908 and 1910 and the potentially commercially important stocks extending upstream through Brantford, Paris, and as far as the confluence with the Speed River. In 1909, a location near the lower dam at Brantford was considered the best place for mussels, “as to size, quantity, and variety” (Detweiler 1918: 79). The first report of Ontario mussels being shipped south of the border to support the US button industry was in 1913 or 1914, where five or six railway cars of shell from ~1 km south of York, Ontario, were reportedly shipped to Buffalo, New York (Detweiler 1918).

These button manufacturers were involved to varying degrees with the direct exploitation of Ontario mussels. In an advertisement, the Windsor Pearl Button Company (1917) declared that it was the “largest manufacturer of fresh water pearl buttons in Canada”. There are records of the company receiving imported US shell from the Illinois River (Evening Record 1908), but none indicating the use of shell from Ontario. In 1929, the company was sold to Alfred Pollock of Montréal, for $90 000 (Burlington Hawk Eye 1929). Although clearly a major player in the Ontario pearl button industry, no records could be found indicating that the operation ever relied on the Ontario harvest.

The Gateman Comb and Button factory started operating in Elmira, Ontario in August 1909 and J.B. Gateman hired Mr. Kruger, from Springfield, Massachusetts, to run the pearl button division of this factory (Elmira Signet 1909). In 1910, Gateman proposed disposing of his factory in Berlin in favour of improvements to his Elmira factory (Elmira Signet 1910a). He would partner with Arthur Ullyot later that year (Elmira Signet 1910b). It is not explicit where this company’s shell material came from; however, as Ullyot is known to have been harvesting shell from the lower Grand River at this time, it is reasonable to conclude that Grand River shell supported this new partnership (Ullyot 1917). Ullyot’s next venture, the Canadian Pearl Button Company in Trenton, opened in early 1911 (Trenton Courier 1911b). He started with imported shell from Mississippi, USA, but suspected that local shell procurement would be possible (Trenton Courier 1911a). In March, an article in the Trenton Courier (1911c) estimated that the operation, when fully running, would employ ~100 people. By April 1917, the company was looking for harvesters and placed an ad in the Canadian Fisherman noting the “large profits” available (Canadian Pearl Button Co. 1917).

A significant impediment to the early shell harvesters was incomplete knowledge of Ontario’s freshwater mussel fauna. Before the early 20th century, formal surveys had not occurred in most watersheds. It was not until John D. Detweiler undertook a survey of various watersheds in Ontario as part of a project of the Biological Board of Canada in 1916, with the purpose of determining the “abundance, species, and commercial value of the mussels” that detailed information about Ontario mussel distributions started to become available (Detweiler 1918: 75).

Detweiler (1918) conducted surveys of the Grand River (Lake Erie watershed), the River Aux Sables (now Ausable River, Lake Huron watershed), Point Edward Bay (St. Clair River watershed), and the Nottawasaga River (Lake Huron watershed). He confirmed the well-known mussel beds in the lower Grand River that Ullyot was already fishing and a smaller but potentially commercially important fauna in the Ausable River; he believed that Point Edward and the Nottawasaga River did not offer a commercially viable resource. In addition to the surveys, he recommended further investigative work in other major rivers of southern Ontario, such as the Thames (Lake St. Clair watershed), Sydenham (Lake St. Clair watershed), Welland (Niagara River watershed), and the Saugeen (Lake Huron watershed) which have all subsequently proven to have substantial mussel assemblages (McNichols-O’Rourke *et al.* 2012; Wright *et al.* 2017). With the exception of the Thames, none of these rivers would apparently ever be subjected to commercial mussel harvest. The Grand and Thames rivers appear to have been the focus of the Ontario button shell fishery and the following sections detail what is known about the harvest there.

The Grand River harvest

Detweiler (1918: 77) asserted that the "Grand River contain[ed] more mussels of commercial value than any other Ontario waters". The shells found in this area were reported to have compared well to US shells (Detweiler 1918) and the Grand River (Figure 2) would eventually become the focus of the Ontario fishery. In 1910, Ullyot discovered a bed of what he called "Threeridge" in the lower Grand River (Ullyot 1917). (Difficulties in reconciling common names make precise species attributions difficult, but see section *The species in the harvest.*) He then employed a "great number of fishermen" between 1910 and at least 1917 and paid the Ontario Government $1 for every imperial ton (1 imperial ton = 1.1 tonne) fished (Ullyot 1917: 282). By 1916, he had rights to the fishery in the Dunnville area, which he continued to hold at least through 1917 (Ullyot 1917). In 1915, 291 tonnes of shell were shipped from a point about a kilometre north of Port Maitland, with the bed apparently showing "no signs of depletion" (Detweiler 1918: 78). However, when 286 tonnes were shipped from an area upstream of Dunville the following year, the area was "not as productive as was anticipated" (Detweiler 1918: 78). By the next year, Ullyot (1917: 282) noted the "inevitable result that the supply each year is diminishing" as a result of the harvest. The question of renewability of mussel shells as a resource was a concern commonly remarked on during the early years of the fishery by those involved on both sides of the Canada–US border: however, the harvest continued. By 1921, elementary school children from Stromness, a town northeast of Port Maitland, earned money (10 cents/hour) separating meat from shell and as many as seven cartloads of shell at a time were sent from this endeavour to Kitchener and further points onward on the Toronto, Hamilton, and Buffalo Railway (Warnick 2003).

A decade or more later, W.H. Robinson would begin his operation further upstream in the Grand River at Caledonia, with the first recovered permit dated 1936 listing a harvest fee of $5 per imperial ton (Figure S1). During the span of his operation, Robinson recalled the price per imperial ton varying from $35 to $100, with an average of 30–60 imperial tons (33–66 tonnes) of shell harvested each summer

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FIGURE 2. Location of the Grand River watershed in southwestern Ontario. A.A. Ullyot's harvesting operation was focussed around the Dunnville area, while W.H. Robinson and his team worked further upstream near Caledonia.

(Figure S2). He noted that Americans could not hold the licence necessary for mussel fishing in Ontario, which was how his family became involved in the industry (Figure S2). Correspondence between Robinson and Carl Jungbluth, president of the American Pearl Button Company of Washington, Iowa (Figure S3), and between Robinson and Henry Umlandt, president of the Automatic Button Company of Muscatine, Iowa (Figure S4), in May 1944 suggest a burgeoning bidding war for his Grand River material. Each of these US buyers was offering $80 per imperial ton, with Umlandt offering an additional $5 per imperial ton bonus if Robinson could provide 60 imperial tons (66 tonnes) as requested. In his letter (Figure S4), Jungbluth expressed his displeasure at having his bid shared with other firms who “might be a little hard up for shells and raise the price just a little in order to get them”. It is unclear who won the rights to Robinson’s Grand River shell that summer. The fisheries were active from May or June through to mid-October, as described by those involved. Robinson described the work as a “summer operation, and only possible when the weather and water warmed up” (Figure S2).

Collection methods were labour intensive and typically involved a “hands-on” approach. Ullyot’s lower Grand operation used the methods of crowfooting, scooping, and collection by hand. Crowfooting (Figure 3) was the most common technique, using a device consisting of wire hooks attached to the ends of cords, tied to a piece of pipe, then dragged behind a boat (Ullyot 1917). In the scooping method, two flat-bottomed scows were fastened rigidly together with planks behind a gasoline-powered launch (Ullyot 1917). A man would stand in each scow with a scoop net that was affixed with spikes and then dragged through the riverbed (Ullyot 1917). Detweiler observed that two men and two boys, using these two methods, were able to fish and clean (i.e., boil and remove the soft tissue) four and a half tonnes of shell in just three and a half days (Detweiler 1918). Lloyd Newth who, as a 16-year-old, worked on Robinson’s operation in Caledonia, reported using a hook and boat method (likely crowfooting) upstream near Caledonia (Newth pers. comm. 2012). Gathering by hand was considered quickest, but only possible in shallow water, which was often not where the beds were located (Ullyot 1917).

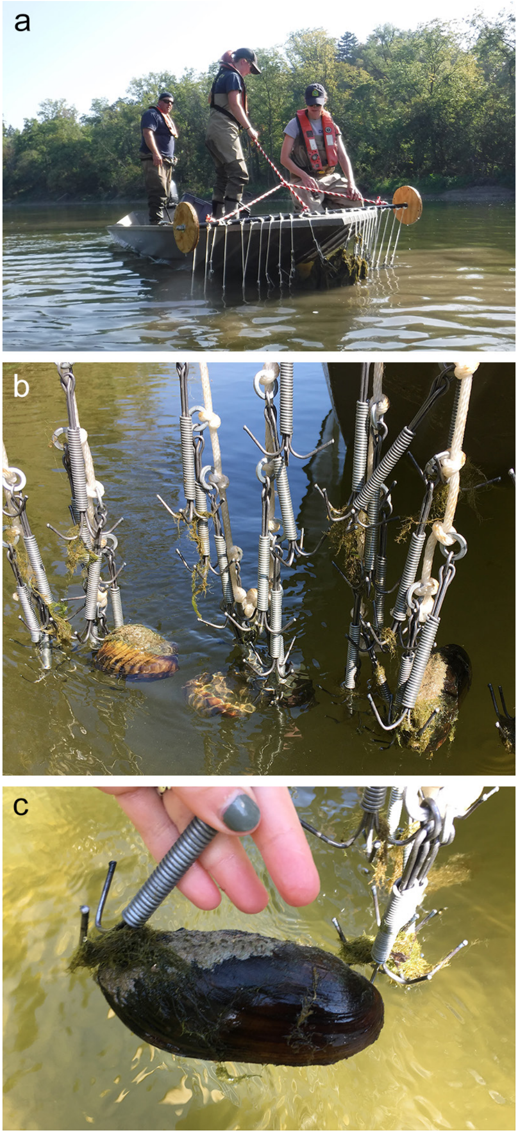

Figure 3. a. Modern-day application of the crowfooting technique being used to sample freshwater mussels on the lower Grand River near Brantford. b. Retrieval of the device (brail) showing multiple freshwater mussels attached to the crowfeet. c. A mature female Black Sandshell (*Ligumia recta*) grasping the tine of a crowfoot. Photos: Fisheries and Oceans Canada.

The Thames River harvest

The Thames River was not included in Detweiler’s 1916 survey but was believed to be part of an area that contained commercial shells (Detweiler 1918). As such, the operation of G. Frank Neely is the only significant source of information so far available. Neely harvested mussels from the Thames from ~1935 to at least 1945 (Figure S5; Stewart 1992). An article purportedly in the London Free Press (it had been retyped with an incomplete date) stated that he held a permit on the Thames from Putnam to Chatham, which comprised most of the lower Thames River (~200 river km; Figures 4 and S5). An area below the Munsee–Delaware First Nation Reserve,

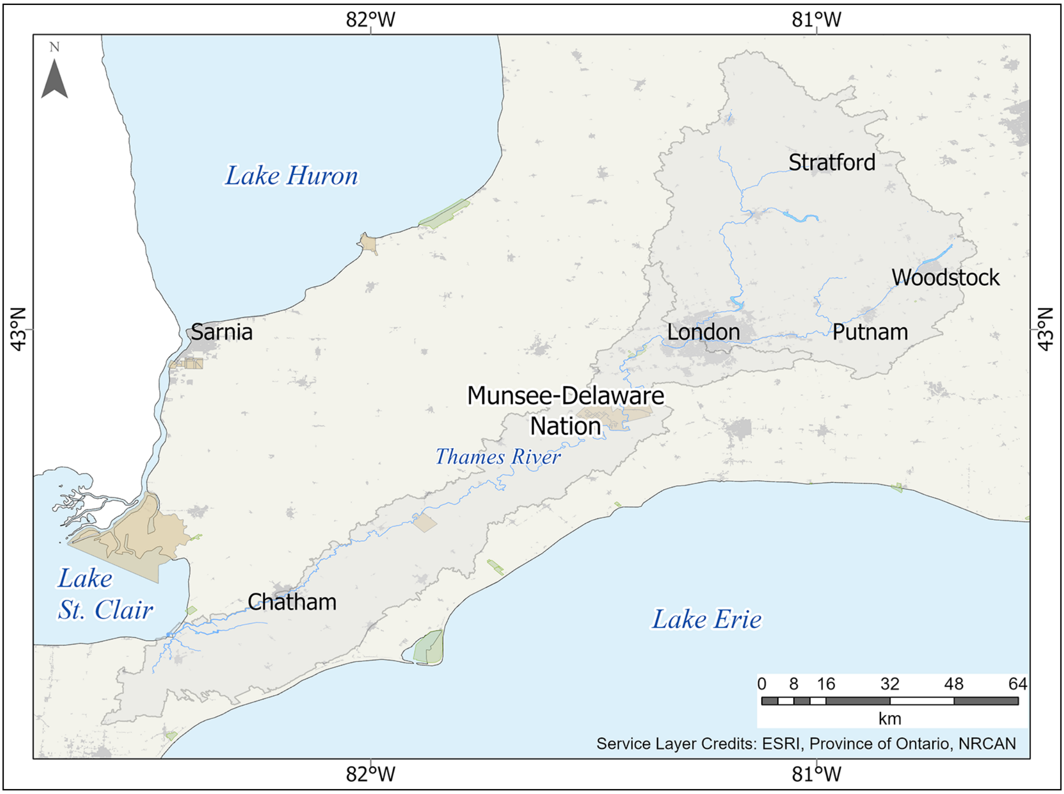

FIGURE 4. Location of the Thames River watershed in southwestern Ontario. G. Frank Neely held exclusive rights to the mussel fishery on the river from Chatham upstream to Putnam.

~25 km downriver from London, Ontario, was identified as one of the "best clam beds in North America" with the area below the dam at Springbank Park, in London, identified as another particularly productive stretch (Figure S5). The area below the Munsee–Delaware First Nation Reserve was of particular abundance, and Neely reported finding an "inexhaustible supply of clams in that bed" (Figure S5). The Munsee location was mainly harvested with farm forks, where one could harvest as many as 13 mussels "in one fork full", while the Springbank site in one instance produced 8.25 tonnes in two days (Figure S5). No other comment on the methods used by the Neely operation has been found. In 1945, The royalty per imperial ton reported in 1945 was $5 (Figure S5). Stewart (1992) reports that ~110 tonnes of shell were shipped yearly to factories including the Dominion Button Manufacturers of Kitchener. However, factories in Guttenberg and Muscatine, Iowa, reportedly received most of the shell material from Neely's operation at this time (Figure S6).

In 1945, Neely appealed to the city of London, Ontario, to stop sewage pollution in the Thames River because it was believed to be diminishing the quality of his shell material (Figure S5). Individuals from the Guttenberg factory had arrived to investigate the cause of "purplish patchy discoloration" in the Thames River Black Sandshell (*Ligumia recta*) and to determine why the Thames River, "a main stay of the button industry" was turning out inferior shells (Figure S5). Paper mill runoff was proposed as a source of pollution but, without a mill in the watershed, the problem was attributed to pollution from London's disposal works (Figure S5). A letter from Mrs. A.Z. Neely (wife of G. Frank Neely), dated 10 February 1965 stated: "The water is so polluted that it is difficult to get white shells without discoloration from the sewage being dumped in the river" (Figure S6). The shells of Black Sandshell in this area continue to have a patchy purple colouration (Figure 5).

The species in the harvest

Across the North American industry, the ideal shell for button processing was "unstained, white or iridescent nacre of moderate thickness and without exterior sculpture, which made shells difficult to cut" (Haag 2012: 304). As a result of these preferences,

Figure 5. Mature male Black Sandshell (*Ligumia recta*) collected recently from the Thames River watershed showing purple colouration in the umbo region similar to that described by G. F. Neely in 1945. Photo: Todd J. Morris.

knowledge of species' distributions was valuable to harvesters and button producers. Prospecting of this sort is responsible for some early records and was the impetus for Detweiler's 1916 surveys (Detweiler 1918). Medium-sized individuals were the original targets, because small shells provided few "blanks" (raw button plugs before finishing) and larger ones resulted in more waste, but the North American industry became less selective as beds were depleted (Haag 2012).

Although detailed catch records are not readily available, a number of people involved in the Ontario harvest kept records that allow for a general look at the species composition. In some cases, collection records contain scientific names, while others rely only on common names. In both cases, there are difficulties in matching historical collection reports with modern species accounts because taxonomy has changed over the last century and common names are known to be regional specific and, in some cases, culturally inappropriate/offensive (see Pfeiffer *et al.* 2024 for a discussion). In some cases, US involvement in the developing Ontario industry likely resulted in local American names being assigned to Canadian specimens bearing a similar appearance (e.g., butterfly or washboard). We have attempted to reconcile the historically provided common/scientific names with the modern scientific literature and our current understanding of species distributions within Ontario. Where common names have been deemed to be inappropriate or offensive they have been redacted.

Detweiler (1918) identified nine commercially important species in the lower Grand River (Table 1), with Threeridge (*Amblema plicata*) and Pink Heelsplitter (*Potamilus alatus*) the two most likely commercially harvestable species. He did, however, note that the pink nacre of Pink Heelsplitter reduced its value to button manufacturers. Of the mussels that Ullyot reported (Table 2), Threeridge appears to have been the target species of his operation just as Detweiler had predicted (Ullyot 1917). Robinson's operation further up the river at Caledonia in the 1930s and 1940s reportedly encountered six or seven species but without the inclusion of scientific names it is difficult to narrow down the exact species that were the focus of this operation (Table 3). In the Thames River, a London Free Press article (Figure S5) identified eight species that were likely part of Neely's harvest although the focus was apparently on Black Sandshell, Mucket (*Actinonaias ligamentina*), Plain Pocketbook (*Lampsilis cardium*), Round Pigtoe (*Pleurobema sintoxia*), and Threeridge (Table 4).

TABLE 1. Species present in the Grand River in 1916 and of commercial importance (Detweiler 1918).*

Detweiler's name	Current name
Pink heelsplitter (*Lampsilis alata*)	Pink Heelsplitter (*Potamilus alatus*)
Fat mucket (*Lampsilis luteola*)	Fatmucket (*Lampsilis siliquoidea*)
Black sand-shell (*Lampsilis recta*)	Black Sandshell (*Ligumia recta*)
Pocketbook (*Lampsilis ventricosa*)	Plain Pocketbook (*Lampsilis cardium*)
Three-horned warty-back (*Obliquaria reflexa*)	Threehorned Wartyback (*Obliquaria reflexa*)
Maple leaf (*Quadrula lachrymose*)	Mapleleaf (*Quadrula quadrula*)
Blue-point (*Quadrula plicata*)	Threeridge (*Amblema plicata*)
Wabash pig-toe (*Quadrula rubiginosa*)	Wabash Pigtoe (*Fusconaia flava*)
Three-ridge (*Quadrula undulata*)	Threeridge (*Amblema plicata*)

*Detweiler's (1918) names have been matched to contemporary species following the nomenclature of Williams *et al.* (2017).

TABLE 2. Species occurring in the Grand River fishery at Dunnville (Ullyot 1917).*

Ullyot's name	Current name
Butterfly (*Pegiola securis*)†	Likely Deertoe (*Truncilla truncata*)
[Redacted] (*Quadrula ebena*)†	Likely Round Pigtoe (*Pleurobema sintoxia*)
Pig-toe (*Quadrula undulata*)	Threeridge (*Amblema plicata*)
Three-ridge/washboard (*Quadrula heros*)†	Likely Threeridge (*Amblema plicata*)

*Ullyot's (1917) names have been matched to contemporary species following the nomenclature of Williams *et al.* (2017). The common name deemed racially or culturally inappropriate has been redacted.

†Species as identified does not occur in Canada, but matched to Grand River species with similar morphology.

TABLE 3. Species occurring at W.H. Robinson's Grand River fishery at Caledonia (Figure S2).*

Robinson's name	Current name
Threeridges	Threeridge (*Amblema plicata*)
Mucket	Mucket (*Actinonaias ligamentina*)
Pocketbook	Plain Pocketbook (*Lampsilis cardium*)
Redacted	Creeper (*Strophitus undulatus*)
Sheepnose†	Likely Round Pigtoe *Pleurobema sintoxia*)
Pigtoes	Likely Round Pigtoe (*Pleurobema sintoxia*) or Wabash Pigtoe (*Fusconaia flava)*

*Robinson's (Figure S2) names have been matched to contemporary species following the nomenclature of Williams *et al.* (2017). The common name deemed racially or culturally inappropriate has been redacted.

†Species as identified does not occur in Canada, but matched to Grand River species with similar morphology.

Numbers of mussels harvested

In an effort to convert the catches reported by Ullyot and Neeley in tonnes to a measure of individuals, we examined a collection of recently surveyed shells (within the last five years) maintained by Fisheries and Oceans Canada at the Canada Centre for Inland Waters in Burlington, Ontario, Canada (Table 5). The average mass of a single valve of each species was determined and the number of individuals required to equal one tonne of shell was calculated using the following equation:

$$\text{No. individuals}_{\text{tonne}} = 2\ \frac{1\,000\,000\ \text{g/tonne}}{\text{mass}_{\text{valve}}\ (\text{g})}$$

This approach assumes that the shell mass of individual species has remained constant over the last 100 years in these rivers, an assumption that we can not verify given the lack of historical shell material. We also have no information on the relative proportions of each harvested species in the reported catches and believe it is unlikely that the harvesters were collecting single species. However, as discussed above, the catch likely consisted of a combination of the species

Table 4. Species occurring at Neely's Thames River fishery (Figure S5).*

Neely's name	Current name
Black Sand clams	Black Sandshell (*Ligumia recta*)
Mucket	Mucket (*Actinonaiais ligamentina*)
Pocket Book	Plain Pocketbook (*Lampsilis cardium*)
Pig Toes	Likely Round Pigtoe (*Pleurobema sintoxia*) or Wabash Pigtoe *Fusconaia flava*)
[Redacted] Heads†	Likely Round Pigtoe (*Pleurobema sintoxia*)
[Redacted] Foot	Creeper (*Strophitus undulatus*)
Three Ridge	Threeridge (*Amplema plicata*)
Warty Backs	Likely Purple Wartyback (*Cyclonaias tuberculata*)

*Neely's names have been matched to contemporary species following the nomenclature of Williams *et al.* (2017). Common names deemed racially or culturally inappropriate have been redacted.

†Species as identified does not occur in Canada, but matched to Grand River species with similar morphology.

Table 5. Mean shell mass of three species of freshwater mussel collected during the last five years from southern Ontario rivers.

Species	No. of valves	Mean shell mass, g/valve (SE)	No. individuals/tonne*
Mucket *(Actinonaias ligamentina*)	15	105.01 (17.71)	4761 ± 1023
Threeridge (*Amblema plicata*)	18	92.18 (14.14)	5423 ± 1585
Round Pigtoe (*Pleurobema sintoxia*)	24	26.59 (2.17)	18 791 ± 2583

*The number of individual animals required to equal one tonne was determined using the equation:

$$\text{No. individuals}_{\text{tonne}} = 2\ \frac{1\,000\,000\ \text{g/tonne}}{\text{mass}_{\text{valve}}\ (\text{g})}$$

(and perhaps others) represented in Table 5. As such, we believe our equation represents a reasonable approach to translate the reported masses into estimates of number of individuals harvested.

Both Ullyot (1917) and Detweiler (1918) have indicated that the most commercially viable and targetted species in the lower Grand River fishery was Threeridge, so it is reasonable to use that value from Table 5 to estimate population scale harvests in the Grand River. Detweiler (1918) reported approximate catches of 291 tonnes in 1915 and 286 tonnes in 1916. If we assume a catch comprising only Threeridge, we estimate that ~ 2.86 million individual mussels were removed over that two-year period. In the decades to follow and a little further upriver, the Robinson camp set up operation on the west bank of the river about 150 m downstream of the bridge in Caledonia. Although they only operated in a short 3-km stretch of the river, they processed a large number of shells annually (Newth pers. comm. 2012; Figure 6). Robinson reports harvesting ~33–66 tonnes annually of a number of species including Mucket, Threeridge, and what we believe was likely Round Pigtoe. Using the values in Table 5 we estimate that the Caledonia harvest ranged from 142 000 (pure Mucket) to 1 125 000 (pure Round Pigtoe) animals per year depending on the species composition and yearly harvest rates. A mixed harvest, the likely scenario, results in estimates intermediate to the two presented above.

In the Thames River, the Neely operation apparently also harvested a mixture of species. Given the broad geographic range of the Neely harvest, extending from the shallow, clear waters of the upper Thames down through the deeper, turbid reaches of the lower river, it is likely that the species assemblage differed greatly across his permitted range, making harvest of a single species impossible (Figure S5). Operating for at least a decade, Neely and his crew reportedly collected around 110 tonnes per year on average. A harvest of that scale could result in the collection of 474 000–1 870 000 animals per year depending on which species contribute to the harvest. Over the decade of operation, the harvest would not have been insignificant at ~5.5–12 million animals.

Implications of historical harvests on today's mussel populations

While the absence of detailed catch records coupled with the lack of historical time series of mussel sampling and abundance in these rivers makes it difficult to properly assess the long-term impacts of these commercial harvest activities, it is likely that these harvests negatively impacted the populations

FIGURE 6. Large pile of shells collected by the W.H. Robinson operation near Caledonia, Ontario. Harvested animals have been boiled to remove the soft tissue and shell material is being prepped for shipment to button factories by rail. Source: W.H. Robinson (Figure S2).

in ways that are still evident today. Haag (2012) described harvest methods that targetted mature individuals of medium to large size while Haag and Rypel (2011) have shown that many of the species targetted in the Ontario harvest demonstrate late maturity and long life spans (i.e., Threeridge up to 54 years; Mucket 50 years; *Pleurobema* spp. 45 years). Species with these characteristics are defined as equilibrium life history strategy species (Haag 2012) and are known to be common in stable, unchanging habitats. Young and Koops (2011: 4) characterized these species as "adult survival dominant", while van der Lee and Koops (2023) demonstrated that altering adult survival rates (e.g., targetting adults for harvest) has the largest proportional impact on population growth rates and ultimately the long-term viability of these populations, particularly when these populations are near carrying capacity.

By the mid-1940s, the North American shell button industry was in steep decline (Haag 2012). Overfishing and pollution had contributed to declines in mussel stocks and the introduction of plastic buttons and the zipper had changed the market forever. The Canadian shell button industry seems to have followed suit, with A.Z. Neely in 1965 stating that "no one has taken clams from that spot since [1945]", referring to the location of the Neely operation (Figure S6). Robinson's operation on the Grand also appears to have run its course by this time. Even during the early years of the fishery, Ullyot (1917: 282) lamented the "diminishing supply" and wondered whether the cause was "the quantity we have fished". While it is encouraging to see that all of the species identified as targets of the Grand and Thames River harvest can still be found in these systems 60–70 years later (McNichols-O'Rourke *et al.* 2012), it would be unwise to think that the harvest had no impact. The very nature of a commercial mussel harvest, targetting large mature individuals, particularly those adapted to stable non-changing habitats, is a recipe for disaster. Minke-Martin *et al.* (2015) surveyed five sites in the lower Grand River at Dunnville in the area where Ullyot operated a century earlier and, despite investing 30 hours of searching, found not a single live Threeridge—the species that was the target of the early Grand River fishery so many years ago. Modern day efforts to protect and recover freshwater mussel populations in these two rivers (e.g., DFO 2019) may be hindered by the lasting effects of this poorly understood but important historical harvest.

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Author Contributions

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SUPPLEMENTARY MATERIALS:

Scans of correspondence and other supplementary materials:

FIGURE S1. Ontario Game and Fish permit #168, 23 April 23 1936, authorizing W.H. Robinson to collect clam shells by hand from the Grand River.

FIGURE S2. Memoir of the Robinson Grand River clam fishery by W.H. Robinson.

FIGURE S3. Correspondence between Grand River shell fisherman W.H. Robinson and Henry Umlandt, president of the Automatic Button Company of Muscatine Iowa, 16 May 16 1944.

FIGURE S4. Correspondence between Grand River shell fisherman W.H. Robinson and Carl Jungbluth, president of the American Pearl Button Company of Washington Iowa, 26 May 1944.

FIGURE S5. Correspondence between Eileene Stewart and William G. Stewart, 23 January 1992, containing text of an article purportedly written by G. Frank Neeley and published in the London Free Press in April 1945.

FIGURE S6. Correspondence between A.Z. Neely and Eileene Stewart, 10 February 1965, discussing Neely's recollections of her husband's shelling operation on the Thames River.

The Canadian Field-Naturalist

Habitat, dispersal, and distribution of the rare Orange-fruit Horse-gentian (*Triosteum aurantiacum* E.P. Bicknell; Caprifoliaceae) in northern Nova Scotia, Canada

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Abstract

Why some plant species are rare and how rare species persist are foundational questions in community ecology. In 2015 we repeated a 2006 survey of three river valleys in rural Antigonish County, northern Nova Scotia, Canada, which support populations of the rare herb Orange-fruit Horse-gentian (*Triosteum aurantiacum* E.P. Bicknell) to see how the populations had changed over a decade and to learn more about why the plant remains rare. Our survey confirms previous observations that Orange-fruit Horse-gentian is largely restricted to the understorey of hardwood and mixedwood stands, on bare ground within and near river floodplains, often with White Ash (*Fraxinus americana* L.). Predictive maps based on geographic information system modelling led to the discovery of new occurrences of the species along the three original rivers and along a fourth river, including a dense cluster in mature hardwood forest, which had not previously been considered habitat. Measurements of photosynthetic capacity using pulse-amplitude modulation (PAM) fluorometry showed significant stress on horse-gentian plants growing in full sunlight or light shade compared with plants beneath closed canopy confirming this plant is shade-adapted. Late-autumn observations of potential consumers of horse-gentian fruit suggest that White-tailed Deer (*Odocoileus virginianus*) may be the primary long-range disperser of seeds. Hence, this species may remain rare in northern Nova Scotia because its optimal habitat (mature, closed-canopy forest with open understorey and calcium-rich soil) is rare and distributed in disjunct patches (mostly along floodplains) and seed dispersal is limited by the range size of the deer.

Key words: Floodplain; GIS; rarity; shade tolerance; soil preference; White-tailed Deer

Résumé

La question de pourquoi quelque d'espèces de plantes reste rares et comment ils survivent en face de la compétition sont primordial en écologie. En 2015, nous avons répétées un levé de 2006 des populations de Trioste orangé (*Triosteum aurantiacum* E.P. Bicknell), une plante herbacée rare qui pousse dans les vallées de trois rivières dans la Comté d'Antigonish, au nord de la Nouvelle-Écosse, pour vérifier la grandeur des populations après neuf ans et comprendre pourquoi l'espèce reste rare. Notre levé a confirmé que l'habitat de Trioste orangé est presque limitée au sous-bois des peuplements feuillus et mixtes, sur sol nu, dans ou près des plaines inondables des rivières, et fréquemment avec Frêne blanc (*Fraxinus americana* L.). L'espèce ne se rencontre le long de deux autre rivières. Néanmoins, les cartes prédictives basées sur la système d'information géographique ont facilitées la découverte des nouveaux sous-populations de Trioste orangé le long des trois rivières originales et aussi le long d'une quatrième rivière, ça incluant un bouquet dense des plantes dans une forêt des feuillus matures, précédemment négligé. Comme mesurée par fluorimétrie, la capacité du photosynthèse de Trioste orangé poussant en plein soleil ou sous un ombre légère est réduite considérablement comparé à des plantes sous un ombre lourde, qui confirme que l'espèce est adapté à l'ombre. Des observations en automne de consomption des fruits de Trioste orangé suggèrent que Cerf de Virginie (*Odocoileus virginianus*) peut être le disperseur des semences primaire à longue distance. Donc, Trioste orangé peut reste rare au nord de la Nouvelle-Écosse parce-que leur habitat optimal (la forêt mature avec l'ombre lourde, sous-étage ouvert et sol riche en calcium) est lui-même rare, et distribué en carrés dissociés (la plupart des plaines inondables des rivières) et le dispersion des semences est limités par le taille de l'aire de répartition de Cerf de Virginie.

Mots-clés : plaine inondable; SDG; rarité; tolérance à l'ombre; préférence du sol; Cerf de Virginie

Introduction

A rare plant is one that has a low frequency of occurrence at some level of spatial resolution (Rabinowitz 1981). Why are some species rare and others common? How does the abundance of a rare species vary through space and time? More practically, to what degree are rare species vulnerable to extinction and what steps can be taken to protect them? Although rarity does not invariably predict extinction, it can increase the probability of local or global extinction (Fagan *et al.* 2001; Matthies *et al.* 2004; Tscharntke and Brandl 2004).

The rarity of plant species has been shown in some studies to correlate with life history characteristics such as height, reproductive strategy, and number of seeds per fruit (Kunin and Shmida 1997; Eriksson and Jakobsson 1998; Hedge and Ellstrand 1999; Guo *et al.* 2000; Farnsworth 2007). An analysis of New England plants showed that rare taxa are more likely to be obligately insect pollinated, have short-range seed dispersal, and be near the northern edge of their range than more common species (Farnsworth and Ogurcak 2008). However, the only finding that was robust across studies in a meta-analysis of 54 life history studies of rare plants at different spatial scales was that rare species tend to produce fewer seeds than common ones (Murray *et al.* 2002).

These correlations provide insight into the characteristics typical of rare plant species, but they do not reveal why those species are rare, i.e., the ecological forces that keep their abundances low. Evolutionarily, rare species are often seen as less competitive than common species (Dawson-Markus *et al.* 2012), which has resulted in rare species evolving to occupy specialized niches in space (habitat) or time (phenology). Rare plant species are often restricted to rare habitats, such as lakeshores, serpentine soils, or alvars, where they are better adapted than more common species and can avoid competitors (Kruckeberg and Rabinowitz 1985; Baskin and Baskin 1988; Morris *et al.* 2002; Jeffrey 2003). These habitats are likely to be scattered in discrete patches within a matrix of non-habitat, creating the problem of dispersal from one patch to another. For plants whose seeds are dispersed by animals, habitat fragmentation may create barriers between used and unused habitat that some dispersers do not cross, limiting seed dispersal and colonization of new habitat (Rodríguez-Cabal *et al.* 2007).

The seed limitation hypothesis (Eriksson and Ehrlén 1992) suggests a plant's dispersal is limited by the number of seeds it can produce (source limitation) or the ability of the seeds to reach patches of suitable habitat (dispersal limitation). In contrast, the establishment limitation hypothesis (Clark *et al.* 2007) says that the primary limitation on the colonization of a plant species is the quality and number of microsites for establishment. These two hypotheses are related because a species limited to a few microsites would need abundant seeds or effective dispersal to guarantee colonization of new sites. Nevertheless, establishment limitation implies that a plant that colonizes a new site may not necessarily persist there if the site quality is poor, as Jacquemyn and Brys (2008) observed for understorey herbs on reclaimed agricultural land.

Orange-fruit Horse-gentian (*Triosteum aurantiacum* E.P. Bicknell; hereafter horse-gentian) is an uncommon, perennial herb that grows in rich deciduous forests of eastern North America. Plants are rhizomatous, each with multiple, pubescent, unbranched stems (up to 1 m) bearing pairs of decussately opposite, lanceolate leaves with wide petioles. Flowers are borne in the leaf axils. The fruit is a fleshy drupe, ~1 cm diameter, turning bright orange in autumn and containing three pyrenes (Roland 1998).

Triosteum aurantiacum is one of three North American *Triosteum* L. species that have overlapping distributions in the USA (Gould and Donoghue 2000) but the only member of the genus in New Brunswick (Hinds 1986) and Nova Scotia, where it grows at the northeastern limit of its distribution (Mazerolle *et al.* 2018). The species occurs in five Canadian provinces and 30 states, as far west as Nebraska and south to Georgia (USDA 2016). It is considered Vulnerable (S3), Imperilled (S2), or Critically Imperilled (S1) in seven eastern states, from Maine (DACF 2022) to Georgia (NatureServe 2023), and rare and Endangered in New Hampshire (NHDFL 2020).

Horse-gentian has long been considered a rare species in Nova Scotia (Mayer *et al.* 1978; Pronych and Wilson 1993) and is considered Vulnerable (S3) in both Nova Scotia and New Brunswick. Based on records held at the Atlantic Canada Conservation Data Centre, populations in Nova Scotia extend from northern Cape Breton south to the Meander and Herbert rivers, near Windsor, all on the north side of the province. The plant occupies upland forest in northern Cape Breton, but most other records in the province are from floodplains of 16 river systems. In no area is horse-gentian considered abundant, and historical observations, mostly in relation to medicinal plants, indicate it was never found in great numbers (Bigelow 1817; Barton 1818).

A previous survey of horse-gentian in northern Nova Scotia (Taylor and Tam 2012) revealed a patchy distribution along select river floodplains and a close association with White Ash (*Fraxinus americana* L.). Horse-gentian occurred primarily in areas of bare ground in regenerating hardwood forest but not in mature mixed forest or coniferous stands. The plant appears to favour partial shade but not dense underbrush or full sunlight. Taylor and Tam (2012) showed that horse-gentian prefers circumneutral soils, which is consistent with historical observations of it growing in limestone-rich areas (Bigelow 1817; Barton 1818) and its absence in acidic, spruce-dominated, upland forests.

Horse-gentian is an excellent candidate for studies of the causes and consequences of rarity in understorey plants. It has a large geographical range but occurs at low frequency in most places in its range. Although it grows in a variety of forest habitats in much of its range, in Nova Scotia it is restricted to specific habitats, mostly river floodplains and calcareous forests. While horse-gentian is uncommon to rare regionally, the plant is sufficiently abundant in suitable habitat patches to test hypotheses and support habitat modelling. Yet the species is absent from large areas of apparently suitable habitat along several river valleys in Nova Scotia, suggesting that a dispersal limitation perpetuates its rarity. The conspicuous fleshy fruits suggest zoochory, but while horse-gentian in northern Nova Scotia is restricted mostly to floodplains, most floodplains do not support horse-gentian, which suggests that the dispersal agent is either incapable of crossing ridges or does so infrequently. Determining the key species dispersing seeds would help answer this question. Studies on the factors limiting the distribution and abundance of horse-gentian may, in turn, shed light on the nature of rarity in plants generally.

The objective of our study was to assess the distribution, relative densities, and demographic characteristics (genet size, stem height, fecundity) of Orange-fruit Horse-gentian in Antigonish County to see how these population features have changed since the previous survey. From this information we sought to better understand the ecological causes of the plant's rarity. First, we resurveyed the three river valleys (Pomquet, West, South rivers) and other locations where Taylor and Tam (2012) reported finding horse-gentian in 2006 to see if those populations remained extant a decade later. To better understand the size and extent of the populations, we searched new areas of floodplain along two of these rivers (Pomquet, West) and added two others (Tracadie River, Brierly Brook) to look for plants that may have been overlooked before. We used these observations to create simple, predictive maps of habitat for the species along West River and previously unsurveyed Rights River. We then made ground searches based on these maps to efficiently search for more overlooked plants and to test whether our predictions of horse-gentian habitat were accurate. Second, we made demographic measurements of plants in three locations to test whether the quality of habitat could be inferred from plant size and fecundity. To test whether the occurrence of horse-gentian in young forest reflected a habitat requirement for light shade, we used pulse-amplitude modulation (PAM) fluorometry to assess the degree of stress experienced by plants growing in different habitats, from open ground to closed-canopy forest. Finally, we used motion-activated cameras and direct observation to identify organisms feeding on horse-gentian fruit, to address whether poor seed dispersal contributes to the patchy distribution of the species.

Methods

Population surveys

Between 16 June and 28 August 2015, we resurveyed horse-gentian populations surveyed by Taylor and Tam in 2006 (South River, Black Avon/Pomquet River, West River; Figure 1). We also surveyed upstream areas of West River floodplain not explored in 2006. The purpose of these surveys was to determine the relative abundance and size of the plants along each river and document the common habitat conditions in which they were growing.

We did not attempt to survey the entire length of these river valleys or to produce quantitative estimates of plant density. We surveyed 4 km along West River (mostly the north bank), 1.2 km along lower Black Avon River, 1 km along Pomquet River, and 1 km along South River (west bank), all within Antigonish County. We surveyed 1 km of lower Tracadie River in 2021. One observer cumulatively surveyed ~1 km of Brierly Brook, a major tributary of West River, from 2015 to 2020. Most survey sites lay within river floodplains but three survey sites along South River (Frasers Mills Upland, St. Andrews, Lower South River) and two sites along West River were in forests above the floodplain. The total area and number of sites surveyed along a river were determined by the presence of presumed habitat (young deciduous forest, sparse underbrush, bare ground) along the river and site accessibility. We attempted to survey the sites covered in Taylor and Tam (2012), using notes and coordinates from the earlier work, although changes to land cover (houses, thickets, channel shaping) since their surveys sometimes made that impossible.

We walked in pairs during the surveys, ~5 m apart, along a path parallel to the river or through upland habitat. When we found a horse-gentian, we marked its location with a global position system unit (Garmin eTrex Legend, Olathe, Kansas, USA) and recorded the number of stems, canopy cover, ground cover (along West and Pomquet rivers only), the identity of the two nearest trees, and the approximate distance from the river. We subjectively ranked canopy cover as open (1), mostly open (2), mostly closed (3), or closed (4). We recorded ground cover as bare ground, leaf litter, grass, moss, ferns, forbs, woody underbrush, or any combination of these. We noted damage to the leaves (insect damage, fungal growth) or the stems (deer browse, broken stems) of horse-gentian. Once all data were collected for a plant, we conducted a fine-scale search over ~10 m in all directions, seeking other individuals. If no more plants were detected,

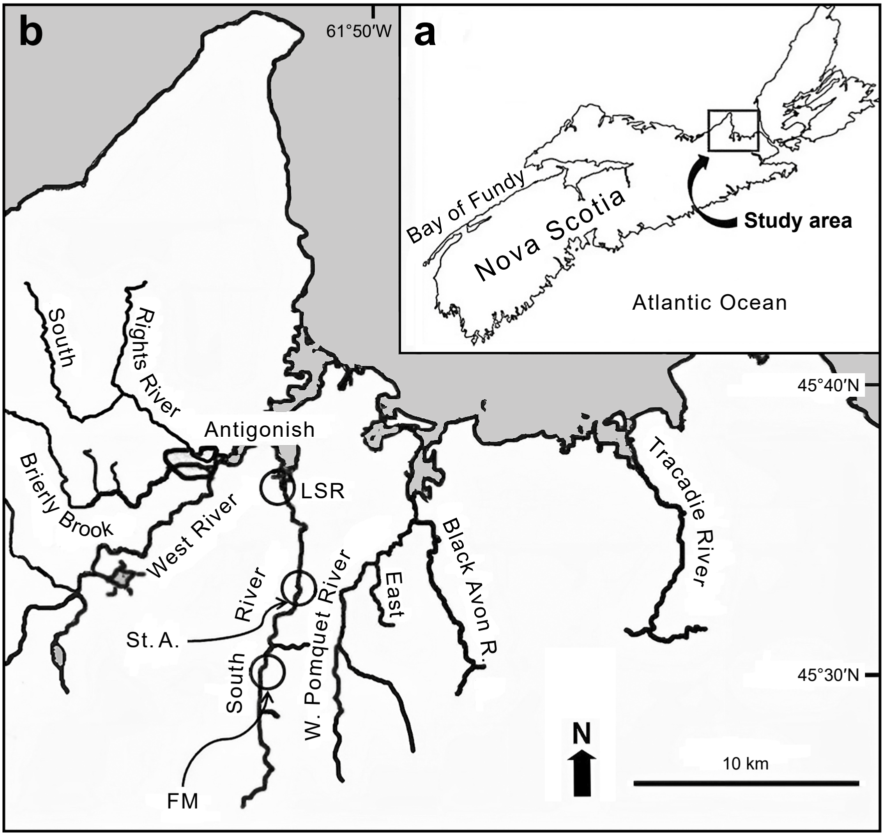

FIGURE 1. Maps of a. Nova Scotia and b. the rivers in Antigonish County surveyed for Orange-fruit Horse-gentian (*Triosteum aurantiacum*). Circles along South River indicate locations mentioned in the text: LSR = Lower South River; St. A = St. Andrews; FM = Frasers Mills.

we continued along the original line until the vegetation changed or no more horse-gentian was found.

At one site along South River and two sites along West River, where the channel was wadable, we crossed the river to determine if patches of horse-gentian on one bank extended across the channel. On most excursions, we also conducted brief surveys of presumed non-habitat (conifer stands, mature forest, areas of dense underbrush) next to presumed habitat.

We conducted demographic surveys on subsets of the horse-gentian populations along Pomquet River (25 genets, 115 stems), West River (13 genets, 95 stems), and Frasers Mills Upland (14 genets, 74 stems) from 13 to 30 September 2015. The Frasers Mills Upland data are part of a long-term study (B.R.T. unpubl. data). For each plant (genet) we recorded the number of stems, height of each stem, and number of fruits per stem. We measured stem height from the ground to the top of the apical buds. Each rhizome of Orange-fruit Horse-gentian produces a clump of stems (ramets) which collectively constitute the genet, the whole plant. Stems all arise from the same base, so it is easy to count the number of stems in each genet. We never encountered two plants so close together that the genets could not easily be distinguished.

Mapping

Using georeferenced locations of horse-gentian plants from the 2015 survey, we created predictive maps of horse-gentian habitat using ArcGIS 10.3 (ESRI, Redlands, California, USA). We acquired GIS files of forestry inventory data (NSDNR 2007) and soil survey data (AAFC 2010) and produced maps of the intersection, or areas of overlap, between soil types and forest types where the plants had been observed.

Field observations revealed a strong association between hardwood tree species and occurrence of horse-gentian (Figure 2), suggesting that hardwood forests would provide the best habitat. We defined forests as "predominantly hardwood" if they supported >70% hardwood species cover in forest inventory maps from NSDNR (2007). Areas containing

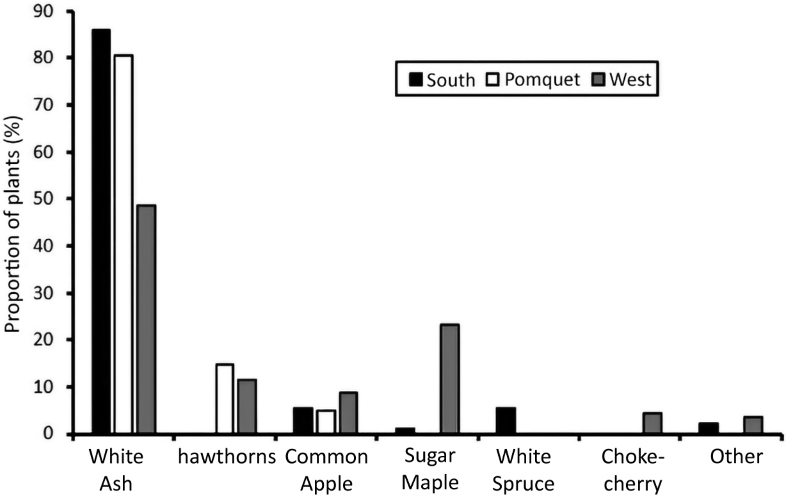

FIGURE 2. Nearest canopy trees to Orange-fruit Horse-gentian (*Triosteum aurantiacum*) genets along South, Pomquet, and West rivers in Antigonish County, Nova Scotia, in 2015.

>70% softwood (conifer) trees were classified as "softwood" and forest between these limits were classified "mixed forest". We mapped hardwood forests as potential horse-gentian habitat.

Examining the known locations of horse-gentian against the soils in the area showed that the plant has a high affinity (68% of georeferenced plants) for Orthic Humic Regosols (Entosols in the USDA classification), a weakly developed mineral soil formed from unconsolidated sediments that lacks a developed B horizon but contains an organic A horizon (Soil Classification Working Group 1998). Habitat for horse-gentian was then predicted to lie in areas of hardwood forest growing in Orthic Humic Regosols. Because these soils develop from fluvial sediments, they are concentrated in river valleys. Known locations of horse-gentian were also associated with flat to gently sloping land. However, slope was not included in the predictive GIS maps because it proved redundant with soil given that Regosols in the study area develop in floodplains.

We initially generated GIS-based, predictive maps for West, South, and Pomquet rivers. We undertook ground surveys to confirm occurrence of the plant in predicted locations along West River in 2015 (28–29 September, 5 October), 2016 (22 September), and 2017 (11–19 September, 19 October). In addition, anecdotal reports in 2018 suggested an un-surveyed population was growing along the floodplain of Rights River, which flows through the Town of Antigonish from the north (Figure 1). We created a predictive GIS map for Rights River using the same criteria as before. We undertook ground-truthing of those habitat predictions from 9 July to 20 August 2018.

Chlorophyll fluorescence

We used pulse-amplitude modulation (PAM) fluorometry to measure the quantum yield of photosystem II in selected Orange-fruit Horse-gentian genets as an index of photosynthetic efficiency and hence vigour of the plant. A low quantum yield could be a sign of stress and an indicator of a sub-optimal habitat (Murchie and Lawson 2013; Kalaji *et al.* 2016). Between 20 July and 3 September 2015, we measured quantum yield on nine genets (29 stems) from the lower Pomquet River floodplain and 19 genets (63 stems) from four sites in the South River valley. Two sites along South River (St. Andrews Upland, Frasers Mills Upland) were anomalous locations identified in Taylor and Tam (2012) where horse-gentian grows along the slope of the river valley, well above the floodplain. We paired these sites with floodplain sites (St. Andrews Floodplain, Frasers Mills Floodplain) directly downslope and <0.5 km distant. Two of the plants surveyed at Frasers Mills Upland had no canopy cover (because of recent forest harvesting), so we analyzed these separately to test for stress caused by lack of cover.

We estimated photosynthetic performance of horse-gentian leaves by measuring the maximum quantum yield of photosystem II, a measure of photochemical efficiency, using a portable PAM fluorometer (Diving-PAM, Heinz Walz, Effeltrich, Germany). We calculated maximum quantum yield as:

$$QY(II)_{max} = (F_m - F_o)/F_m = F_v/F_m$$

where F_o is the minimal value of chlorophyll *a* fluorescence in photosystem II in a dark-adapted leaf and F_m is the maximum chlorophyll *a* fluorescence of that leaf during a saturating flash, a non-modulated flash of light that fully reduces photosystem II. The difference between the minimum and maximum fluorescence values, F_m–F_o, is the variable fluorescence, F_v. Maximum quantum yield is therefore the ratio of variable fluorescence to maximum fluorescence; in unstressed leaves this value is consistently ~0.83 (Murchie and Lawson 2013). Stresses that influence photosynthetic performance may be reflected in lower values of F_v/F_m (Kalaji *et al.* 2016).

To measure quantum yield, we selected four leaves equidistant along each of 1–8 stems on each genet, to compensate for the effect of declining light intensity below the top of the plant. Portions of each selected leaf were enclosed in dark leaf clips and allowed to dark adapt for 10–15 min before measurements were taken. The intensity of the PAM fluorometer's monitoring beam, used to measure F_o, was 0.04 μmol photons/m^2/s, and the intensity of the saturating flash (0.8 s) was 10 000 μmol photons/m^2/s. We noted the health of the leaves, including colour, damage, and presence of fungi. Weather does not influence these measurements because the instrument measures the photosynthetic capacity of the leaf by subjecting isolated portions to flashes of light.

Dispersal agent survey

We set up motion-sensitive cameras with built-in flash (Wingscapes Wildlife Cam, Ebsco Industries, Birmingham, Alabama, USA; 8.0 MP, focal length 30 cm–infinity) facing relatively large genets (15 and 25 stems) above the South River floodplain at Frasers Mills on 17–19 October and 24–31 October 2015, when ripe fruits were abundant on the stems. We redeployed one camera to face the 25-stem genet from 5 November to 13 December 2015, after which snow cover was expected. Fruits do not persist over winter; they become soft and rot. We inspected photographs for the presence of animals near the plants or feeding on the fruits, which presumably would be dispersal agents. We tallied the number of days in which an animal was recorded near the plant and the number of distinct visits each species made.

Statistics

We compared canopy cover among the three river valleys using the χ^2 test. We compared stem height and number of fruits per stem (log-transformed) using one-way analysis of variance (ANOVA) followed by Tukey's test. Because fruits are borne in the leaf axils, number of fruits is correlated with stem height (r = 0.68, P < 0.001, n = 268). Therefore, we included stem height as a covariate in the ANOVA comparing fecundity among sites. We compared quantum yields among sites using a two-factor ANOVA on location and date, followed by Tukey's test. To avoid an unbalanced design, we averaged the results from the five stems with the highest quantum yields at each site and used these data to compare sites. Preliminary analysis revealed no significant difference (P < 0.05) in average quantum yield among leaf positions. Therefore, data from each site were not divided by leaf position. Statistical analyses used Statistix® v.10 (Analytical Software 2013).

Results

Population surveys

The survey of known horse-gentian habitat revealed that populations are more extensive and more dynamic than previously reported. We found 287 plants (1026 stems) along the three river floodplains in 2015 (Table 1). West River supported the largest population and Pomquet/Black Avon River the smallest. (Note: Pomquet River bifurcates near the mouth. The west branch is called West Pomquet River and the east branch is the Black Avon River but it is all the Pomquet River system; Figure 1.) Taylor and Tam (2012) reported only 96 plants in the 2006 survey, with the largest counts along Pomquet River and smallest along West River. We found horse-gentian 10 km further upstream along West River than Taylor and Tam (2012), in previously unexplored habitat (Figure 1). All the plants observed in 2015 in the Black Avon/Pomquet River system were growing along the Pomquet River main stem. We found no horse-gentian along either bank of Black Avon River, despite an extensive search, nor along lower Tracadie River or Brierly Brook.

Forays across South River revealed no horse-gentian on the bank opposite where the species was found. We did encounter horse-gentian along both banks of West River, but these patches were not

TABLE 1. Counts of Orange-fruit Horse-gentian (*Triosteum aurantiacum*) in each of three river valleys in Antigonish County, Nova Scotia, 2015, compared with counts from a 2006 survey.

Variable	Pomquet/Black Avon River	South River	West River	Total
Genets 2006*	66	22	8	96
Genets 2015	41	108	138	287
Stems 2015	207	394	425	1026

*Taylor and Tam (2012).

directly opposite each other.

We confirm that Orange-fruit Horse-gentian tends to grow in hardwood or mixedwood stands, closely associated with White Ash and to a lesser extent hawthorn (*Crataegus* L.) and Common Apple (*Malus domestica* (Suckow) Borkhausen). The plants we found along West River in 2015 sometimes occurred in more mature forest dominated by Sugar Maple (*Acer saccharum* Marshall; Figure 2). Among 179 plants for which we recorded ground cover, we observed bare ground around all but eight (96%), sometimes with cover of leaf litter or scattered grass and moss (Figure 3). We rarely found horse-gentian among other forbs, ferns, or woody underbrush.

Most horse-gentian plants were growing within a few metres of deer trails, as was noted in the 2006 survey. Of 287 genets recorded in 2015, 43 plants (15%) displayed truncated or broken stems, presumably caused by White-tailed Deer (*Odocoileus virginianus*) browsing. We noted insect damage on 150/287 plants (52%), although it was rarely severe. Conspicuous fungal infection was never observed.

Among 287 observations of tree cover above horse-gentian, almost half (45%) were in cover class 3, indicating mostly closed canopy. Virtually all the remainder was in cover classes 2 and 4. We found only seven plants (2.4%) in the open, cover class 1, and two of those were in recent clear-cuts. Median cover class was 3 overall, but cover class differed significantly among sites ($\chi^2_6 = 87.6$, $P < 0.0001$). Median cover class was 3 (mostly closed) along Pomquet and West rivers, but 2 (mostly open) along South River. Hence, plants along South River were exposed to more intense sunlight than in the other two river valleys.

Horse-gentian genets typically had one to three stems (Figure 4), with some individuals reaching 25 (South River), 32 (Pomquet River), and 55 stems (West River). The median number of stems/genet was two at South and West rivers, but three in Pomquet River, which had relatively fewer one-stemmed plants and more large, multi-stemmed plants (>10 stems; Figure 4).

Horse-gentian was found in substantial numbers at three upland sites along South River: Lower South River, St. Andrews, and Frasers Mills (Figure 1). The last two sites seem to be extensions of the populations in the floodplain; we consider all the plants in one river valley as a single population. The upland plants at Frasers Mills were growing in dense hedgerows and second-growth forest, often beneath apple trees. Median cover at this site was 3 ($n = 16$). The Lower South River site is an area of calcareous ground around gypsum outcroppings. The upland site at St. Andrews lies in a small (<1 ha) stand of White Ash, along the edge of a hayfield, and separated from the South River floodplain by a steep slope and a gravel road. The 2015 survey (in June) discovered 38 genets in this patch, compared with 35 in 2007. The median number of stems/genet was two in both surveys. The number of stems/genet was distributed almost identically between the two surveys (Figure 5). Hence, the population at this site appears to be stable.

Demographic data reveal that the West River population had significantly taller stems ($F_{2,282} = 12.78$, $P < 0.001$) than plants from Pomquet River or Frasers Mills Upland. Comparing the number of fruits per stem among sites, using stem height as a covariate, revealed a clear distinction among sites ($F_{2,281} = 45.5$, $P < 0.001$), with Frasers Mills Upland > Pomquet River > West River. Hence, plants in the thickets at Frasers Mills, just above the South River floodplain, were shorter but most fecund while plants along West

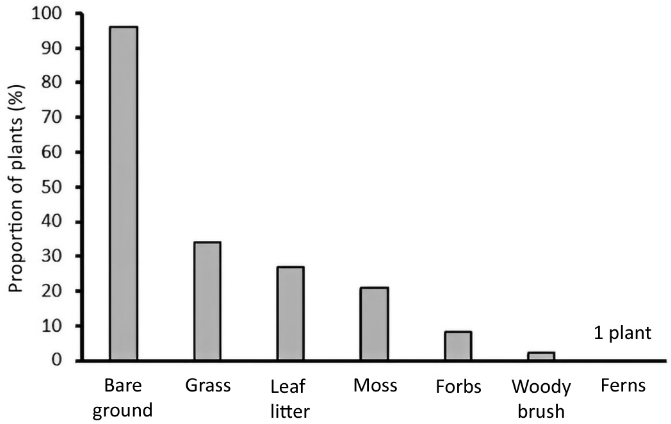

FIGURE 3. Distribution of ground cover around 179 Orange-fruit Horse-gentian (*Triosteum aurantiacum*) plants in South, Pomquet, and West river valleys, Antigonish County, Nova Scotia, in 2015. More than one kind of ground cover could surround an individual plant; therefore, columns do not add to 100%.

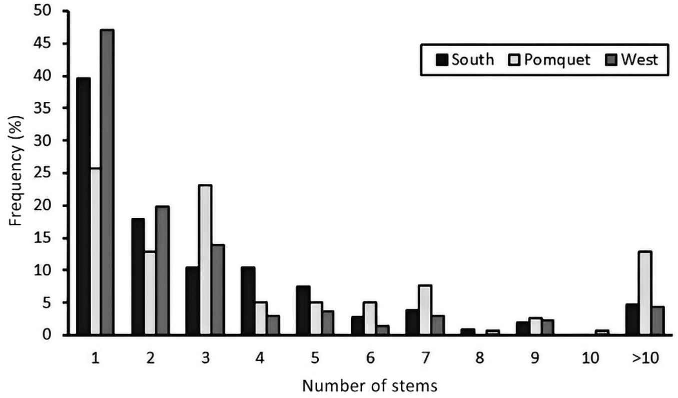

FIGURE 4. Distribution of number of stems/genet among Orange-fruit Horse-gentian (*Triosteum aurantiacum*) plants from South, Pomquet, and West rivers, Antigonish County, Nova Scotia, in 2015.

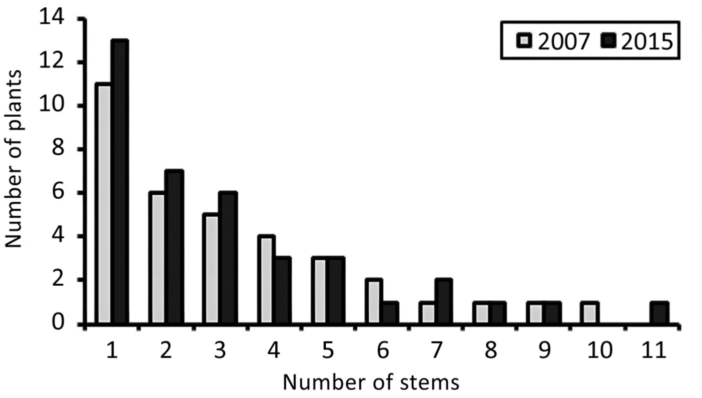

FIGURE 5. Distribution of number of stems/genet of Orange-fruit Horse-gentian (*Triosteum aurantiacum*) in a confined stand of White Ash (*Fraxinus americana*) along South River, near St. Andrews, Nova Scotia, in 2007 (Taylor and Tam 2012) and 2015.

River were taller but least fecund. The Pomquet River population was intermediate in both characters. In the 2006 survey, Pomquet River plants were both taller and more fecund than those in South River floodplain (Taylor and Tam 2012).

Habitat mapping

The GIS exercise revealed substantial areas of potential horse-gentian habitat along all three river valleys. As expected, potential habitat was mostly limited to the river floodplains, usually within a few decametres of the river channels. Habitat was distributed as elongate, linear patches interrupted by river sections running through steeper valleys where the floodplain was restricted. Occasional patches of potential habitat were revealed in isolated upland areas, especially near West River, and along wider tributaries to the main-stem rivers.

Ground-truth surveys of West River from 2016 to 2018 revealed over 200 plants at five new locations predicted by habitat mapping (Figure 6). Many of these plants were growing in places previously thought to be suboptimal habitat for the species, such as mature forest and mixedwood stands with numerous softwood trees. The species was abundant wherever it was found. We did not find horse-gentian at two predicted locations (Figure 6). One of these was a large alder swamp; the other was too dense with underbrush to constitute habitat.

The ground-truth survey in 2017 unexpectedly revealed one new patch of horse-gentian growing in mature hardwood forest on a steep slope ascending from the West River floodplain. This site is only ~200 m × 60 m, yet we recorded 141 Orange-fruit Horse-gentian in this small area. These plants were growing in an open understorey among large Sugar Maple (trunk diameter 24–68 cm, $n = 9$), White Ash (46–65 cm, $n = 2$), Trembling Aspen (*Populus tremuloides* Michaux;

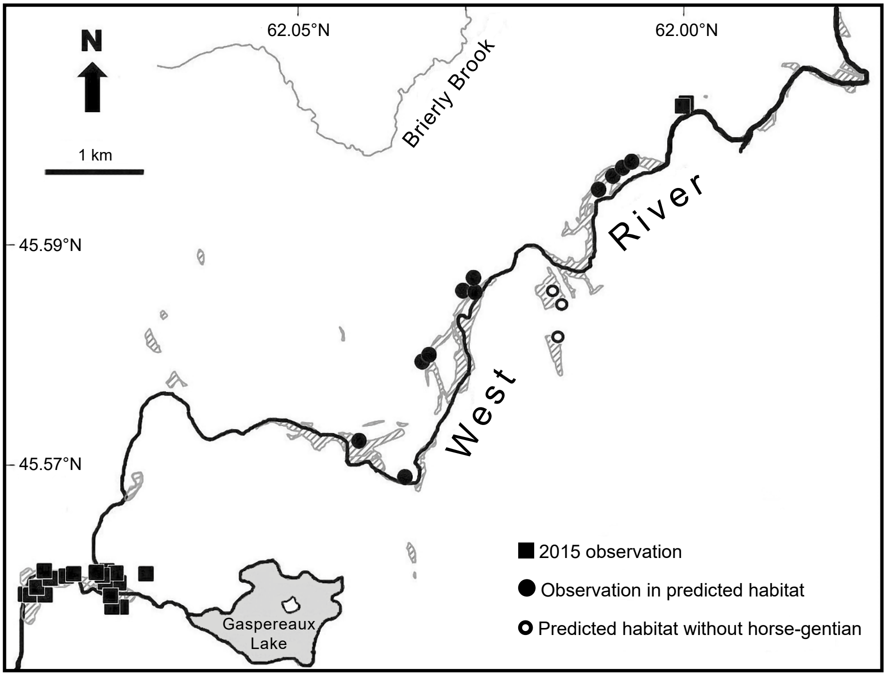

FIGURE 6. Map of West River, Antigonish County, Nova Scotia, showing predicted habitat (grey diagonal lined) for Orange-fruit Horse-gentian (*Triosteum aurantiacum*).

30–35 cm, $n = 6$), and American Beech (*Fagus grandifolia* Ehrhart).

The ground-truth survey of Rights River covered ~1.5 km along the South Branch (Figure 7). Horse-gentian was scattered throughout the surveyed reach and grew in such abundance that recording locations of all plants became impractical; we thus stopped doing so after the first 323 plants encountered. Plants along the east-flowing, lower reach (Figure 7) were growing in typical floodplain habitat, on flat ground dominated by young hardwood forest (White Ash, Sugar Maple, birch [*Betula* L.], and Chokecherry [*Prunus virginiana* L.]). Farther upstream, along the south-flowing channel, we discovered many plants on a steeply sloping hillside covered with mature, mixed forest of the above species plus White Spruce (*Picea glauca* (Moench) Voss) and Eastern Hemlock (*Tsuga canadensis* (L.) Carrière). Horse-gentian association with White Ash was strong at this site. Only 12/323 records of horse-gentian along Rights River do not report White Ash as one of the two closest trees. Median cover index was 3. Ground cover was universally bare ground with leaf litter.

Most horse-gentian plants along Rights River were short and appeared to be young. Over 80% of 323 genets recorded had only one (59%) or two (23%) stems (median one). Large, multi-stemmed plants were rare: only 4% of genets had >5 stems, compared with 12–27% in the other river valleys; the largest plant had 11 stems.

Chlorophyll fluorescence

Our analyses revealed a significant difference in the average quantum yields among horse-gentian populations at the sites surveyed ($F_{3,5} = 6.33$, $P < 0.001$; Figure 8). Quantum yields at four of the five sites were similar and close to the typical value of 0.83. Quantum yields of plants at the upland St. Andrews site, a compact group of 38 plants in a stand of White Ash and not in the flood plain, showed no significant difference from the floodplain plants downhill from them, nor from floodplain plants along Pomquet River. Surprisingly, mean quantum yield of plants at the Frasers Mills Upland, a scattered group of plants growing in hedgerows and second-growth forest and not in the flood plain, was significantly greater than that of plants growing in the forested floodplain below (Figure 8). Floodplain plants at Frasers Mills had the lowest quantum yield of any shaded site. Mean quantum yield of plants lacking tree cover at Frasers Mills Upland was also significantly less than shaded plants at the same site (Figure 8), confirming that Orange-fruit Horse-gentian is a shade-adapted species.

Dispersal agent survey

The field cameras caught White-tailed Deer near

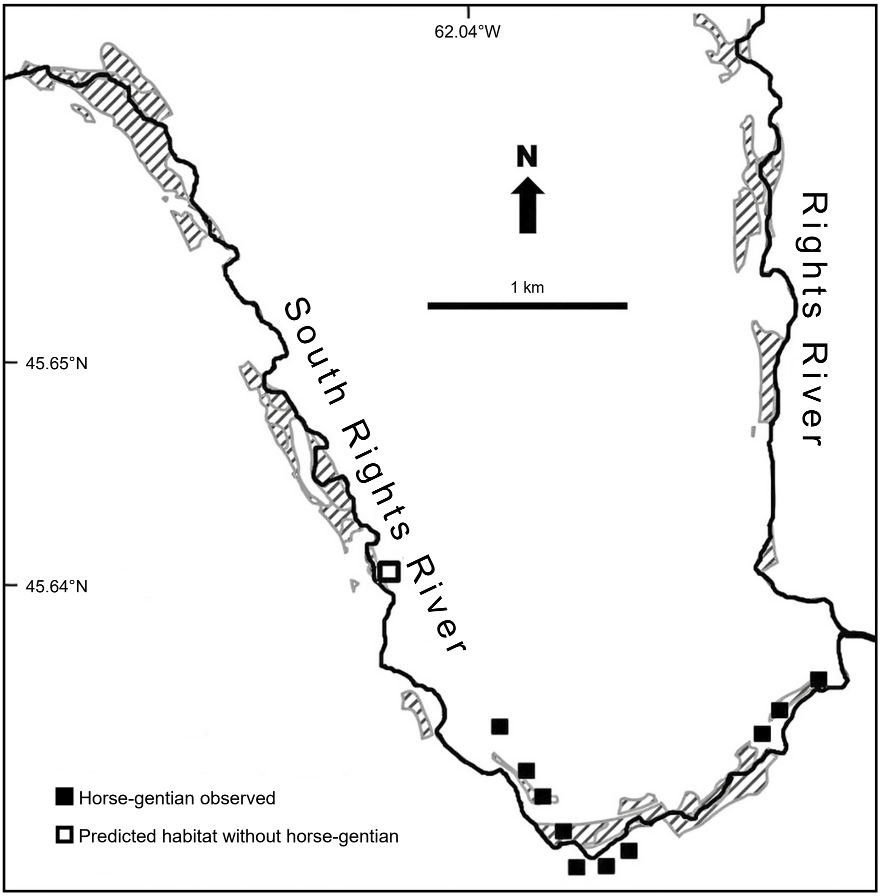

FIGURE 7. Map of lower West Branch, Rights River, Antigonish County, Nova Scotia, showing predicted habitat (grey diagonal lined) for Orange-fruit Horse-gentian (*Triosteum aurantiacum*).

horse-gentian on seven days (eight visits). Although not the most frequent visitor, the deer showed great interest in the plant, and some photo series show clear foraging behaviour, indicating that deer were consuming the plant with the attached fruits. Snowshoe Hare (*Lepus americanus*) was photographed on the most days (12 days, 20 visits). An Eastern Chipmunk (*Tamias striatus*) was photographed on two days, and in one picture its cheeks are full, an indication that it had been foraging. The other mammalian captures were Raccoon (*Procyon lotor*) and North American Porcupine (*Erethizon dorsatum*), which were each seen on two days (two visits each). The only birds captured were a Black-capped Chickadee (*Parus atricapillus*) and an American Robin (*Turdus migratorius*), which were each noted in only a single visit.

Damage apparently from deer browsing was observed on multiple plants over the course of the survey, at one or more sites along each river. Deer damage was seen on 8% of Frasers Mills plants, 6% of Pomquet River plants, and 50% of West River plants. Fruits were observed on the stems well into the fall, also suggesting distribution by foraging animals. Deer and deer tracks were commonly observed at the Frasers Mills Upland site and in all river valleys during our research, showing that deer are common in known horse-gentian habitat.

Discussion

Our study revealed new information about the distribution of Orange-fruit Horse-gentian in northern Nova Scotia and about some factors limiting that distribution. Horse-gentian grows primarily in closed canopy hardwood or mixed forest with open ground and Orthic Humic Regosol soil. These conditions occur most often in river floodplains. However, its occurrence well above the floodplain in Frasers Mills and St. Andrews and far upslope from Rights River demonstrates that the restriction to Regosol is not absolute. Soils at these upland sites are Orthic

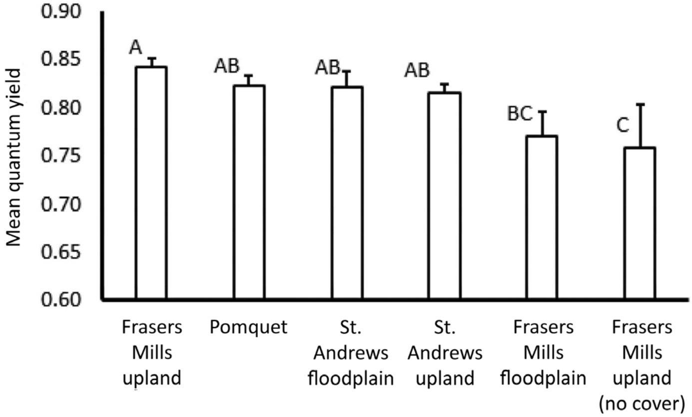

Figure 8. Mean quantum yield of chlorophyll in leaves of Orange-fruit Horse-gentian (*Triosteum aurantiacum*) from different habitats along South and Pomquet rivers, Antigonish County, Nova Scotia. Treatments sharing the same letter are not significantly different (Tukey's test, $P < 0.05$). Error bars are SD. Plants in Frasers Mills Floodplain are significantly more stressed than those in the upland nearby; a plant deprived of shade by forest harvesting shows significant stress compared with shaded plants. Unstressed leaves consistently have a value of ~0.83 (Murchie and Lawson 2013).

Humo-Ferric Podzols (USDA Cryorthod or Haplorthod), by far the most common soil type in northern Nova Scotia (AAFC 2010). Humo-Ferric Podzols, developed over unsorted glacial till, are rich in organic matter but highly leached, acidic, and nutrient poor. Evidently, horse-gentian may be catholic in its soil preference if other conditions are suitable.

In appropriate habitat, the species appears to be more abundant and widespread than previously documented in Nova Scotia. We discovered many more plants along South River and West River than in the 2006 survey. This increase was partly because we surveyed a larger area; apparent distributions of rare species are strongly influenced by search effort (Kadmon *et al.* 2004) and ease of access (Keith 2000). We found plants along West River growing 10 km upstream, beyond the previously known extent of the population and sometimes in places that would not previously have been considered habitat for the species. The same may be said for the population growing in mature, closed-canopy forest along upstream Rights River.

In contrast, the total plant count for the Pomquet/Black Avon River system was lower in our survey than in 2006 because we found no horse-gentian along Black Avon River, where Taylor and Tam (2012) found 20. Our survey was guided by location data and notes from Taylor and Tam (2012) but also covered a larger area along the floodplain. While a survey can never prove the absence of the target species, a sharp decline in the number of horse-gentian plants along Black Avon River is evident. The underbrush (mostly thickets of Chokecherry) had grown denser along both the Pomquet and Black Avon rivers in the nine years between surveys, making the floodplain difficult to search and perhaps reducing habitat quality for horse-gentian. Floodplain forests in Antigonish County have developed on abandoned farmland (Gentilcore 1956). Early successional stages on this land often develop dense thickets of Chokecherry and other short-lived tree species, which may be detrimental to horse-gentian.

Where horse-gentian occurred it was usually relatively abundant, and all other local populations appear to be stable in number or growing. Despite the loss of the species along Black Avon River, the frequency of its occurrence along the floodplains of South and Pomquet rivers did not noticeably change between the two surveys. However, the Pomquet River population had more large plants (more stems) and fewer single-stemmed (presumably younger) ones than populations along the other rivers, which suggests poor recruitment; fecundity at this site appears to have declined compared with 2006 (Taylor and Tam 2012). The size of the population above the floodplain at St. Andrews has remained stable (35–38 genets) for a decade. Size and fecundity of the plants at Frasers Mills are assessed every autumn in a long-term study (B.R.T. unpubl. data); that population also appears to be slowly increasing.

Ground-truth surveys suggest that predictive habitat mapping based on forest cover and soil type was generally successful in identifying potential habitat. These maps indicate scattered, often elongated, patches of habitat along all the surveyed rivers and some tributaries. Perhaps because the maps were extrapolated from surveys of river valleys, they do not predict occurrences in upland areas, where the species was also sometimes encountered. For example, while GIS-generated maps correctly predicted habitat along the floodplain of lower Rights River (South Branch), they failed to predict the extended population throughout the hillside forest farther upriver.

The application of GIS to locating horse-gentian in Antigonish County provides the basis for a general approach to surveying occurrence of rare plants when some aspects of the environment and community structure are known (Sperduto and Congalton 1996; MacDougall and Loo 2002; Draper *et al.* 2003; Neigel *et al.* 2022). For Nova Scotia and most of southern Canada, land cover, soil types, and hydrology have been mapped in detail (see Methods). The GIS approach directly predicts sites suitable for ground truthing (Wu and Smeins 2000; Aitken *et al.* 2007). Mann *et al.* (1999) used a similar approach to predict the location of rare, calcareous soil habitat. Although our GIS model was comparatively simple, it proved immediately useful by identifying potential new sites, with considerable accuracy, and thereby greatly increasing the efficiency of field surveys.

Moreover, GIS mapping of West River led to the discovery of a remarkably dense cluster of Orange-fruit Horse-gentian (over 140 plants) growing in mature, closed-canopy forest that would not have been considered habitat based on previous surveys. This forest stand was probably spared from historical logging because it grows on a steep slope. The discovery of many plants beneath a canopy of large White Ash, maple, and Red Oak along West River, and again in mature mixed forest along Rights River, suggests that young deciduous forest stands, such as those along most floodplains here, are not prime habitat for the species. The species may be encountered most often beneath suboptimum early second-growth forest (White Ash, Common Apple, cherry, young maple) because the preferred habitat—mature, late-successional forest—is so rare in northern Nova Scotia. Thus, horse-gentian may be rare at least partly because its habitat is rare. Creating similar habitat maps for other regional rivers would help in locating additional unknown patches of horse-gentian and determining whether lack of habitat limits the abundance of the species.

The frequency with which horse-gentian is found in the floodplains of Antigonish County may be explained by the relatively high pH there compared with upland sites. Hill and Garbary (2011) and Taylor and Tam (2012) found that the upland sites of Antigonish river valleys were significantly more acidic than the floodplains. Hill and Garbary (2011) also concluded that soil calcium is a determining factor in the presence of large-seeded herbs, including horse-gentian. Preference for high-calcium soils would align with the historical pattern of finding horse-gentian in limestone-rich areas elsewhere (Barton 1818; Ogle 1980; Laughlin and Uhl 2003; Mazerolle *et al.* 2018) and is consistent with the robust population of the species among the gypsum cliffs of Lower South River.

The PAM fluorometry confirms that Orange-fruit Horse-gentian is a shade-adapted plant that is stressed by exposure to full sunlight. However, the observation of apparent stress among floodplain plants along South River and unstressed functioning among upland plants nearby questions the conclusion that horse-gentian grows best in moist floodplains. Plants growing in Frasers Mills Upland also had the highest density of fruits per unit stem length among the sites compared. Taken together, these data suggest that South River floodplain provides less favourable habitat than other river floodplains or even some upland sites. The important difference appears to be the lower canopy cover (class 2, mostly open), and hence greater understorey light penetration, along South River compared with the other river valleys (class 3, mostly closed). Most flowers develop fruits, so pollination does not appear to be limiting. These observations support the contention that ideal habitat for horse-gentian is mature, closed-canopy forest with open understorey, and the association of the species with river valleys arises independently from a preference for calcium-rich soil.

This conclusion calls into question earlier suggestions that periodic disturbance is necessary to maintain habitat for Orange-fruit Horse-gentian (Ogle 1980; Laughlin and Uhl 2003). Taylor and Tam (2012), noting the association of horse-gentian with early successional trees in the river valleys and its absence in closed-canopy forest nearby, suggested that the plant may depend on disturbance to create and maintain habitat. However, it now appears more likely that mature forest, such as along West and Rights rivers, provides better habitat and disturbance is important only where it prevents growth of dense thickets of other plants. Then why does horse-gentian not occur in mature, hardwood forest farther upstream in the Pomquet/Black Avon and South River systems? It is possible that the species is rebounding from a historical decline due to land clearing and has yet to recolonize upstream habitat.

Seed dispersal in horse-gentian is probably by endozoochory, possibly dominated by White-tailed Deer. The fruits float, so dispersal by hydrochory cannot be ruled out. However, the presence of large patches of horse-gentian on one bank of South and West rivers, but not on the other, suggests that rivers may be acting as barriers, rather than vectors, to dispersal. Moreover, the upland sites at Frasers Mills and

St. Andrews were atop a steep incline from the floodplain and further separated by a long-extant gravel road. Therefore, the uphill slope was not a barrier to dispersal, nor was the road. The population scattered along upper Rights River was also far uphill from the river. These observations reinforce our hypothesis that horse-gentian is dispersed by means other than, or in addition to, hydrochory.

Additionally, horse-gentian stems with deer damage were recorded throughout the course of the study and along all four rivers, indicating that deer browsing is widespread. Damage from deer browsing was particularly evident along West River, which supports the largest horse-gentian population. We do not speculate on the reason for the apparent different browsing pressure among rivers and there appear to be no deer density data for the area. We have direct photographic evidence of a deer consuming a plant with fruits. We observed many genets of horse-gentian along deer trails.

Endozoochoric dispersal by deer also helps explain: (1) the association of horse-gentian with Common Apple along all three rivers (Figure 2), and (2) why some habitat that appears to be suitable for the species is not colonized. Deer readily feed on fallen apples and therefore spend time beneath apple trees. Horse-gentian seeds excreted in their faeces are likely to accumulate beneath apple trees. Of 30 horse-gentian plants recorded at Frasers Mills Upland, 18 grew near apple trees.

Female White-tailed Deer are strongly territorial (Beier and McCullough 1990), occupying home ranges of 20–140 ha from which they rarely stray (Beier and McCullough 1990; Storm *et al.* 2007; Walter *et al.* 2009). A doe with a territory encompassing a river valley is unlikely to cross into another valley. Horse-gentian dispersal by deer to more distant patches of new habitat would thus depend on occasional dispersal by young deer (Long *et al.* 2005) or migrations between summer and winter habitat (Messier and Barrette 1983). Deer are apparently responsible for dispersal of White Trillium (*Trillium grandiflorum* (Michaux) Salisbury) over distances of several hundred metres to 4 km; many herbs lacking obvious long-term dispersal mechanisms may be occasionally dispersed by deer (Vellend *et al.* 2003).

The browse selection of Snowshoe Hare often overlaps with that of White-tailed Deer (Telfer 1972), so both species may be consuming horse-gentian. Yet the hare's preference for woody shrubs (Turkington *et al.* 2002) and a lack of observed damage from hares (whose incisors clip stems cleanly, compared with rough breakage from deer) throughout our survey suggest it is unimportant compared with deer. Other possible mammalian dispersers (chipmunks, Raccoon, porcupines) were infrequently observed and have even smaller home ranges than White-tailed Deer (Forsyth and Smith 1973; Banfield 1974). We never observed birds feeding on the fruits. Therefore, endozoochory may impose a dispersal limitation (Eriksson and Ehrlén 1992), which impedes colonization of all available habitat. If a local population of horse-gentian is extirpated, as may have happened along lower Black Avon River, it may be many years before a deer travels far enough to bring in new seeds. Collection of seeds from deer faeces would be necessary to confirm this dispersal mechanism. Longevity of the seedbank is unknown.

The upper limit of dispersal by White-tailed Deer, specifically the distance a deer can travel on the maximum gut retention time, may exceed 10 km (Vellend *et al.* 2003). Dispersal limitation may explain the absence of horse-gentian from apparently suitable habitat along Tracadie River, which lies 15 km east of Pomquet/Black Avon River, but not from the floodplain of Brierly Brook, which lies between Rights and West rivers (Figure 1). No horse-gentian has been found along Brierly Brook despite extensive searches by Taylor and Tam (2012) and us. White-tailed Deer are common along the brook, even within Antigonish, so dispersal limitation is unlikely. The high electrical conductance (a measure of dissolved ion concentration) of Brierly Brook compared with other regional streams (B.R.T. unpubl. data) argues against calcium deficiency, and physical habitat in its floodplain is indistinguishable from floodplains along other rivers. The remaining possibility is that floodplain forest along this historically disturbed stream has only recently matured and a colonization event has not yet occurred.

Conclusions

It appears that both habitat limitation (Clark *et al.* 2007) and dispersal limitation (Eriksson and Ehrlén 1992) contribute to the rarity of Orange-fruit Horse-gentian in Antigonish County. Combined habitat and dispersal limitation is likely to apply to any rare plant species restricted to isolated patches of habitat embedded in an inhospitable landscape, such as often created by human disturbance. How readily new plants establish in a habitat patch may depend not only on the size and geographical isolation of that patch, but also on the efficacy of vectors carrying propagules from one patch to another. Both these factors may contribute to maintaining rarity of a species. Our study also highlights the difficulty of identifying best habitat for a species (here, probably mature hardwood forest) when good habitat is so rare that most plants occur in sub-optimal habitat (early successional forest). A GIS-based modelling approach continues to prove useful for directing field searches toward the most promising sites. Further work is needed to confirm whether Orange-fruit Horse-gentian can survive in what appears to be unoccupied habitat, such as along Brierly Brook, and whether White-tailed Deer is a key vector of seed dispersal. The implications for the species given expected future changes in land use, climate, and species abundances in Nova Scotia also remain to be explored.

Author Contributions

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

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Note

Probable predation by an American Black Bear (*Ursus americanus*) on a Gray Wolf (*Canis lupus*) pup in northwestern Wisconsin

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Abstract

On 13 June 2023, we noted probable predation by an American Black Bear (*Ursus americanus*) on a male Gray Wolf (*Canis lupus*) pup in pine barrens of northern Bayfield County, Wisconsin. The wolf pup, which had been captured and radio-collared on 11 May 2023, was detected by mortality signal on 8 June 2023. Predation by black bears has previously been reported on Eastern Wolf (*Canis lycaon*), but our observation represents the first documentation of probable predation on Gray Wolves of which we are aware.

Key words: American Black Bear; *Ursus americanus*; predation; Gray Wolf; *Canis lupus*

Bears are known to be occasional predators of wolves in North America, but only two cases of predation by an American Black Bear (*Ursus americanus*) on wolves (*Canis* spp.) have been reported in the literature (Pimlott *et al.* 1969; Mills *et al.* 2008). In both studies, bears killed Eastern Timber Wolf (*Canis lycaon*). Ballard *et al.* (2003) summarized 26 interactions between black bears and wolves from studies published between 1944 and 1999, but they list only a single killing of an adult female eastern wolf reported by Pimlott *et al.* (1969); most were with Gray Wolf (*Canis lupus*) and did not involve killing. Mills *et al.* (2008) reported an American Black Bear killing an Eastern Timber Wolf pup. Because American Black Bear predation on Gray Wolves has previously not been reported, we provide documentation of such an event, observed in spring 2023.

The Red Cliff Band of Chippewa, Treaty Natural Resource Division, has monitored wolf packs on the Red Cliff Reservation and adjacent areas of the Bayfield Peninsula since 2014 by collaring adults through live trapping and hand capturing pups at den sites (Gable *et al.* 2024). The Battle Axe pack occurs in portions of Moquah Barrens (46.63°N, 91.26°W) in the Chequamegon-Nicolet National Forest, Bayfield County, Wisconsin, USA. The barrens are representative of an area of outwash sand plains savannah dominated by Jack Pine (*Pinus banksiana* Lambert), Red Pine (*Pinus resinosa* Aiton), Northern Pin Oak (*Quercus ellipsoidalis* E.J. Hill), and Trembling Aspen (*Populus tremuloides* Michaux) with an understorey made up of Sweet Fern (*Comptonia peregrine* (L.) J.M. Coulter), Sand Cherry (*Prunus pumila* L.), Little Bluestem (*Schizachyrium scoparium* (Michaux) Nash), Ricegrass (*Oryzopsis asperfolia* Michaux), Pennsylvania Sedge (*Carex pensylvanica* Lamark), and various other shrubs, forbs, and grasses. Along with Gray Wolves, common mammals in this area include Coyote (*Canis latrans*), Red Fox (*Vulpes vulpes*), American Black Bear, Fisher (*Pekania pennanti*), American Badger (*Taxidea taxus*), Bobcat (*Lynx rufous*), White-tailed Deer (*Odocoileus virginianus*), Plain's Pocket Gopher (*Geomys bursarius*), Thirteen-lined Ground Squirrel (*Ictidomys tridecemlineatus*), and various other small mammals.

Wolf pups were captured by hand at den sites using methods similar to those described by Gable *et al.* (2024). Attempts were made to capture pups at about 4–6 weeks of age. Captured pups were fitted with breakaway expandable collars with VHF capacity (M1930 Mammal Collar, Advanced Telemetry Systems, Isanti, Minnesota, USA), and passive integrated transponders were implanted subcutaneously at the base of the neck and the lower right front leg. After weighing, processing, and examining for injuries, pups were released at site of capture.

On 11 May 2023, male Gray Wolf pup W465 (5.1 kg, appeared healthy, and ~5 weeks old) was captured with sibling male pup W355 (5.6 kg) ~285 m south of the pack's den site. These were the only pups seen at the time, although four wolves were seen at the den on 1 May 2023. On 15 May, an adult wolf was observed at the den site by trail camera, and on 25 May both pups were alive. When checked on 8 June, W465's signal indicated possible mortality, but we were unable to search for the carcass until 13 June. We found the remains at 1033 (CDT) in a small open patch in a dense brushy area of Jack Pine and aspen, with an understorey of Hazelnut (*Corylus americana* Walter) and other shrubs, forbs, and graminoids, 870 m south of the pack's main den and 800 m west of the nearest forest road.

The carcass consisted of twisted hide with legs and head; the trunk, including organs, vertebrate, ribs, and pelvis, was missing (Figure 1). The pup appeared to have been dead for a week or more. The hide had been pulled back along the legs, like a pair of pants partly removed to expose muscle. Hide remained only on the lower portions of the feet and on the skull with the skin on the skull displaced, i.e., one eye opening was not over the eye socket. A fracture was visible on part of the base of the skull (Figure 2), above the roof of the mouth, but there were no visible puncture wounds, suggesting that the skull had probably been broken by some form of blunt trauma, such as swatting of a large paw. Except for some minor chewing on the back of the right scapula, there was no evidence of feeding on bones. The radio collar was still in place around the neck, and both passive integrated transponders were functioning, further confirming the identity of W465. There was some evidence of possible bruising on the inside of the hide, but it was difficult to distinguish from post-mortem manipulation of the carcass.

Along with the adult visit at the natal den on 15 May 2023 as detected by the trail camera, adult wolf tracks were found 620 m east of the natal den on 22 May and 910 m north of the den on 25 May. Sibling W355 remained in the den area until 29 June, when he was detected 390 m southwest of the den after which his signal was lost. The regular occurrence of adults near the den and continued use of the den site by the sibling suggests that pups had not been abandoned.

Based on our observations, black bear predation seemed the most probable cause of death for wolf W465. Our observations are consistent with descriptions of typical American Black Bear predation on smaller mammals as described by Acorn and Dorrance (1990), Elbroch (2003), and VerCauteren *et al.* (2005). Elbroch (2003: 725) states that "An inverted carcass, inside out, is definitely a bear kill". Black bears are also known to drag carcasses into dense cover to feed, consistent with our observations.

American Black Bear predation has been previously reported on an adult female Eastern Wolf (Pimlott *et al.* 1969) and pup (Mills *et al.* 2008); thus, similar predation on Gray Wolf pups seems probable. American Black Bears readily hunt and kill White-tailed Deer fawns (Kunkel and Mech 1994; Warbington *et al.* 2017).

The Moquah Barrens lie within Wisconsin Bear Management Zone A, which covers 24 292 km^2 in the northwestern part of the state (Wisconsin DNR Advisory Committee 2019). In 2023, Zone A had an estimated population of 7710 bears or a density of 31.7 bears/100 km^2 (Margenau and Whipple 2024). This part of northwestern Wisconsin has a wolf density >2.5 wolves/100 km^2 (McDonnell *et al.* 2023). As a regular predator on neonate deer, it seems logical that bears would also opportunistically select other similar-sized neonate mammals, especially where bears occur at relatively high densities. Although we acknowledge that scavenging by a bear could have occurred, the fractured skull and careful skinning of the hide suggest direct predation by a bear.

Mortality factors for wolf pups are poorly known; intraspecific mortality from adjacent packs, disease, and starvation are the most common (Boyd *et al.* 2023). Predation by other carnivores, such as black bears, may also occur, but the frequency of this type of mortality for wolf pups is likely hard to detect and is currently unknown.

Author Contributions

Writing – Original Draft: A.P.W.; Writing – Review & Editing: R.N.J., A.E., E.R.O., and A.P.W.; Conceptualization: A.P.W.; Investigation: R.N.J., A.P.W., and E.R.O.; Methodology: R.N.J. and A.E.; Funding Acquisition: R.N.J. and A.E.

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FIGURE 1. Remains of Gray Wolf (*Canis lupus*) pup W465 on 13 June 2023, in the Moquah Barrens of northwestern Wisconsin. Photo: Ron Nordin.

the capture of the wolf pups and the search for wolf 465. We followed guidelines of the American Society of American Mammalogists to minimize any impact of our handling on wolf pup welfare (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

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FIGURE 2. Jaw of Gray Wolf (*Canis lupus*) pup W465 found dead on the Moquah Barrens of northwestern Wisconsin on 13 June 2023. The roof of the mouth shows a fracture resulting from trauma that apparently killed the wolf. Photo: Ron Nordin.

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Stream restoration: a key to the survival and recovery of the Endangered Western Brook Lamprey (*Lampetra richardsoni*), Morrison Creek population

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Abstract

Aquatic ecosystems and species are increasingly threatened by anthropogenic activities. Stream restoration has therefore become a necessary conservation strategy to improve habitat quality and quantity, which are key components of productive, healthy, resilient aquatic ecosystems. The Morrison Creek watershed on Vancouver Island, British Columbia has been impacted by anthropogenic activities resulting in the degradation of aquatic habitat. For an Endangered, range-restricted species like Western Brook Lamprey (*Lampetra richardsoni*), Morrison Creek population, which only occurs in this one watershed, any habitat-related impacts have the potential to cause population level declines, thereby increasing the risk of extinction. Stream and riparian restoration were therefore undertaken to ameliorate the species' Critical Habitat, which no longer supported spawning and early rearing. Effectiveness of restoration was determined through the use of restored areas for spawning, increased hydraulic complexity, and reduced sedimentation. Lamprey (adults and larvae) and salmonids (*Oncorhynchus* spp.) had not been observed in this habitat since 2005; however, following habitat restoration in 2021, 10 different lamprey nests were observed being tended in the restored habitat in 2022. Salmonids were also observed using the newly created habitat for spawning in fall 2021 and fry and smolts used pools and riffles for rearing the following spring and summer. Our work demonstrates specific types of habitat restoration that are effective for lamprey conservation and validates that complex restoration activity can occur when there is effective collaboration.

Key words: Lamprey; conservation; restoration; Endangered species; Western Brook Lamprey; Morrison Creek Lamprey

Introduction

Stream restoration has become a necessary conservation strategy to help mitigate the significant declines in salmonids and other aquatic species attributed to declining habitat quality and quantity (Gessner *et al.* 2004; Opperman and Merenlender 2004; Rumps *et al.* 2007; O'Neal *et al.* 2016; Anderson *et al.* 2019). Although the direct or proximate causes of decline vary by species and geographic areas, it is often a result of the cumulative impacts of multiple stressors (Moyle and Leidy 1992). Species that have specialized life histories and/or are endemic with small distributions also tend to be among those most at risk of extinction (Moyle and Leidy 1992; Purvis *et al.* 2000).

The increasing knowledge of direct and indirect impacts to aquatic species has resulted in a greater understanding of the need to protect aquatic biodiversity and has resulted in large amounts of funding spent to improve freshwater habitat (Opperman and Merenlender 2004; Bennett *et al.* 2016; O'Neal *et al.* 2016; Roni *et al.* 2018; Anderson *et al.* 2019). While there is information available on restoration techniques to improve productivity (Roni *et al.* 2018), there is often a lack of monitoring to evaluate the effectiveness of restoration projects and the benefit to aquatic species is often uncertain (Bennett *et al.* 2016; Roni *et al.* 2018; Anderson *et al.* 2019). Typically, examples of responses to restoration actions are limited to reach-scale studies because of associated challenges to evaluate effectiveness at the watershed scale (Liermann and Roni 2008; Anderson *et al.* 2019). However, the need for monitoring is recognized and well documented (O'Neal *et al.* 2016) and reach-scale results can inform population-level effects of restoration, especially for species with small distributions.

The opportunity to monitor and evaluate the effectiveness of restoration activities existed within Arden Creek (49.6832°N, 125.0168°W) on Vancouver Island, British Columbia. Arden Creek (3 km long) is part of the Morrison Creek watershed, which also includes Morrison Creek (24 km) and spring-fed headwaters (543 ha). The watershed in its entirety supports a diverse range of aquatic species from Pacific Lamprey (*Entosphenus tridentatus*), Coho (*Oncorhynchus kisutch*), Pink (*Oncorhynchus gorbuscha*) and Chum (*Oncorhynchus keta*) Salmon, Threespine Stickleback (*Gasterosteus aculeatus*), and several trout species (*Oncorhynchus* spp.; Wade *et al.* 2015). It also contains the entire population of a unique and at-risk freshwater lamprey species, the Western Brook Lamprey (*Lampetra richardsoni*), Morrison Creek population also known as the Morrison Creek Lamprey.

In 2003, the Morrison Creek Lamprey was listed under Canada's *Species at Risk Act* (SARA Public Registry 2023) as Endangered because of its small distribution and ongoing declines in habitat quality in Arden Creek and the larger Morrison Creek watershed. This endemic freshwater population is unique in its reproductive and life history traits. Adults create nests or depressions in sand or gravel substrates to spawn in the spring (~April–June). Eggs hatch within 12–30 days, and larvae remain buried in the streambed, filter-feeding. Lamprey larvae generally rear for up to seven years before undergoing metamorphosis into adults (Dawson *et al.* 2015). Morrison Creek Lamprey undergoes metamorphosis in late summer or early fall (COSEWIC 2010). This population is unique in that after metamorphosis, adults emerge as either parasitic or non-parasitic forms, each with distinct ecological roles and physical traits. Non-parasitic adults, smaller and darker than their parasitic counterparts, cease feeding after metamorphosis, relying on energy reserves from their larval stage. They mature quickly after metamorphosis, spawn and subsequently die in the spring following their transformation. In contrast, parasitic adults delay spawning for a year, develop prominent teeth and a silvery colouration, and actively feed on salmonids during this period (COSEWIC 2010). This enables parasitic adults to grow larger and accumulate energy reserves which may potentially increase reproductive success the following spring. Like their non-parasitic form, they die after spawning, completing their life cycle. The presence of both parasitic and non-parasitic forms within a single population is highly unusual, and these forms are indistinguishable until after metamorphosis (COSEWIC 2010).

For most aquatic species, maintaining habitat quality is important for survival, but this is particularly true for range-restricted Endangered species whose ecology is poorly understood (Beamish 2013). Canada's *Species at Risk Act* (SARA) recognizes the importance of habitat that is necessary for the survival and recovery of species and provides legal protection for identified Critical Habitat. For the Morrison Creek Lamprey population, Critical Habitat has been identified and includes Arden Creek, underscoring the importance of safeguarding this unique habitat to ensure the population's persistence.

The habitat requirements for this population include sand and gravel substrate, pools, riffles, and hydraulic complexity for nest building, spawning, egg incubation, and rearing, in addition to adequate food supply (COSEWIC 2010; Wade and Grant 2022). Adults excavate a small depression (10–12 cm wide, 5 cm deep) used as a nest for spawning and egg incubation from April to June (COSEWIC 2010; Wade and Grant 2022). Spawning habitat includes areas with small riffles (i.e., turbulent water flowing over shallow substrates across short distances with either complete or partial channel coverage, which enhances dissolved oxygen levels in the system) in proximity and a mix of sand and gravel for nest building (1–100 mm diameter; Stone 2006; Gunckel *et al.* 2009) with low flow (0–0.7 m/s; Pletcher 1963; Stone 2006; Gunckel *et al.* 2009).

The habitat that supports larval lampreys is generally similar across species (Dawson *et al.* 2015). Larval-rearing habitats are typically characterized by reaches with hydraulic complexity, including cool, oxygenated, but slower flowing water, which facilitates the accumulation of sediments suitable for burrowing (Farlinger and Beamish 1984; Stone and Barndt 2005; Smith *et al.* 2011; Ferreira *et al.* 2013; Gonzalez *et al.* 2017). Larvae also tend to prefer stream margins (Farlinger and Beamish 1984; Stone and Barndt 2005). Although dense canopy has been shown to have a negative effect on larval habitat suitability (Stone and Barndt 2005), riparian vegetation can help maintain larval habitat by stabilizing stream banks and regulating water temperatures through the shade it provides (Macey and Potter 1978; Arakawa and Yanai 2021). Furthermore, the leaves and detritus from riparian vegetation contribute organic material that serves as a substrate and nutrient source for periphyton and microbes, which form a vital part of the food web supporting larval lamprey development (Evans and Weber 2019).

Arden Creek has experienced substantial degradation over time because of growing urbanization pressures. Key impacts include the removal of riparian vegetation, which has destabilized stream banks, a reduction in channel complexity that has diminished habitat diversity, and increased sediment loadings that have smothered aquatic substrates. Together, these changes have severely disrupted the creek's ecological integrity, threatening its ability to support healthy aquatic ecosystems (COSEWIC 2010). Although several small-scale bank stabilization and fish passage projects have been undertaken, the cumulative impacts of land use changes became increasingly evident after 2005, when lamprey and salmonids stopped spawning in Arden Creek. In 2019, these impacts were further exacerbated by the development of a disc golf course, which increased sediment inputs. This sedimentation led to a low-gradient stream profile with negligible water flow, creating stagnant, muddy areas with poor water quality and likely reduced dissolved oxygen levels, further degrading the habitat's suitability for aquatic species. A multi-stakeholder initiative was therefore developed to restore the legally protected Critical Habitat for Morrison Creek Lamprey.

While management strategies have been developed to identify conservation needs of lamprey, and lamprey have benefited from broader habitat restoration projects (Clemens *et al.* 2021), this is one of the few projects where restoration activity has specifically targetted lamprey, while indirectly benefiting co-occurring salmonids and other aquatic species. Herein, we give details on the restoration methods used and then present monitoring results to evaluate the effectiveness of our efforts on Morrison Creek Lamprey. These data provide valuable insights that could help prioritize other lamprey-specific benefits in future restoration projects, ensuring that the unique needs of lamprey are more effectively addressed in planning and implementation.

Methods

Restoration planning and activities

In-stream restoration plans were designed to match the physical and hydraulic characteristics of the stream with the needs of fish populations and ecological health, with a particular focus on Morrison Creek Lamprey and salmonids. Based on the best available knowledge, this included creating habitat suitable for lamprey spawning as well as suitable rearing habitat for ammocoetes (larval lamprey).

The treatment reach of Arden Creek circumnavigated two large school fields. These reaches were excavated in 1964 to reduce surface flow elevations of the fields resulting in straight, low gradient (<1%) channels, with highly incised banks. The channel was over-widened that resulted in slow flow velocities and low hydraulic complexity. The combination of sedimentation, reduced flow variability, and diminished hydraulic complexity rendered Arden Creek unsuitable for any life stage of lamprey or salmonid. Thus, it was necessary to recreate hydraulic conditions throughout the habitat that would support: 1) increased localized flow and overall hydraulic complexity, 2) decreased sedimentation, 3) bank stabilization, 4) the creation of refuges, and 5) increased spawning and early rearing habitat. In upstream and downstream areas, in-stream restoration involved the installation of features such as wing deflectors and woody debris structures to constrict and increase local flow and promote scouring. Small rocks, pea gravel, and sand were added in key areas to provide spawning habitat for lamprey and salmonids.

In-field surveying of Arden Creek occurred in 2021 based on standard restoration methods as described in Newbury and Gaboury (1993) and Slaney and Zaldokas (1997). Measurements, including stream profile elevations, water depth, and high-water conditions and were recorded approximately every 20–30 m, depending on the terrain. For each site, substrate type was recorded as silt (0–0.06 mm), sand (0.06–2.0 mm), gravel (2–64 mm), cobble (65–100 mm), or small rock (101–200 mm) based on categories modified from Wolman (1954). Terrestrial areas which could benefit from an increase in riparian diversity and density were also identified. This information was used in conjunction with Geographic Information Systems-based technologies to create a stream profile including a cross-section to inform engineering plans. Specific restoration sites were identified over an ~800 m length of Arden Creek and incorporated both in-stream and riparian restoration.

The engineering plans included the installation of two rock riffles, 74 boulder clusters, 77 pieces of large woody debris structures, and 28 wing deflectors (i.e., triangular projections placed in shallow over-widened stream channels to promote localized scour and hydraulic complexity). The structures were constructed on a triangular framework or base of boulders sequentially top-dressed with cobbles, then with a select bank pit run mixed with 10% pea gravel. The placement of cobbles followed by the gravel mix was intended to help seal the structures and promote local scour. Deflectors were oriented to promote a meandering channel path and constructed with the apex of the triangle to pinch the creek to an approximate width of 0.75–1.5 m from an existing bankfull width of 4.1 m. During construction, large accumulations of small woody debris, largely resulting from the Red Alder (*Alnus rubra* Bongard)-dominated riparian vegetation community, were removed from the channel by volunteers. This improved hydraulic conveyance of the treatment reach. Because very little substrate suitable for lamprey spawning and early rearing was found, the installation of pea gravel in and around these features was key to increasing habitat availability.

In all, 156 tonnes of 300–600 mm boulder, 104 tonnes of "overs" (mix of gravel and cobble substrate ranging from 100 to 260 mm diameter), 143 tonnes of select bank pit run gravel (2–64 mm), and 14 tonnes of fine gravel and pea gravel (1–15 mm diameter) were used in restoration activities. Pit run is unsorted, naturally occurring gravel deposit and was selected from exposed banks that have reduced fines as a result of being washed by rain. Pit run used for this project was relatively low in fines with a higher component of coarse sand.

Riparian restoration included three main activities: 1) planting of native trees and shrubs, 2) relocating portions of the trail system, and 3) delineating sensitive riparian habitat with fencing. To enhance the Critical Habitat of lamprey within restoration sites identified along the 800 m of Arden Creek, more than 1900 native plants (>25 different species) were planted with the assistance of students and volunteers. Both coniferous and deciduous plants were planted, including for example, Grand Fir (*Abies grandis* (Douglas ex D. Don) Lindley), Sitka Spruce (*Picea sitchensis* (Bongard) Carrière), Salmonberry (*Rubus spectabilis* Pursh), Thimbleberry (*Rubus parviflorus* Nuttall non. cons.), Western Sword Fern (*Polystichum munitum* (Kaulfuss) C. Presl), and Devil's Club (*Oplopanax horridus* (Smith) Miquel). This work occurred in the autumn of 2021 when rain was imminent to maximize the potential for survival of planted stock.

A 125 m section of trail running alongside Arden Creek was decommissioned and relocated to reduce its environmental impact. The decommissioned trail, identified as a significant source of sediment during rainy months, had caused damage to riparian vegetation and sediment release due to uncontrolled public access to the creek. The old trail was replaced with woody debris and native plants to stabilize the area and restore riparian habitat. A new trail, located ~3–5 m away from the creek to protect sensitive habitats, was constructed with compacted pit run to provide a durable and stable surface for recreational use. Furthermore, invasive plants such as Scotch Broom (*Cytisus scoparius* (L.) Link), English Holly (*Ilex aquifolium* L.), Himalayan Blackberry (*Rubus bifrons* Vest) were removed, and dead trees available on-site were used to flank the trail to provide a visual cue to discourage the creation of additional paths within the riparian area.

To encourage people to stay away from the creek and on trails, split rail cedar fencing was installed in the elementary school yard adjacent to Arden Creek as well as in the heavily used disc golf area. Native plants were planted between the creek and the fence. In total, 4300 m^2 of riparian habitat along Arden Creek was restored, 470 m of split-rail cedar exclusion fencing was installed, and more than 650 m of pedestrian trails were created.

Aquatic restoration took place between mid-July and mid-August 2021; riparian planting and fence building occurred in October and November 2021.

Pre- and post-restoration lamprey surveys

Pre-restoration surveys for adult Morrison Creek Lamprey have been conducted regularly by the Morrison Creek Streamkeepers and other stakeholders to monitor population presence and habitat use. In early July 2021, prior to in-stream construction, targetted surveys were carried out using a combination of visual observations, standardized kick sampling, and sampling and filtering of sediment with aquatic nets. Visual surveys focussed on potential presence of adults, while kick sampling and net collection were used to locate larval lamprey within fine sediment deposits.

Given that lamprey were not spawning in Arden Creek prior to restoration or used this creek for rearing, we wanted to determine if restoration activities resulted in a successful response for the target species. Post-restoration surveys of Arden Creek occurred between the end of May and beginning of July 2022 to identify active lamprey nesting during the known spawning window for Morrison Creek Lamprey (Wade and Grant 2022); this spawning window is similar to that reported for Western Brook Lamprey in other locations and depends on temperature (Stone 2006; Gunckel *et al.* 2009). Surveys were conducted by walking along the creek from the first restored feature to the last, downstream to upstream. Surveys took place between early morning and mid-afternoon. If lamprey were actively tending nests or engaging in spawning activity, the geolocation and number of lamprey were recorded.

Environmental data and nest dimensions were taken only if lamprey moved away from the nesting area to minimize any interruption of nesting activities. Temperature, pH, electrical conductivity (EC; µS/cm), and total dissolved solids (TDS; ppm) were measured using a handheld Hanna Combo meter (H1989129, Hanna Instruments, Woonsocket, Rhode Island, USA); dissolved oxygen (DO) was measured using an OxyGuard Handy Gamma meter (OxyGuard International, Farum, Denmark). These handheld instruments were used immediately downstream of active nests. Nest dimensions and depth were measured using a ruler. In addition, two HOBO TidbiT v2 (Onset Computer Corporation, Bourne, Massachusetts, USA) water temperature loggers were placed in separate locations in the creek to collect hourly temperature data during the spawning season (~April–June).

Results

In-stream restoration features were successful in increasing localized scour, improving hydraulic complexity, and improving refuge for fish (Figure 1) based on observations of localized increases in water movement and fish behaviour. Areas that previously had been stagnant settling areas for sediment deposition now had flowing water, which helped maintain alluvial substrate complexity with a well-graded mix of gravel and small stones. The constructed deflectors and large woody debris structures effectively increased local flow velocities (not quantitatively measured) and created scour points that mobilized deep (15–70 cm deep) accumulations of fine sediments in the over-widened channel. In the spring and throughout the summer, salmon fry were observed using riffles and taking refuge downstream of large woody debris features.

Pre-restoration surveys did not detect adult lamprey use since 2005 (DFO [Fisheries and Oceans Canada] unpubl. data), and no adult or larval lamprey were detected at any of the identified restoration sites during pre-restoration targetted surveys. Post-restoration, between 23 May and 5 July 2022, surveys were conducted 18 times along the restored area of Arden Creek (Table 1). A total of 10 unique lamprey nests were seen being tended by Morrison Creek Lamprey, and many nests were used more than once. No nesting or spawning activity was observed on the first (23 May) or last three days (27 and 28 June, and 5 July) of the observation period. The maximum number of active nests in any survey was four and the number of lamprey for each survey ranged from 0 to 17. Nest 2 was the most consistently active nest over the survey period with 23 lamprey seen actively tending the nest or spawning from 24 May to 22 June (Table 1).

Length and width of eight of the 10 nests were measured to calculate nest area. Nest 2, measured five times between 24 May and 22 June, increased in area from 504 cm^2 to 4125 cm^2, with little change in nest depth (8–9 cm). Overall, the depth of water in which active nests were observed varied from 6 to 26 cm and the nest area varied from 100 to 4125 cm^2. Lamprey were observed singly or in multiples using their oral disc to move stones from the nesting area and fanning the substrate with their bodies. On several occasions, females were seen anchored to rocks using their oral disc while a male attached to the head of the female and coiled around the female as part of their spawning behaviour. It was possible to distinguish the sexes based on the secondary sexual characteristics of lamprey as summarized in Kott *et al.* (1988). These mating occurrences would be interrupted by bouts of nest construction before recommencing. This behaviour is typical of that described for Western Brook Lamprey as well as other lamprey species (Stone 2006; Wade and Grant 2022).

Water quality ranges measured immediately downstream of the 10 active lamprey nests were: pH 6.40–7.95 (*n* = 13), EC 197–326 µS/cm (*n* = 13), TDS 98–151 ppm (*n* = 11), DO 9.00–9.96 mg/L (*n* = 7), and water temperature 11.1–14.7°C. Water temperature was also recorded on the two data loggers from 29 May to 6 July. The average temperature over the

FIGURE 1. Arden Creek stream restoration for the Western Brook Lamprey (*Lampetra richardsoni*), Morrison Creek population at the most downstream riffle near the confluence with Morrison Creek. a. pre-restoration, b. immediately after riffle installation, and c. one year post-restoration. Photos: Joy Wade and Paul Grant.

TABLE 1. Surveys of Western Brook Lamprey (*Lampetra richardsoni*), Morrison Creek population nesting in restored areas of Arden Creek, 2022. 1–10 refers to nest number.

Survey date	Number of lamprey in each unique nest										Total number of lamprey
	1	2	3	4	5	6	7	8	9	10	
23 May											0
24 May	2	3									5
27 May		1									1
28 May	3		1								4
30 May		2		1							3
1 June				3	1						4
3 June											0
8 June			5			2	9		1		17
8 June		1		1			3				5
9 June		2									2
10 June							1				1
11 June		3									3
16 June		4						4			8
20 June		4								6	10
22 June		3									3
27 June											0
28 June											0
5 July											0
Total	5	23	6	5	1	2	13	4	1	6	

entire time period was 13.4°C (range 9.8–17.5°C; Figure 2). Over the period in which lamprey were seen building nests and spawning and loggers were in place (29 May–2 June), the average temperature was 12.5°C (range 9.8–15.1°C). No lamprey were seen on nests after 22 June (Figure 2). The average water temperature for the remainder of the logger deployment (23 June to 6 July) was 14.8°C (range 11.1–17.7°C).

Discussion

Freshwater ecosystems are increasingly threatened by anthropogenic activities and are considered the most imperilled on Earth (Strayer and Dudgeon 2010; Lapointe *et al.* 2014). Species that depend on these systems are also experiencing some of the highest extinction rates across ecosystem types and are in need of immediate protection (Opperman and Merenlender 2004; Lapointe *et al.* 2014; Barnas *et al.* 2015). Species with specialized life histories, or those that are endemic with small distributions, tend to be at the greatest extinction risk (Moyle and Leidy 1992). While causes of decline vary and are often a result of cumulative effects, decline in habitat quality is widely recognized as one of the key proximate causes of decline among aquatic species (Moyle and Leidy 1992; Lapointe *et al.* 2014; Barnas *et al.* 2015).

Stream restoration has therefore become a necessary conservation strategy to help mitigate the significant declines in aquatic species (Opperman and Merenlender 2004; O'Neal *et al.* 2016; Anderson *et al.* 2019). The challenges are how to prioritize areas for restoration in the context of: 1) limited capacity and funding; 2) sufficient understanding of the species' biology, ecology, and habitat requirements across life stages; and 3) evaluating activities to ensure conservation goals are being met.

Restoration projects often prioritize species that have economic, social, or more obvious and quantifiable ecological value, such as salmonids (Bash and Ryan 2002; Barnas *et al.* 2015; Anderson *et al.* 2019) and tend to overlook other aquatic species such as lamprey, where public perception can pose a barrier to their conservation despite their significant ecological importance (Clemens *et al.* 2021; Clemens and Wang 2021). While management strategies have been developed specifically for lamprey to improve access to spawning and larval rearing (Clemens *et al.* 2021) and lamprey have benefited from other habitat restoration projects (Clemens *et al.* 2021), ours is one of the few projects where restoration activity has specifically targetted lamprey.

Somewhat uniquely for lamprey, the prioritization of Arden Creek for restoration was driven by public interest in conserving this population. Even with

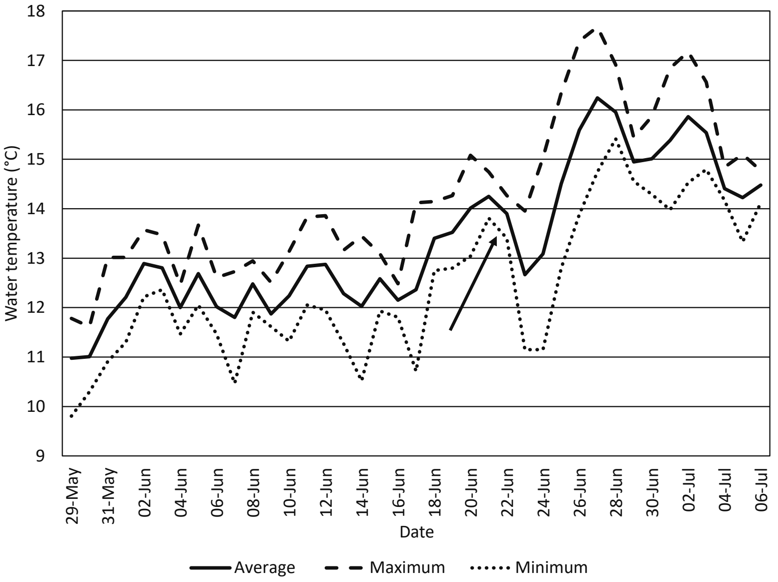

FIGURE 2. Daily water temperatures (average, maximum, and minimum values) from two water temperature dataloggers deployed in Arden Creek (May–July 2022). Arrow indicates when the last Western Brook Lamprey (*Lampetra richardsoni*), Morrison Creek population nesting activity was observed.

the legal requirements of habitat protection under SARA, our restoration work was only accomplished as a result of a collaborative effort among stewardship groups, communities, individuals, and government to help ensure the continued survival of an evolutionarily significant population at risk of extinction. This highlights the value and importance of improved coordination and collaboration among the aforementioned diverse entities to achieve successful conservation outcomes for aquatic species (Maitland *et al.* 2015; Clemens *et al.* 2021).

Restoration of aquatic habitats also requires sufficient understanding of the target species' biology, ecology, and habitat requirements across life stages, ecological processes, and the engineering required to enable these specific changes. In this case, Arden Creek and the Morrison Creek watershed had been affected by a number of anthropogenic activities over time. Prior to the restoration work, in-stream habitat in this area of Arden Creek was of little value to either Morrison Creek Lamprey or salmonids. This was primarily because of extensive fine sediment deposits throughout the targetted reach, caused by erosion that had degraded the stream. This had transformed it into an over-widened, low-gradient channel, characterized by areas of minimal flow and stagnant, low-oxygen conditions. Our measure of restoration success for Morrison Creek Lamprey, in the short-term, was the confirmed use of habitat for nest building and spawning. The in-stream restoration activity was successful in providing the necessary habitat for Morrison Creek Lamprey to build nests and spawn in an area of Arden Creek that had been devoid of such activity since 2005. Moreover, nest building and spawning was not just observed in the restored area in general, but specifically in the features and gravel that were added. Restoration also proved beneficial to salmonids. In the fall of 2021, both Coho and Pink Salmon were seen in the creek, using the new beds of sand and gravel for their spawning activities (DFO unpubl. data). The following spring, salmonid fry were found taking refuge behind large woody debris and holding in pools created by feature-driven pinch points diverse in substrate.

Restored areas now contain patches of alluvial, size-graded substrates interspersed within pools as well as shallow habitat and increased hydraulic complexity—particularly at riffles; all these features are known to be used by lamprey for nesting (Gunckel *et al.* 2009). As the restored riparian areas become more established, they too will contribute to spawning habitat by providing shade, woody debris, and bank stability, thus decreasing sedimentation. Controlled public access will also mitigate sediment sources and facilitate the establishment of functional riparian vegetation communities.

The restoration of this section of Arden Creek has successfully created habitat conditions that are now suitable for adult Morrison Creek Lamprey, marking a significant improvement in habitat quality. However, determining the suitability of the restored habitat for larval rearing will require long-term monitoring to fully evaluate its effectiveness. The restoration approach was carefully designed to address key habitat requirements, incorporating deeper sediments and fine gravel to provide potential larval rearing areas. Enhanced water flows were also established to improve oxygenation, a critical factor for supporting larval development (Gonzalez *et al.* 2017). While the restoration has transformed this once impaired section of the creek into a functional habitat capable of supporting both spawning adults and potentially rearing larvae, ongoing monitoring will be essential to confirm larval use and ensure the long-term success of the restored habitat.

Although critical knowledge gaps remain regarding the conservation of Morrison Creek Lamprey, there is sufficient understanding of their habitat requirements to guide effective restoration efforts. Ensuring that engineering outcomes create habitat characteristics that improve conditions such as flow, oxygen levels, and substrate type is essential not only for the survival and recovery of this species but also for supporting a diverse range of aquatic life. Substrate preferences for both adult and larval lamprey have been documented, highlighting the importance of suitable fine sediments for larvae and coarser substrates for spawning adults. Incorporating these habitat requirements into restoration designs benefits not just lamprey, but also enhances ecological health, processes, and the integrity of food webs for the entire aquatic ecosystem (Wade and Grant 2022).

Many authors have highlighted the importance, and often the lack, of monitoring to evaluate the effectiveness of restoration projects (Bash and Ryan 2002; Liermann and Roni 2008; O'Neal *et al.* 2016; Roni *et al.* 2018). Pre- and post-restoration surveys are essential to determine if conservation goals have been met. The temporal and spatial scales for monitoring should also be considered when designing effective monitoring programs. Monitoring at the watershed scale is more effective at detecting changes in abundance at the population level (Liermann and Roni 2008). However, there are often financial and capacity constraints that make this larger scale monitoring unfeasible for most projects (Liermann and Roni 2008; Anderson *et al.* 2019). Nevertheless, monitoring at the reach-scale can evaluate effectiveness of restoration activities, especially when the focus is on the habitat use of target and co-occurring species. Such monitoring plans should be conducted for multiple years to evaluate the long-term effectiveness of restoration on both species as well as habitat and ecosystem processes.

Lamprey are relatively cryptic non-charismatic species (Clemens and Wang 2021), which bring many unique challenges to their management and restoration (Clemens *et al.* 2021). Our study demonstrates the benefit of management actions for the conservation of an at-risk species and what can be accomplished when effective collaboration among stakeholders occurs. It also contributes to furthering our understanding of habitat requirements of lamprey as well as the specific types of restoration activities conducive to restoring severely degraded and previously non-functional habitat, which should be informative and applicable for other lamprey species.

Author Contributions

Writing – Original Draft: J.W., W.F., and P.G.; Writing – Review & Editing: J.W., W.F., and P.G.; Conceptualization: J.W. and P.G.; Investigation: J.W., W.F., and P.G.

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Note

Reaching new heights: novel use of alpine talus by a Red Squirrel (*Tamiasciurus hudsonicus*)

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Abstract

Red Squirrel (*Tamiasciurus hudsonicus*) is common in the boreal forest, where it is chiefly arboreal and intricately tied to conifer trees for food and shelter. As such, these squirrels are found in close association with contiguous conifer forest. However, we observed a Red Squirrel in a talus patch in an alpine valley in southwestern Yukon, Canada. The valley was devoid of trees, with the nearest conifer ~3.6 km away and contiguous conifer forest ~4.8 km from our observation. How or why the Red Squirrel came to be in the alpine talus is unknown; however, it likely represented an unusual natal dispersal event. Our observation provides a novel record of this arboreal species in a talus patch located in an alpine valley that lacked trees.

Key words: Arboreal mammals; Kusawa Territorial Park; natal dispersal; talus

Red Squirrel (*Tamiasciurus hudsonicus*) is an arboreal mammal that is widely distributed across North America, where it is closely associated with boreal forests that consist of abundant conifer trees (Obbard 1987; Steele 1998; Steele and Koprowski 2001; Yahner 2003; Nagorsen 2005). Red Squirrels are highly dependent on conifer trees, particularly spruces (*Picea* spp.) and pines (*Pinus* spp.), for shelter and food (i.e., seed cones; Boonstra *et al.* 2001). As such, they are often common in conifer forests, and records of this species outside contiguous conifer forest are rare. Here, we report the occurrence of a Red Squirrel above the treeline in an alpine valley, far from the nearest conifers.

On 24 August 2023, while conducting surveys of Collared Pika (*Ochotona collaris*) in an alpine valley in Kusawa Territorial Park in southwestern Yukon, Canada (60.55513°N, 136.24769°W), we observed a Red Squirrel in talus (i.e., a boulder field) above the treeline. The animal was readily identified as a Red Squirrel based on its size, bicoloured coat, white eye ring, and long, bushy tail (Obbard 1987; Steele 1998; Steele and Koprowski 2001; Yahner 2003; Nagorsen 2005; Figure 1). Similar species, such as Collared Pika, Least Chipmunk (*Neotamias minimus*), Arctic Ground Squirrel (*Urocitellus parryii*), and Ermine (*Mustela erminea*), are somewhat common in our survey area, but these talus-dwelling species are readily distinguished from Red Squirrels based on diagnostic physical characteristics such as coat colouration and body size and shape (Obbard 1987; Steele 1998; Yahner 2003; Nagorsen 2005). The Red Squirrel did not vocalize during our observation (which is also a

Figure 1. A Red Squirrel (*Tamiasciurus hudsonicus*) observed in a talus patch in an alpine valley in southwestern Yukon, Canada, on 24 August 2023. Photo: T.S. Jung.

diagnostic trait; Obbard 1987; Steele 1998; Steele and Koprowski 2001; Yahner 2003; Nagorsen 2005), and it was seemingly leery of our presence, periodically disappearing into the talus, under the rocks, and reappearing several seconds later 10–15 m away from us. Altogether, we spent about 10 min observing and photographing the Red Squirrel to confirm its identification (Figure 1).

Our observation occurred in a broad alpine valley that was devoid of trees or tall (>2.0 m) shrubs (Figure 2). Ground cover consisted of low (<0.5 m tall) shrubs, dry heath, wet hummocks, and talus (Figure 2). The valley was ~4.7 km long and the squirrel was observed roughly in the middle of the valley. We observed the Red Squirrel ~3.6 km from the nearest conifer and ~4.8 km from contiguous spruce forest (Figure 3).

Our observation occurred in August, when juvenile Red Squirrels were dispersing from their natal range and establishing their own territories (Larsen and Boutin 1994; Sun 1997). During our brief observation, there was no indication that the squirrel had permanently settled at this site (i.e., no food caching, midden material, or territorial vocalizations). Dispersing Red Squirrels are known to be transient through suboptimal habitat, such as forest gaps (Bakker and Van Vuren 2004), and we may have encountered it in suboptimal habitat while it was in transit between forest patches. Natal dispersal by Red Squirrels varies with individuals and personalities (Cooper *et al.* 2017), and the fitness benefits of dispersal also vary among individuals (Martinig *et al.* 2020).

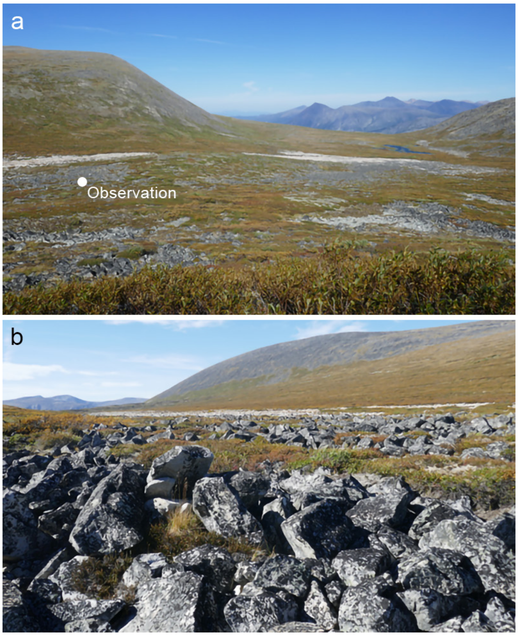

FIGURE 2. Landscape views of the location of an observation of a Red Squirrel (*Tamiasciurus hudsonicus*) in an alpine valley in southwestern Yukon, Canada. a. Looking east and showing the location of the observation. b. Looking west from the observation point. There are no trees in this broad valley. Photos: T.S. Jung.

Figure 3. Site of an observation of a Red Squirrel (*Tamiasciurus hudsonicus*) in an alpine valley in southwestern Yukon, Canada, showing the approximate location of the nearest, sparse White Spruce (*Picea glauca* (Moench) Voss) trees and the limit of contiguous White Spruce forest. Scale bar is approximate. Source: Kusawa Territorial Park, Yukon, 60.55513°N, 136.24769°W. Google Earth Pro 7.3.1.4507. Imagery date: 31 December 2020. Data provider: Maxiar Technologies 2018. Accessed: 11 October 2023.

Although Red Squirrels may cross suboptimal forest clearings (Bakker and Van Vuren 2004), our observation is noteworthy with respect to the distance between contiguous conifer forest and the alpine talus patch (4.8 km). In a study of gap crossing in Alaska, a long-distance crossing was classified as >100 m, and crossings >400 m were rare (Bakker and Van Vuren 2004). In Yukon, the longest dispersal distance recorded for 176 Red Squirrels was 566 m (average = 102 m; Cooper *et al.* 2017). These distances are also consistent with the perceptual distances (i.e., the maximum distance an animal can perceive the presence of habitat patches; Zollner 2000) of other arboreal squirrels, which include 300 m for Eastern Gray Squirrel (*Sciurus carolinensis*) and 400 m for Fox Squirrel (*Sciurus niger*; Zollner 2000). As such, the observation of a Red Squirrel nearly 5 km from a patch of forest is exceptional.

Collectively, we have observed and heard of reports from others of Red Squirrels in alpine tundra habitats, where sparse spruce trees occur above the continuous treeline. However, to the best of our knowledge, this is the first record of a Red Squirrel in alpine tundra far from any conifers. This is also the first record of a Red Squirrel in an alpine talus field, which it apparently used as shelter in lieu of conifers, similar to small, alpine mammals such as Collared Pika and Least Chipmunk. Our observation is of interest because it may indicate that Red Squirrels will explore or traverse novel habitats without conifer cover, and while doing so use available habitat features, such as talus, for shelter. However, a small percentage of dispersing Red Squirrels survive (Larsen and Boutin 1994) and the fate of the individual we observed is uncertain without nearby conifers for food and shelter.

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Snow-surface activity of California Snow Scorpionfly, *Boreus californicus* (Mecoptera: Boreidae), in western Montana, USA

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Abstract

The flightless California Snow Scorpionfly (*Boreus californicus* Packard) has rarely been studied, and knowledge of its distribution and activity on snow remains fragmentary. I found it on snow surfaces in western Montana, USA, from valley grasslands to subalpine conifer forests and above the tree line. At lower elevations (991–1500 m), *B. californicus* was present on snow from early November to early March, at higher elevations (1800–2850 m), from early October to early January as well as late June. The species has now been documented in western Montana over an elevation gradient of nearly 2000 m and is probably active somewhere on snow in most months except in mid- and late summer. When the insect was present on snow, surface temperatures ranged from −5.0°C to 5.5°C. Pairs *in copula* ($n = 26$) were found when snow surface temperature was −0.5°C to 5.5°C. Mating occurred on snow at low elevations from November to late February, at high elevations in late June. The mating period in subalpine habitat, and probably above the tree line, includes early summer as well as late autumn to spring because of the colder temperatures and lingering snow in spring and earlier snowfall in autumn. Temperature and snow-cover characteristics affect the snow-surface ecology of *B. californicus* across its range in western Montana. Mating on a snow cover is likely related to greater mobility (ability to jump) on snow surfaces, aiding the search for mates and contributing to greater dispersal of eggs and reduced inbreeding.

Key words: *Boreus californicus*; California Snow Scorpionfly; ecology; mating; Mecoptera; Montana; snow cover; supranivean; temperature; winter

Introduction

Among the dark specks scattered on snow in winter landscapes is the occasional snow scorpionfly of the genus *Boreus* Latreille (Mecoptera: Boreidae), which constitutes a relatively little-studied group of winter-active insects with a holarctic distribution (Penny 1977). Where snow can persist for several months during winter, *Boreus* lay their eggs during winter in the subnivean space among low-stature mats of bryophytes (mosses and club mosses), where larvae pupate and where adults also occur; both larvae and adults feed mostly on mosses (Penny 1977). Adults are occasionally active on the snow surface throughout winter when temperatures are near 0.0°C (Sömme and Östbye 1969; Courtin *et al.* 1984; Aitchison 2001; Hågvar 2001), a capability attributable in part to elevated concentrations of trehalose, glycerol, and perhaps additional compounds in the hemolymph (Husby and Zachariassen 1980; Vanin *et al.* 2008). Adults exhibit additional adaptations to "supranivean" (snow surface) living, such as long legs, dark exoskeletons (for absorbing incident long- and shortwave radiation), flightlessness, and an ability to jump (Courtin *et al.* 1984; Roff 1990; Hågvar 2010).

Most studies describing the ecology, reproductive biology, and winter physiology of *Boreus* have focussed on just a few species, such as Mid-winter Boreus (*Boreus brumalis* Fitch) in eastern North America, and *Boreus hyemalis* (L.) and *Boreus westwoodi* Hagen in Europe (e.g., Crampton 1940; Fraser 1943; Sömme and Östbye 1969; Courtin *et al.* 1984; Maier 1984; Hågvar 2001; Vanin *et al.* 2008). Far less is known about the ecology of other species, including most of those inhabiting western North America. Much of the information on the latter species has been obtained by passive sampling through use of pitfall traps and sticky boards (Maier 1984; Schmidt and Lockwood 1992; Looney *et al.* 2019). The presence and mating ecology of most western North American *Boreus* species on snow is poorly described, especially as related to ambient conditions, and merits additional study.

California Snow Scorpionfly (*Boreus californicus* Packard) is relatively widespread, ranging from British Columbia and Alberta in Canada to California, Nevada, and Arizona (Penny 1977) in the United

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States, but little has been published regarding the species' ecology other than the summary in Penny (1977) and the accounts of Chapman (1954) from western Montana, USA, and Looney *et al.* (2019) from south-central Washington, USA. I expand on Chapman's (1954) brief observations of snow-surface ecology of adult *Boreus unicolor* Hine, now considered a junior synonym of *B. californicus* (Penny 1977). I describe the annual phenology of activity by adult *B. californicus* across a range of elevations in western Montana, temperature and weather conditions as they relate to adults on snow and the occurrence of mating pairs (Figure 1), and the behaviour and rate of dispersal on snow as they may relate to mating. I place my observations in the context of literature on *B. californicus* and other *Boreus* species and speculate on why *B. californicus* sometimes occurs on snow. Less frequently, I encountered a second species, Reduced Snow Scorpionfly (*Boreus reductus* Carpenter), but will not discuss it further.

Methods

Observations were made west of the continental divide in Montana, mostly from 1994 to 1998 on transects (n = 50) that I walked or skied at eight locations in the lower mountains surrounding Missoula, Missoula County, Montana, <15 km from downtown (46.868°N, 113.997°W). A few transects were farther from Missoula: at Lolo Pass (46.635°N, 114.565°W) on the Montana–Idaho state line (n = 4) and at Willow Mountain (46.320°N, 113.910°W) in Ravalli County (n = 1). Maximum elevations varied from 991 to 1433 m above sea level (asl) for the eight transects near town, 1800 m at Lolo Pass, and 2432 m at Willow Mountain. I also include opportunistic observations at Ward Mountain (46.183°N, 114.245°W, 1830 m; Ravalli County) in 1994, Lolo Pass area (1875 m) in 2000, Saint Mary Peak (46.512°N, 114.244°W, 2758–2850 m; Ravalli County) in 2000, and near Polebridge Ranger Station in Glacier National Park (48.776°N, 114.272°W, 1122 m; Flathead County) in 2013. All transect lengths and elevations are from topographic maps.

Forested habitat at lower elevations included Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), Ponderosa Pine (*Pinus ponderosa* Douglas ex P. Lawson and C. Lawson), and Western Larch (*Larix occidentalis* Nuttall), with Lodgepole Pine (*Pinus contorta* Douglas ex Loudon), Subalpine Fir (*Abies lasiocarpa* (Hooker) Nuttall), and Engelmann Spruce (*Picea engelmannii* Farrar) at subalpine locations and Whitebark Pine (*Pinus albicaulis* Engelmann) and Subalpine Fir krummholz above the tree line. One location near Missoula was open grassland dominated by Flat-stem Bluegrass (*Poa compressa* L.) with a diversity of dried forbs projecting above the snow.

I conducted transects mostly from 1994 to 1998 between 5 November (1996, the earliest) and 12 March (1997, the latest), except at Willow Mountain on 22 June 1995. Transects were on established trails or old forest service roads, generally when fresh snow (2–40 cm) covered the ground; fresh snow was often on top of older, firmer snow up to 80 cm thick. Transect lengths were 1.2–6.4 km (mean 3.2 km) and ended when I reached a turn-around point or completed a loop, traversed at a pace of ~1–2 km/hr when walking or skiing. I recorded ambient temperature <1 cm above the snow surface using a pocket thermometer accurate to 0.5°F with the thermometer bulb shaded, similar to the method of Chapman (1954), with readings later converted to °C. Thermometer readings were made at several locations on each transect then averaged or recorded when I encountered *B. californicus* opportunistically.

I used a non-parametric Spearman rank correlation to examine the relation between numbers of mating pairs and ambient temperature near the snow and a non-parametric Wilcoxon rank sums test or a two-sample t-test (if variances were similar) to examine differences in sample mean values of temperature when *B. californicus* was present or absent on the snow or when mating pairs were or were not present. Values are means ± SD; statistical significance was assumed if $P < 0.05$. All statistical analyses were conducted using Statistix 8 (Analytical Software, Tallahassee, Florida, USA).

FIGURE 1. Mating pair of California Snow Scorpionfly (*Boreus californicus*) near Polebridge Ranger Station, Glacier National Park, Flathead County, Montana, 13 February 2013. Male (below) grasping female to his back with modified wings; individuals are ~4.0 mm in length. Photo: P. Hendricks.

Results

Boreus californicus was widespread, both in habitat and elevation, occurring in mixed grassland and lower-elevation mixed conifer forest as low as 991 m asl but also subalpine mixed conifer forests of Lodgepole Pine, Subalpine Fir, and Engelmann Spruce, and above the tree line near margins of Whitebark Pine and Subalpine Fir krummholz at the summit of Saint Mary Peak (2849 m) in the Bitterroot Mountains. The species was also present in a six-year-old Lodgepole Pine burn on Ward Mountain (Bitterroot Mountains) and a regenerating pole–sapling Lodgepole Pine stand in a 25-year-old stand-replacement burn near Polebridge Ranger Station in Glacier National Park.

Boreus was not encountered on 19 snow transects between 27 November to 12 March (all years combined; mean distance travelled: 3.4 ± 1.2 km) when ambient temperature averaged −6.2 ± 3.4°C (range −13.0 to −1.0°C). On transects when *B. californicus* was detected on snow between 5 November to 22 June (all years combined; $n = 28$), the ambient temperature averaged 0.4 ± 2.2°C (range −5.0 to 5.5°C), significantly warmer than when they were absent (Wilcoxon rank sums test: $P < 0.001$). Between 5 November and 22 February (all years combined), I found 24 mating pairs on 12 of the 25 transects below 1500 m elevation and on none of the two transects at 1680 m. On 22 June 1995, I encountered two pairs *in copula* on the Willow Mountain transect on a lingering snowbank during light snowfall at 2432 m on the north side of the mountain. Pairs *in copula* were found during overcast conditions, often with light snowfall or rain ($n = 18$), or in shade ($n = 8$), at temperatures near or above freezing (Figures 2 and 3).

The occurrence of pairs *in copula* on transects when *B. californicus* was encountered was significantly related to ambient temperature near the snow surface: 1.5 ± 1.8°C when mating pairs were present (range −0.5 to 5.5°C, $n = 13$) and −0.6 ± 2.1°C when mating pairs were absent (range −5.0 to 3.5°C, $n = 15$; two-sample *t*-test: $t_{26} = -2.82$, $P < 0.01$). The number of pairs encountered *in copula* (1–4) on trips when *B. californicus* was present ($n = 28$ trips; Figure 2) was also significantly correlated with ambient temperature ($r_s = 0.568$, $P = 0.002$). The correlation with ambient temperature remained significant ($r_s = 0.579$, $P = 0.002$) when adjusted for survey effort, expressed as the number of mating pairs/km traversed (Figure 3).

Boreus californicus either jumped or folded their legs and antennae under the body (i.e., "play dead") when first disturbed (poked with a pencil tip). Temperatures averaged 1.3 ± 1.0°C (range 0.5 to 3.5°C, $n = 27$) when the initial response was to jump and −2.1 ± 2.7°C (range −5.0 to 3.5°C, $n = 122$) when the initial response was to "play dead" (Wilcoxon rank sums test: $P < 0.001$). Several individuals jumped when first disturbed then folded their legs and antennae under their body after jumping once.

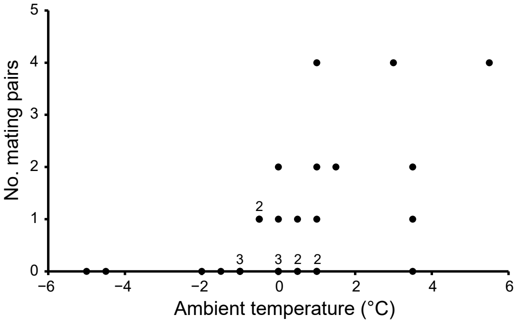

FIGURE 2. Number of mating pairs ($n = 26$) of California Snow Scorpionfly (*Boreus californicus*) on snow in western Montana related to ambient temperature near the snow surface. Points represent survey dates when the species was detected ($n = 28$ surveys). Numbers above some points show the number of surveys sharing that point value.

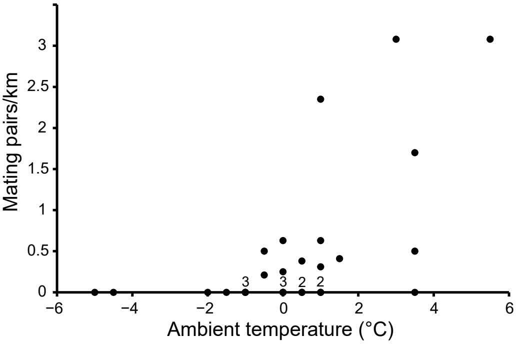

FIGURE 3. Number of mating pairs ($n = 26$) of California Snow Scorpionfly (*Boreus californicus*) on snow/km traversed in western Montana related to ambient temperature near the snow surface. Points represent survey dates when the species was detected ($n = 28$ surveys). Numbers above some points show the number of surveys sharing that point value.

Distances jumped by undisturbed individuals ($n = 21$) varied from 1.0 to 8.0 cm/jump at a rate of 5–7 jumps/min. Jumping was sometimes the response of pairs *in copula* (the male did the jumping while grasping the female to his back with his modified wings; Figure 1), both when disturbed and undisturbed. On 22 June 1995, an undisturbed pair of *B. californicus in copula* at Willow Mountain jumped 10 times in 2 min (temperature 3.5°C), each jump ~2.0 cm. Jumping also occurred regularly when undisturbed individuals travelled in a deliberate direction. On 31 December 2000, one male and two female *B. californicus*, above Lolo Pass at 1875 m elevation (temperature 0.5°C), made 60, 70, and 68 jumps in 10 min and covered straight-line distances of 390 cm, 420 cm, and 620 cm, respectively, the last sequence aided by a slight tail wind of 4–5 km/hr.

Discussion

My observations of California Snow Scorpionfly activity on snow expand on the findings of Chapman (1954) from the same region of western Montana. *Boreus californicus* has now been documented on snow in western Montana at elevations <1500 m asl from at least early November to early April—Chapman (1954) reported them in early February to early April in the same general area near Missoula where I encountered them in early November to early March. The period of adult activity at lower elevations in western Montana now closely matches collection dates across the species range as noted in Penny (1977), as well as capture dates of adults in south-central Washington during continuous and systematic pitfall trapping over four years (Looney *et al.* 2019) and where a snow cover was rarely present.

Chapman (1954) failed to detect *B. californicus* above 1220 m elevation on any of his 21 trips in search of snow insects in western Montana, including six trips at 1825–2438 m during the winter of 1952–1953. Note that, on 20 September, he found an unidentified *Boreus*, possibly this species, under a rock at 2255 m in the Mission Mountains (Lake County) in the absence of any snow. I encountered *B. californicus* on snow on several transects up to 1400 m near Missoula, at 1830 m on 6 November 1994 at Ward Mountain, at 1675–1875 m between 24 November to 1 January (1994–1996) at Lolo Pass, at 2432 m on 22 June 1995 at Willow Mountain, and at 2850 m on 6 October 2000 at the summit of Saint Mary Peak. Thus, *B. californicus* has now been found on snow in western Montana over an elevation range of nearly 2000 m, from valley grasslands and mixed conifer forests to mountains cresting above the tree line, with adults active somewhere across this elevation gradient most months of the year except in mid- to late summer (July to late September). What little evidence is available indicates that some adults are present at subalpine and alpine locations later into spring and early summer than at lower elevations and again appear earlier in autumn. The generality of this conclusion for *B. californicus* is hampered by little data from high elevations, but Colorado Snow Scorpionfly (*Boreus coloradensis* Byers) exhibits a similar period of activity on snow (1 October to 27 May) across a similar range of habitats at higher average elevations in Colorado and Utah (Byers 1955; Penny 1977). The pattern fits expectation in relation to the environmental lapse rate (decrease in temperature with an increase in elevation) of ~6°C/km (MacArthur 1972), which results in snow lingering at high elevations later into summer and appearing earlier in autumn. Across the known range of *B. californicus* in western Montana, the lapse rate translates to an ambient temperature difference of ~12°C between valley bottom and mountain top, an important ecological variable affecting the phenology of *B. californicus,* the adults of which are most active at temperatures near freezing.

I found *B. californicus* moving across snow in western Montana when temperatures near the snow surface were as low as −5.0°C, lower than the minimum of −1.5°C reported by Chapman (1954). However, captives kept outdoors in February were able to slowly "crawl" at −5.5°C, and a few were motionless but survived overnight at −12.0°C, indicating an ability of *B. californicus* to withstand temperatures lower than those encountered when they occur on snow of their own volition. However, my newly presented findings and the observations of Chapman (1954) indicate that this species is most active on snow when temperatures are close to freezing, similar to other *Boreus* species studied (Shorthouse 1979; Courtin *et al.* 1984; Hågvar 2001, 2010).

The jumping response to disturbance exhibited by *B. californicus* is most prevalent when temperatures reach or slightly exceed freezing, an observation also made by Chapman (1954). However, I found that "playing dead" (contracting the legs and antennae under the body), also observed by Chapman (1954), is a more common response to disturbance than jumping when temperatures are below freezing. Jumping is an important ability for *B. californicus* as it may allow them to escape potential predators (some jumps reached 8.0 cm) but especially to disperse long distances across the snow. I documented straight-line travel rates for individuals of 390–620 cm in 10 min, which translates to 23.4–37.2 m/hr if sustained. These rates of travel are similar to those reported on snow for *B. brumalis* in Ontario (Shorthouse 1979) and *B. westwoodi* in Norway (Hågvar 2001, 2010); the observed rates, if sustained, convert to ~24.0 m/hr and ~18.0–72.0 m/hr, respectively, although the longest case of directional movement for *B. westwoodi* was 12.2 m in 30 min (24.4 m/hr) at 5.0°C (Hågvar 2001). Males of pairs *in copula* also jumped, but distances and frequency of jumping may be hindered by the presence of the female. An undisturbed pair of *B. californicus in copula* at 3.5°C jumped at a rate ~6.0 m/hr. Total distances travelled continuously by *Boreus* on snow before they retreat to subnivean spaces are not known, but Hågvar (2001) reported several cases where individuals were 30–50 m out on snow-covered lakes or bogs, and Shorthouse (1979) found one individual 70 m from shore on a snow-covered lake, locations where retreat from the surface would be unlikely.

Mating activity on snow by *B. californicus* in western Montana is clearly related to temperatures at or above freezing near the snow surface (Figures 2 and 3), also noted by Chapman (1954) and by Cockle (1908) in British Columbia. However, mating pairs were encountered infrequently, even at temperatures above freezing. Travelling on snow transects, I found a maximum of ~3.0 pairs/km, but more typically ≤0.5 pairs/km, which is about what Chapman (1954) reported, i.e., three pairs in 9.6 km or 0.3 pairs/km. Pairs *in copula* occurred on snow throughout much of the period when snow cover was present (early November to late February at lower elevations, to at least late June at higher elevations) and when the temperature near the snow was −0.5°C or warmer, most often in shade or when skies were overcast. Similar conditions were reported for pairs of *B. westwoodi* on snow during November to January in Norway (Hågvar 2001), who suggested that surface activity when overcast may reduce the likelihood of being caught on the snow under a clear sky when air temperature drops rapidly at sunset. Interestingly, Hågvar (2001) observed no copulating animals on snow when present at the two highest densities, where 1–10 m separated individuals under overcast skies at 1.0°C. I made a similar observation on 10 November 1995 with falling snow at −1.0°C. I counted 137 *B. californicus* over 6.4 km, but most were concentrated at five sites in groups of 10–20 animals in 2–4 m^2 and with no mating pairs, even though both sexes were present in each group. Thus, *B. californicus* seems to be active on snow for reasons other than just mating.

Female *B. californicus* on snow in early and late winter may carry fully developed eggs more often than females in mid-winter, assuming egg development follows the pattern of *B. westwoodi* (Hågvar 2001); perhaps females are less receptive to males at those times. Of the 26 copulating pairs of *B. californicus* found on snow, 76% were encountered in December through February with 58% in February alone, consistent with this possibility. Mating *B. californicus* at the Willow Mountain transect (2432 m) on 22 June 1995 are pertinent in this regard. Two pairs were found *in copula* during light snowfall along with two single females. Mating activity there probably occurs frequently during late spring and early summer, as well as in the absence of snow during autumn and in the subnivean space throughout winter (Hågvar 2001, 2010). Extensive topographic relief allows snow to linger well into summer at high elevations and appear earlier in autumn, along with accompanying colder and favourable temperatures. This undoubtedly influences the timing of reproduction by *B. californicus* across an elevational gradient and produces a phenological shift in mating, or perhaps an expanded mating season, at high elevations, as is evident by my observations in late June on Willow Mountain, the latest date of the winter active period during which I encountered *B. californicus* on snow, and three females on wind-packed snow above the tree line on 6 October 2000 at the summit of Saint Mary Peak (2849 m), the earliest date I observed the species on snow. Mating probably commences, regardless of elevation or the presence of a snow cover, when ambient temperatures approach freezing.

It is commonly assumed that *Boreus* gains access to snow surfaces by climbing vegetation penetrating the snow or through the air spaces produced around that vegetation and that they retreat to subnivean spaces via the same routes (Shorthouse 1979; Hågvar 2010). Why *Boreus* move to a snow surface (supranivean zone) remains an open question, but it must offer advantages favoured by selection. Possible advantages, proposed by Shorthouse (1979) and Hågvar (2010), are an improved ability to disperse by moving across relatively smooth terrain (perhaps to distribute eggs more widely and reduce inbreeding) and to avoid subnivean invertebrate and vertebrate predators. Little is known regarding predators of *Boreus*, subnivean or otherwise. Subnivean pitfall traps capture few adult *Boreus* (Schmidt and Lockwood 1992; Hågvar and Hågvar 2011), indicating that the space under a snow cover could hinder the ability of boreids, including *B. californicus*, to jump and disperse as effectively as on the surface.

Characteristics of snow cover likely influence the occurrence and abundance of *B. californicus* on snow (Aitchison 2001); thus, better documentation of such characteristics could increase our knowledge of boreid ecology and behaviour associated with their snow-surface activity. Major qualities of snow cover include duration, thickness, hardness, and density (Pruitt 2005). Of special interest is the relation of snow-cover qualities to the critical thickness of snow, the hiemal threshold, where the subnivean space is stabilized at or slightly below 0.0°C and buffered from extreme fluctuations in temperature above the snow cover (Pruitt 1957; Aitchison 2001). The presence and duration of this critical snow thickness (at least 20–30 cm of snow) probably plays an important role in the timing of reproductive activities beneath and on snow by *B. californicus* as related to the broad elevational gradient where the species occurs.

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Distribution and habitat use of Canada Goose (*Branta canadensis*) during spring and fall migration along the James Bay east coast

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Abstract

Canada Goose (*Branta canadensis*) is the main waterfowl harvested by Cree hunters in James Bay. Environmental changes that could affect the number, distribution, and migration patterns of geese have occurred along James Bay's east coast in the last 50 years, including isostatic rebound, climate warming, and hydroelectric development. We determined the spring and fall distribution of Canada Geese along the James Bay east coast in 2018 and identified habitats associated with the greatest goose densities. We conducted four helicopter surveys between Waskaganish and Chisasibi, two each during spring and fall. The main goose concentrations were between Eastmain and Wemindji in both seasons. In spring, goose densities increased with the percentage of salt marshes whereas in fall, the highest densities were in areas with the greatest proportion of tidal flats and turbid water. We did not find any relationships between Common Eelgrass (*Zostera marina* L.) beds and the distribution of Canada Geese although it was an important habitat for geese in the 1970s. Our observations are consistent with surveys conducted in the 1990s that found limited use of eelgrass beds by migrating geese. This suggests that geese may be using alternative habitats during migration following the decline of eelgrass beds reported by Cree land users and confirmed by ground surveys and remote sensing. Changes in distribution and habitat use of goose flocks along the James Bay east coast are probably a consequence of habitat changes, natural and human disturbances, and the increasing number of moult migrant temperate breeding Canada Goose (*Branta canadensis maxima*).

Key words: Aerial surveys; *Branta canadensis*; disturbance; Common Eelgrass; Eeyou Istchee; habitat use; James Bay; migration; Traditional Ecological Knowledge

Résumé

La Bernache du Canada (*Branta canadensis*) est la principale espèce de sauvagine récoltée par les chasseurs Cris de la Baie James. L'abondance, la distribution et les mouvements migratoires des bernaches ont certainement été affectés par les nombreux changements environnementaux qu'a connus la Baie James au cours des 50 dernières années, incluant l'ajustement isostatique, les changements climatiques et les développements hydroélectriques. Nous avons déterminé la distribution des bernaches du Canada le long de la côte est de la Baie James en 2018 et identifié les habitats associés avec les plus grandes densités de bernaches. Pour cela, nous avons mené quatre inventaires aériens entre Waskaganish et Chisasibi, deux au printemps et deux en automne. Au printemps, la densité des bernaches augmentait avec la proportion de marais salés alors qu'en automne, nous avons trouvé les plus grandes densités de bernaches dans les sections avec les plus grandes proportions de vasières et d'eaux turbides. Nous n'avons pas pu établir de relation entre les herbiers marins (*Zostera marina* L.) et la distribution des bernaches bien qu'ils aient constitué un habitat important pour les bernaches dans les années 1970. Nos observations sont cohérentes avec les inventaires menés dans les années 1990 qui ont permis de documenter une utilisation limitée des herbiers marins par les bernaches en migration. Cela suggère que les bernaches utilisent des habitats alternatifs au cours de leur migration depuis le déclin des herbiers marins rapporté par les communautés Cries et confirmé par des inventaires terrestres et la télédétection. Ces changements dans la distribution et l'utilisation des habitats par les bernaches du Canada sur la côte est de la Baie James sont probablement une conséquence de la modification des habitats, des perturbations humaines et naturelles, ainsi que du nombre croissant de bernaches résidentes (*Branta canadensis maxima*) en migration de mue.

Mots clés : Inventaires aériens; *Branta canadensis*; perturbation; Zostère; Eeyou Istchee; utilisation des habitats; Baie James; migration; Savoir traditionnel

Introduction

Canada Goose (*Branta canadensis*) is one of the main waterfowl species harvested by Cree hunters along the James Bay coasts and has been part of their subsistence hunting for centuries (Prevett *et al.* 1983; Berkes *et al.* 1994). The traditional annual spring goose break is important socially and culturally for all coastal communities in Eeyou Istchee, the Eastern James Bay Cree territory (Royer and Herrmann 2013). Canada Geese harvested along the James Bay east coast belong to two subspecies and four populations (Giroux *et al.* 2022). These include the Atlantic Population composed of *Branta canadensis interior* that breeds in northern Quebec with the largest concentrations on the Ungava Peninsula and winters along the Atlantic coast of the United States. The Southern Hudson Bay Population is also composed of *B. c. interior* that breeds in southwestern James Bay (Ontario) and southern Hudson Bay (Ontario and Manitoba) and winters in the Midwest states of the United States. The harvest includes temperate breeding geese (*Branta canadensis maxima*), including individuals from the Atlantic Flyway Resident Population and the Mississippi Flyway Giant Population. Geese from the three latter populations are harvested by Cree hunters as they undertake a moult migration to northern Quebec, most likely after nesting failure (Sorais *et al.* 2023). The *B. c. interior* and *B. c. maxima* subspecies are referred to as short-necked and long-necked geese by Cree hunters, respectively.

Cree land users have reported that fewer short-necked geese migrate along the James Bay east coast compared to the 1980s (Royer and Herrmann 2013; Idrobo *et al.* 2024). They also observed that the fall distribution of geese was less predictable now than in the 1980s when the birds were moving between the coast where they fed on Common Eelgrass *(Zostera marina* L.) and the adjacent tundra where they foraged for berries (Idrobo *et al.* 2024). The distribution of waterfowl along the east coast of James Bay was assessed in the early 1970s before hydroelectric development in Eeyou Istchee through a series of aerial surveys conducted by the Canadian Wildlife Service (Curtis and Allen 1976). In spring, sub-arctic breeding Canada Geese were found wherever there was open water with concentrations in all major bays along the entire east coast. In fall, the greatest numbers of Canada Geese were found north of Wemindji where they were reported to feed extensively on eelgrass beds (Curtis and Allen 1976). In the 1990s, Reed *et al.* (1996) conducted aerial and ground surveys along the northeast part of James Bay after completion of the first phase of the hydroelectric complex on La Grande River, which drains into James Bay. They found that sub-arctic breeding Canada Geese were feeding on different plant species including berries during their fall migration but made limited use of eelgrass beds.

Several environmental changes that occurred since the 1970s along the James Bay east coast might have affected the abundance and distribution of short-necked geese in the area. One noteworthy change observed by Cree land users (Peloquin and Berkes 2009; Dickey 2015; Idrobo *et al.* 2024) and confirmed by ground surveys (Leblanc *et al.* 2022) and remote sensing (Clyne *et al.* 2024) is the decline of eelgrass in subtidal meadows in the late 1980s and 1990s. This decline may have resulted from several environmental stressors including the development of hydroelectricity in Quebec's boreal region and ongoing climate change (Leblanc *et al.* 2022). Using satellite imagery from 1985 and 2020, Olatunji (2022) found an increase of deciduous forests, shrub fens, and shrub swamps that is likely related to the greening of sub-arctic regions of northern Canada (Davis *et al.* 2021; Leipe and Carey 2021). Also, isostatic rebound estimated at 10–12 mm/yr in James Bay (Henton *et al.* 2006) has resulted in a coastal raise of ~35–42 cm in the last 35 years. During this period, the area of tidal flats declined while those of salt marshes and freshwater wetlands increased (Olatunji 2022). In addition, it is estimated that several hundred thousand temperate breeding Canada Geese are now crossing James Bay during their moult migration (Sorais *et al.* 2023). This may also influence the distribution and habitat use of sub-arctic breeding geese during fall because their migration along the James Bay coast overlaps (Sorais *et al.* 2023) and competition between the two subspecies could occur (Ankney 1996; Abraham *et al.* 1999; Sheaffer *et al.* 2007; Luukkonen *et al.* 2008). In spring, short-necked geese (*B. c. interior*) migrate through James Bay before the long-necked geese (*B. c. maxima*; Sorais *et al.* 2023).

The objectives of our 2018 study were to use aerial surveys to update our knowledge of the distribution and habitat use of Canada Geese in Eastern James Bay during their spring and fall migration. Specifically, we assessed the density of geese along the James Bay east coast during migrations. Second, we determined how habitat composition influenced goose density on coastal habitats such as salt marshes, tidal flats, and eelgrass beds.

Methods

Study area

Our study took place in Eeyou Istchee, the territory of the Cree Nation in Quebec's boreal region. The territory covers ~400 000 km^2 and includes lands on the eastern shore of James Bay and southeastern Hudson Bay, as well as the lakes and rivers that drain into them. It is divided into formally recognized family hunting territories, referred to as traplines, the use of which is supervised by a tallyman designated by family members. Cree land user interests, including those of tallymen, are represented at the local and regional level by the Cree Trappers Association. We conducted aerial surveys along ~250 km of coast from Waskaganish to Chisasibi (Figure 1). The coast is highly sinuous with numerous bays, points, and peninsulas fringed by numerous islands, islets, and reefs (Dignard *et al.* 1991). The area is generally low, alternating between flat, gradually sloping shorelines and rockier, hilly shores. Subtidal meadows are characterized by Common Eelgrass beds that vary in density and biomass in time and space (Lalumière *et al.* 1994; Leblanc *et al.* 2022). Vast stretches of mud and sand tidal flats are found on the mainland shore with salt marshes occurring inshore. Islands and exposed points are usually covered by heath with lichens and ericaceous shrubs. White Spruce (*Picea glauca* (Moench) Voss) is the dominant species on the coastline, replaced by Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh) in interior forests (Dignard *et al.* 1991).

Aerial surveys

We conducted two aerial surveys during each of the spring and fall migration of Canada Geese in 2018. We used a Eurocopter AStar 350 helicopter (Airbus Helicopter, Marignane, France) flying from south to north ~100 m above ground along the coastline. We focussed mainly on the shoreline and estimated a maximum width of our observation corridor to be ~500 m on each side of the flight path. Each survey was completed during a single day with low to moderate winds and clear conditions. The spring surveys were 3.6 hr (6 May) and 3.8 hr (13 May) in duration, and occurred between 8 am and 3 pm at an average speed of 140 km/hr. The fall surveys were 5.9 hr (16 September) and 6.2 hr (23 September), and occurred between 7 am and 7 pm at an average speed of 100 km/hr. A few traplines were not surveyed to respect the will of tallymen who were concerned that the helicopter would disturb the geese and consequently their hunting activities. Hence, the number of traplines and distance travelled by helicopter varied among surveys. The same pilot, principal observer, and navigator flew on the four surveys although there was a different second observer assistant from the Cree community for each survey. We recorded the location of the helicopter when a flock of Canada Geese was detected regardless of the distance from the flight path and recorded the number of individuals using the software Avenza Map (Avenza Systems Inc., Toronto, Ontario, Canada) on a tablet computer. The helicopter followed a straight flight path without circling above flocks to avoid disturbing hunting activities. We recorded the flight path of each survey (Figure 1) using a global positioning system (GPS) device. We calculated a goose density index as the number of geese counted in a section of coast divided by the length of the flight path in km within the section.

Habitat mapping

We produced a 15-m resolution habitat map of the east coast of James Bay by classifying a combination of optical and synthetic-aperture radar (SAR) satellite imagery. We acquired optical imagery from the US Landsat-8 Operational Land Imager satellite and SAR imagery from the European Sentinel-1B satellite in 2017, 2018, and 2020 for spring, summer, and fall to consider the phenological stages of the vegetation (Tables S1, S2). The detailed procedure for image classification can be found in Clyne *et al.* (2021) and Sorais *et al.* (2023). Briefly, we re-projected Landsat-8 and Sentinel-1 raw images to a 15-m pixel resolution using the Pansharpening module of PCI Geomatica Banff (PCI, Ontario, Canada). We used the "randomForest" package in R software (version 4.3.3; R Development Core Team 2021) for applying Random Forests to the images, a non-parametric decision tree type supervised classifier that requires delineation of training areas (Breiman 2001). A total of 555 randomly distributed training polygons of 23 classes were delineated from photointerpretation of high spatial resolution (32 to 65-cm pixel size) optical satellite images obtained from the ArcGIS archive (Figures S1–S10). The photointerpretation was also guided by pictures taken in the field by A.L. in 2019 (Figures S1–S10). We further processed the resulting classified images with ArcGIS Pro (ESRI, California, USA) to produce a map with 15 habitat types of which 10 were considered to have potential to explain the density of Canada Geese based on Cree traditional knowledge (Dickey 2015) and field observations of Dignard *et al.* (1991) and Reed *et al.* (1996; Table 1).

Modelling goose density

We wanted to determine if goose density was influenced by the habitats on the coast. Because geese can move a few km between their resting and feeding

FIGURE 1. Helicopter flight paths (dark green line) during the aerial surveys along the James Bay east coast in spring (a: 6 May, b: 13 May) and fall 2018 (c: 16 September, d: 23 September). Traplines are delimited by grey lines.

TABLE 1. Characteristics of 10 habitats used to establish relationships with the density of Canada Geese (*Branta canadensis*) surveyed along the James Bay east coast. Photos and satellite images of each habitat are shown in Figures S1–S10.

Habitat	Description	References
Eelgrass bed (Figure S1)	Vegetation submerged in coastal shallow water dominated by Common Eelgrass (*Zostera marina* L.). Other plants like *Ruppia* spp. and *Potamogeton* spp. are also reported. Use by Canada Geese as a feeding habitat during fall and spring when ice-free.	Dignard *et al.* (1991); Dickey (2015)
Turbid water (Figure S2)	Turbid open water often observed in river estuaries with important amount of transported mineral and organic particles. The presence of submerged vegetation remains undetected. Potential use by Canada Geese as feeding habitat.	Clyne *et al.* (2021)
Shallow water (Figure S3)	Open water with a depth <3 m. Vegetation can be found at the surface of inland bodies of shallow water. Use by Canada Geese as a resting habitat during fall and spring when ice-free.	Dignard *et al.* (1991); Sorais *et al.* (2023)
Tidal flat (Figure S4)	Unvegetated habitat located between minimum and maximum limits of sea level consisting of mud and sand. Use by Canada Geese as a resting habitat during fall and spring when ice-free.	Dignard *et al.* (1991); Sorais *et al.* (2023)
Cobble beach (Figure S5)	Unvegetated habitat located in the upper part of the foreshore consisting mainly of coarse rocks. Use by Canada Geese as a resting habitat during fall and spring when ice-free.	Dignard *et al.* (1991); Sorais *et al.* (2023)
Salt marsh (Figure S6)	Coastal wetlands dominated by low-lying vegetation including Chaffy Sedge (*Carex paleacea* Schreber ex Wahlenberg), Four-leaved Mare's Tail (*Hippuris tetraphylla* L. f.), Needle Spikerush (*Eleocharis acicularis* (L.) Roemer & Schultes), and Marsh Arrowgrass (*Triglochin palustris* L.). This habitat is periodically flooded by saltwater. Use by Canada Geese as a feeding habitat during spring and fall.	Dignard *et al.* (1991); Reed *et al.* (1996)
Freshwater wetland (marsh, open fen, string fen; Figure S7)	Freshwater marshes dominated by low-lying vegetation such as *Carex* spp., open fen with *Carex* spp., and moss permanently saturated with stagnant freshwater, and string fen characterized by an alternance of elevated ground strings and narrow depressions. Potential use by Canada Geese as feeding habitat but data are limited.	Dignard *et al.* (1991)
Tundra (Figure S8)	Heath habitat covered by low-lying vegetation, including Black Crowberry (*Empetrum nigrum* L.) and Mountain Cranberry (*Vaccinium vitis-idaea* L.), associated with subarctic vegetation such as lichens, mosses, herbaceous plants, and shrubs. This habitat is found along the coast above the high-water limits and further inland in the northern part of the study area. Use by Canada Geese as a feeding habitat in fall and to a lesser extent in spring.	Dignard *et al.* (1991); Reed *et al.* (1996)
Deep water (Figure S9)	Open water with a depth >3 m without vegetation. Potential use by Canada Geese as resting habitat during fall and spring when ice-free.	Dignard *et al.* (1991)
Peatland (open bog, muskeg; Figure S10)	Wetland dominated by low-lying vegetation, mainly moss, growing on an organic soil. Potential use by Canada Geese.	Sorais *et al.* (2023)

areas during the day, we wanted to characterize the habitats found in the vicinity of goose observations (i.e., geese were observed at a maximum of 500 m from the helicopter). We assessed the relationship between goose density and habitat coverage using two approaches based on different types of sampling units. The first approach was based on trapline limits because this was relevant for resource management in the coastal communities. Because traplines represent inland geographic entities and we were interested in coastal habitats, we extended trapline limits into the bay following the latitude at the junction between two traplines (Figure 2a,b). For each survey, we set longitudinal limits of trapline sections at 5 km on each side of the flight path. We calculated goose density within each trapline section, as well as the proportion of the 10 potential habitats for geese such as Common Eelgrass beds, tidal flats, and salt marshes (Table 1).

The second approach was based on smaller sampling units that maximized variation in goose density and increased sample sizes (Figure 2c,d). To establish these sampling units, we first created a 1-km wide buffer on each side of the flight path. We then sectioned these buffers every 2 km along the latitudinal axis (south to north). We selected this section length because it maximized the coefficient of variation of

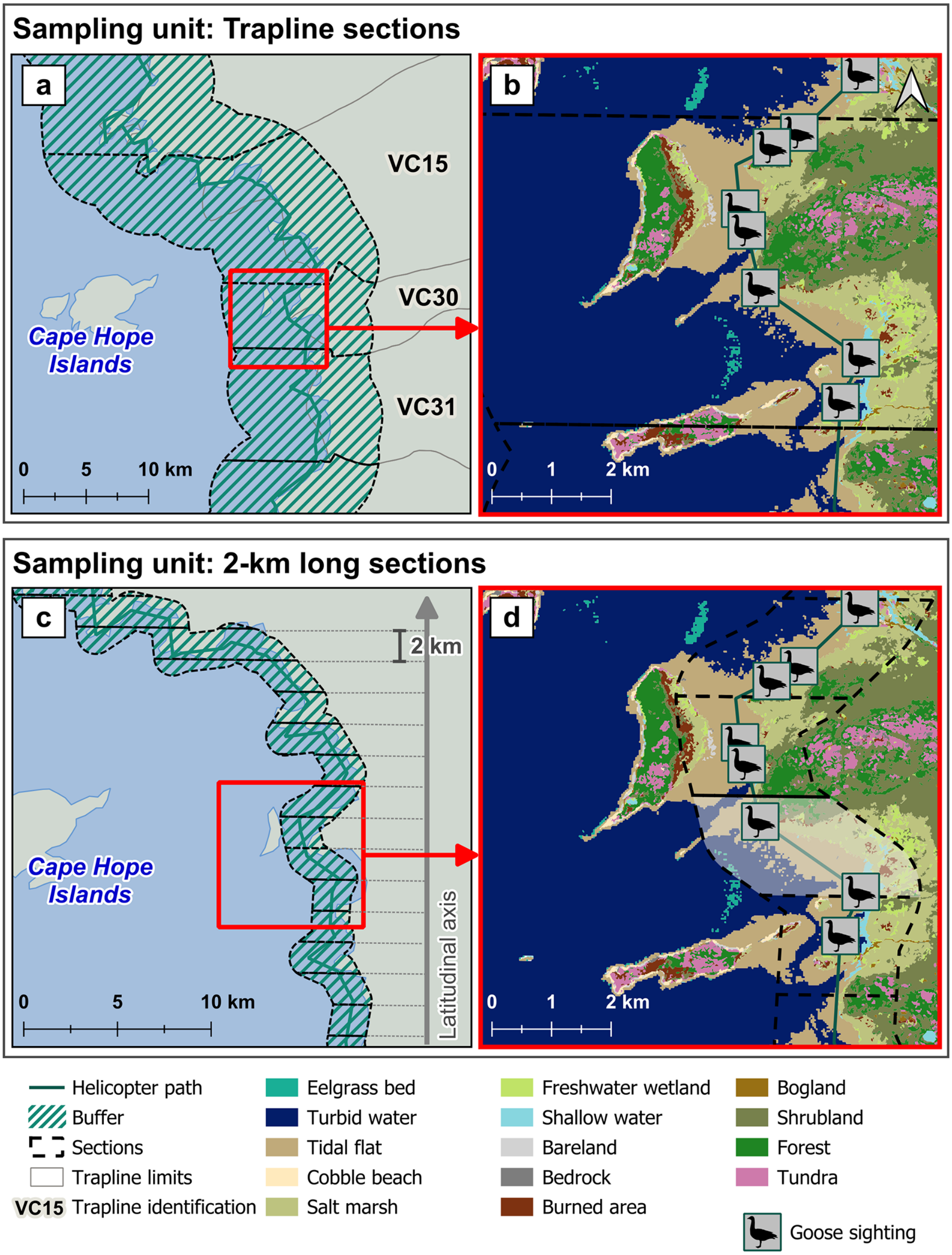

FIGURE 2. Illustration of the two types of sampling units used to study the relationship between Canada Goose (*Branta canadensis*) density and habitats: trapline sections (a, b) and 2-km long sections (c, d). a. A 5-km buffer was delimited on each side of the helicopter flight path and divided into sections following trapline limits that were extended towards the bay. b. Example with the 23 September 2018 goose survey for trapline VC30 and the eelgrass habitat: flight distance = 6941 m; *n* observed geese = 1055; goose density = 152 geese/km; percentage of the section covered by eelgrass beds = 0.2 %. c. A 1-km buffer was delimited on each side of the same helicopter flight path and divided into sections every 2 km following the latitudinal axis. d. Example for the highlighted section: flight distance = 24 501 m; *n* observed geese = 775; goose density = 300 geese/km; percentage of the section covered by eelgrass beds = 0.5 %. Note: these sampling units were used to characterize goose density and the habitats in the vicinity of goose observations. As such, the buffers were established to create trapline sections and 2–km long sections extended beyond the 500-m maximum observation corridor on either side of the helicopter.

goose density among sections when comparing section lengths ranging from 2 to 50 km (Figure S11). We therefore used these 2-km long sections to assess the association between goose density and the proportion of the habitats within each section.

Using these two different sets of sampling units allowed us to analyze goose density variation at a coarse scale (i.e., traplines sections) and finer scale (i.e., 2-km long sections). Because the helicopter followed the coastline as much as possible during each survey, we considered the longitudinal variation between the flight paths to be negligible (Figure 1). However, the length of the flight path differed between surveys based on the number of traplines that we were authorized to fly over at the time. As such, for calculating the Pearson correlation of goose density in traplines between two different surveys, we only considered traplines that we flew during both surveys.

We assessed the relationship between goose density and habitat composition for each survey at the scale of traplines and 2-km long sections. Sample sizes varied among analyses because not all traplines or 2-km long sections were covered during the four surveys. At the trapline scale, we fit multiple linear regressions models to explain the log transformed goose density, i.e., log(density + 1), as a function of the proportion of each potential habitat in the trapline. Using the 2-km long sections, we used two approaches to analyze goose density. Geese were absent in 35–80% of sections according to surveys, which skewed the goose density distribution towards maximum values similar to a Poisson distribution. However, because we wanted to be able to analyze this absence/presence phenomenon, we decided to analyze the presence/absence in sections and the density in occupied sections with geese separately. Hence, we first fit logistic regression models to explain the presence/absence of geese as a function of the proportion of the different habitats in each section. Next, we used the subset of sections where geese were present and fitted a multiple regression model to explain the log-transformed goose density as a function of the proportion of each habitat. For each modelling procedure, we determined the best model using a stepwise approach by testing model performance that maximized R^2 ensuring that predicting variables included in a model were not strongly correlated (Pearson correlation coefficient < 0.6). We verified homoscedasticity and normality of residuals by performing visual diagnosis. We performed statistical analyses using R software (version 4.3.3; R Development Core Team 2021). We used the "ggplot2" package to create graphic representations. We used ArcGIS Pro (ESRI, California, USA) and QGIS 3.34 Prizren (QGIS 2023) for mapping.

Results

Our first spring survey (6 May) occurred before the peak migration of Canada Geese in James Bay as shown by the low number of geese counted ($n = 815$) compared to the number tallied one week later ($n = 11\,332$ on 13 May). We saw no major concentration of geese during the first survey, but we recorded the greatest densities between Eastmain and Wemindji during the second (Figure 3). We found no correlation in goose density calculated within traplines between the first and second survey (Pearson $r_{15} = 0.22$; $P = 0.40$). The presence/absence of geese in 2-km long sections was not significantly influenced by the proportion of any habitat for both surveys. Moreover, we did not find any relationship between goose density estimated during the first survey and habitat composition using either traplines or 2-km long sections. For the second spring survey, however, goose density increased with the percentage of salt marshes in traplines ($F_{1,15} = 8{,}37$; $R^2 = 0.32$; $P = 0.01$) and in 2-km long sections ($F_{1,51} = 10.27$; $R^2 = 0.15$; $P < 0.01$; Figure 4).

The fall surveys were better synchronised with the Canada Goose migration with 8458 and 11 057 birds counted on 16 and 23 September, respectively (Figure 5). We saw the greatest densities in traplines just north of Eastmain. There was a weak correlation in the density of geese between the two fall surveys (Pearson $r_{17} = 0.42$; $P = 0.07$) indicating that some traplines may have been more attractive for geese than others, at least during the period when the two surveys were conducted. However, neither the first fall survey (Pearson $r_{15} = -0.25$; $P = 0.33$) nor the second (Pearson $r_{15} = -0.02$; $P = 0.93$) correlated with the second spring survey, in terms of density in traplines. The presence/absence of geese in 2-km long sections was not significantly influenced by the proportion of any habitats during the two fall surveys. Goose density in traplines increased significantly with the proportion of turbid water ($F_{1,19} = 16.79$; $R^2 = 0.44$; $P < 0.01$) during the first survey and with the proportion of tidal flats ($F_{1,18} = 8.86$; $R^2 = 0.29$; $P = 0.01$) during the second survey (Figure 4). In 2-km long sections, goose density increased with the proportion of tidal flats and turbid water during the first survey ($F_{2,78} = 15.59$; $R^2 = 0.27$; $P < 0.01$). During the second survey, it also increased with tidal flats but slightly decreased with the proportion of freshwater wetlands ($F_{2,73} = 13.68$; $R^2 = 0.25$; $P < 0.01$; Figure 4).

Discussion

These surveys determined how Canada Geese were distributed along the eastern coast of James Bay in spring and fall 2018. Although we could not distinguish between subspecies, most geese counted

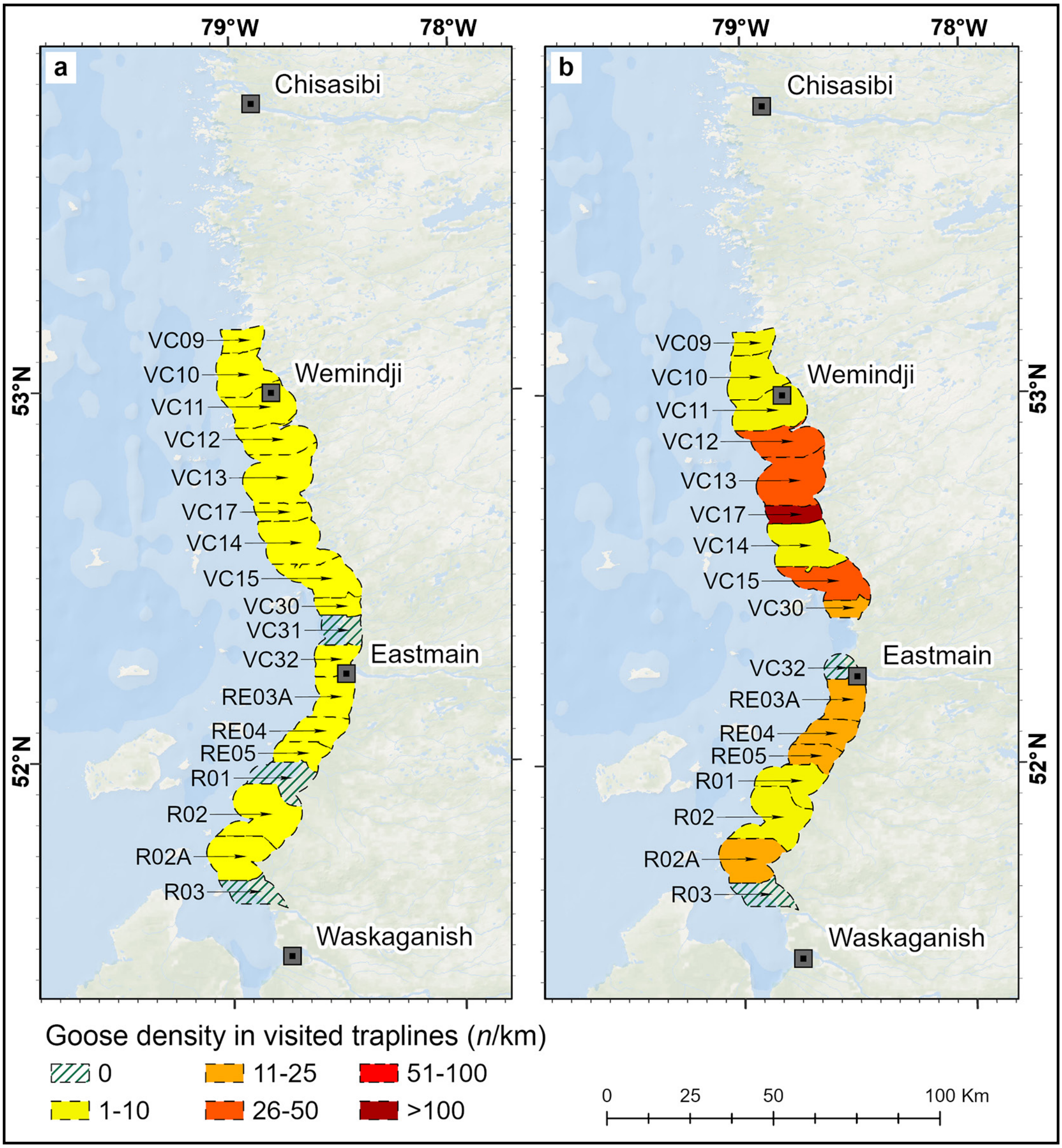

FIGURE 3. Canada Goose (*Branta canadensis*) density (number geese/km of helicopter path) in surveyed traplines on a. 6 and b. 13 May 2018 along the James Bay east coast. Traplines surveyed are identified by their Cree Trappers' Association numbers.

during the spring surveys in May were likely sub-arctic breeding geese because temperate breeding geese that migrate north to moult arrive in James Bay in early June after our surveys (Sorais *et al.* 2023). In fall, however, both subspecies migrate through the area in September and can sometimes be found on the same staging sites as shown by the simultaneous capture of the two subspecies in Boatswain Bay near Waskaganish (Sorais *et al.* 2023). Hence, geese counted in fall were most probably a mixture of the two subspecies. However, several aspects of our study prevented us from drawing general habitat use patterns during goose migration. The spring of 2018 was late and characterized by extensive snow cover persisting throughout northern Quebec, and in particular across the main breeding grounds of the Atlantic Population of Canada Geese (Harvey *et al.* 2018). Consequently, the annual production of juveniles was nearly absent and the worst since 1997 (Lefebvre and Orichefsky 2020). Our results therefore reflect

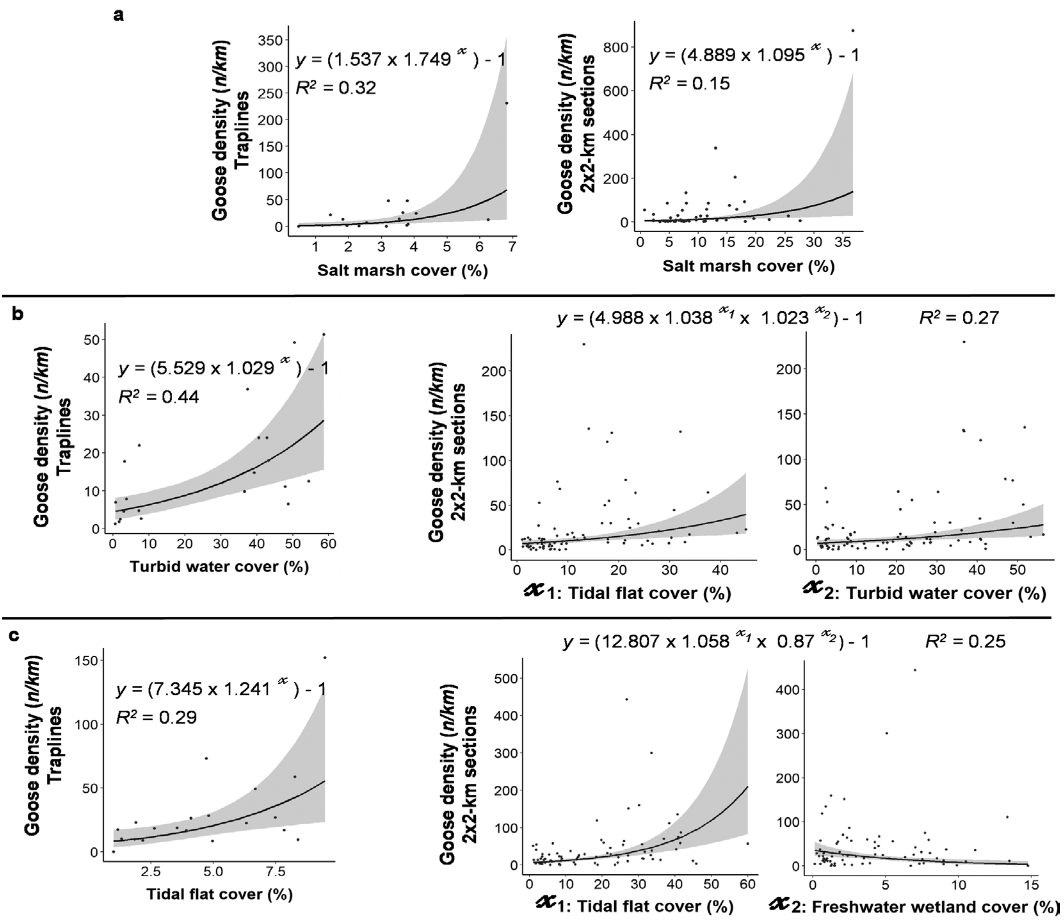

FIGURE 4. Relationships between habitat composition and the density of Canada Geese (*Branta canadensis*) in traplines and 2-km long sections surveyed on a. 13 May, b. 16 September, and c. 23 September 2018.

conditions prevailing during a late spring and in presence of very few juveniles during the fall migration. During both seasons, we saw the greatest concentrations of geese between Eastmain and Wemindji. Unfortunately, our coverage of the coast was incomplete, especially in traplines north of Chisasibi. Nevertheless, our surveys enabled us to highlight some associations between goose density and different coastal habitats.

In spring, the proportion of salt marshes in traplines and in 2-km long sections was the only significant predictor of Canada Goose density. While it explained little variation in goose density ($R^2 = 0.15$), this result is consistent with the observations of Curtis and Allen (1976) along the entire east coast and Reed *et al.* (1996) in the northeastern portion of the bay. The GPS tracking of temperate breeding geese has also shown that moult migrants used salt marshes when staging along the James Bay east coast in spring (Sorais *et al.* 2023). Reed *et al.* (1996) reported that Canada Geese consumed a wide variety of plants during their spring migration including Chaffy Sedge (*Carex paleacea* Schreber ex Wahlenberg), Needle Spikerush (*Eleocharis acicularis* (L.) Roemer & Schultes), Four-leaved Mare's Tail (*Hippuris tetraphylla* L. f.), and Marsh Arrowgrass (*Triglochin palustris* L.) found in salt marshes that are among the first habitats to become available after ice melt in May.

In fall, the greatest goose densities occurred in traplines and 2-km long sections that had a greater proportion of tidal flats and turbid water. The use by Canada Geese of tidal flats where vegetation wrack accumulates was also reported by Curtis and Allen (1976) and Reed *et al.* (1996). The latter suggested

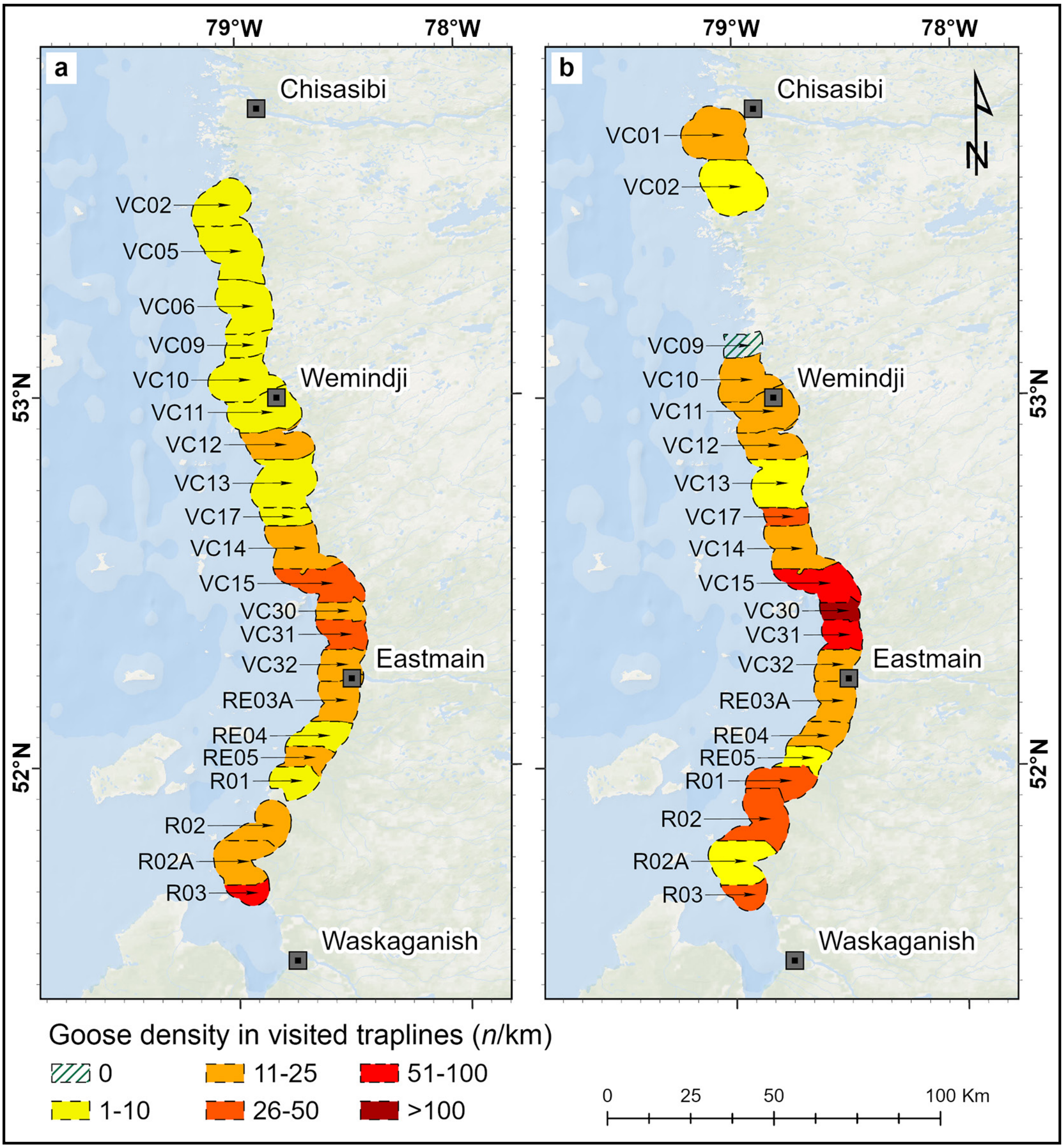

FIGURE 5. Canada Goose (*Branta canadensis*) density (number of geese/km of helicopter path) in surveyed traplines on a. 16 and b. 23 September 2018 along the James Bay east coast. Traplines surveyed are identified by their Cree Trappers' Association number.

that the presence of geese in tidal flats was likely due to their proximity to salt marshes where geese were feeding. The lower portions of salt marshes are dominated by Creeping Alkaligrass (*Puccinellia phryganodes* (Trinius) Scribner & Merrill; Dignard *et al.* 1991), a food item found in the stomach contents of geese examined by Reed *et al.* (1996). However, unlike in spring, we failed to find a relationship between goose density and the proportion of salt marshes in traplines or in 2-km long sections. This could suggest that tidal flats are currently used for resting more than for feeding during fall, thus reducing the importance of salt marshes.

The relationship between goose density in fall and turbid water is not obvious. While this habitat could be used by geese for resting, it may also support submerged vegetation that could not be detected by remote sensing due to murky water. Indeed, eelgrass has been observed by scuba divers at control points in the turbid water habitat (Clyne *et al.* 2024). However, we found no relationship between goose density and the proportion of traplines or 2-km long sections covered by clearly identified eelgrass beds. This contrasts with the observations of Curtis and Allen (1976) who reported extensive use of eelgrass by Canada Geese in fall in the early 1970s, which has been widely corroborated by Cree hunters (Ettinger *et al.* 1995; Peloquin and Berkes 2009; Dickey 2015; Idrobo *et al.* 2024). However, our results are consistent with those of Reed *et al.* (1996) who reported no eelgrass in stomach contents of Canada Geese sampled in the 1990s in northeastern James Bay.

We did not find any association between goose density and the tundra habitat that was previously reported to provide food resource, such as berries of blueberry (*Vaccinium* spp.) and Black Crowberry (*Empetrum nigrum* L.; Reed *et al.* 1996). Cree land users have reported a general decline of berry production in Eeyou Istchee in recent years (Idrobo *et al.* 2024). Moreover, 2018 may have been a year of particularly poor production due to the very late spring. Also, subarctic greening induced by climate warming has reduced the area covered by the tundra habitat (Olatunji 2022).

Finally, we were not expecting a negative relationship between goose density and the proportion of freshwater wetlands in 2-km long sections during the second fall survey because Sorais *et al.* (2023) found that moult migrants were commuting between inland freshwater wetlands and coastal habitats. However, it is possible that freshwater wetlands along the coastline, within 1 km on each side of the helicopter flight path, were more exposed and less suitable for resting and feeding than those further inland.

Conclusion

This study is a description of the distribution of Canada Geese during their spring and fall 2018 migration in Eastern James Bay. It is a reference point in the long-term monitoring of this waterfowl species in a region where and on which local communities strongly rely. Cree hunters of the coastal communities partially attribute their reduced Canada Goose harvest compared to the 1980s to the fact that short-necked geese modified their habitat use strategy (Idrobo *et al.* 2024). We wanted to better understand the relationship between goose distribution and the different habitats available along Eastern James Bay during spring and fall migration. However, we found that habitat composition only partly explains the density of Canada Geese along James Bay east coast. Moreover, because we could not explain the presence/absence of geese in traplines nor in 2-km long sections suggests that their distribution is driven by factors other than those we considered. Several land users suggested that the increasing presence of Bald Eagle (*Haliaeetus leucocephalus*) and increasing use of helicopters for travelling to hunting camps are disturbances that contribute to modifying the distribution of geese along James Bay east coast (Idrobo *et al.* 2024). Also, we did not consider how the distance from human settlements or hunting pressure could factor into explaining the presence/absence of geese along the coast. Finally, the increasing number of moult-migrant long-necked Canada Geese in this area since the 1980s (Giroux *et al.* 2022) could affect habitat use by short-necked geese. It is possible that when using habitats with a diversity of food resources during the fall migration, moult migrant temperate geese act as decoys and attract subarctic breeding geese to these habitats (Sorais *et al.* 2023). Tracking of individual subarctic breeding geese, as has occurred with temperate breeding geese (Sorais *et al.* 2023), would help to better understand the distribution and habitat use by Canada Geese along the James Bay east coast.

Author Contributions

Writing – Original Draft: M.S. and J.-F.G.; Writing – Review & Editing: M.P.-M., B.L., and A.L.; Conceptualization: J.-F.G. and M.P.-M.; Investigation: M.S., M.P.-M., B.L., and A.L.; Formal Analysis: M.S., A.L., and B.L.; Funding Acquisition: J.-F.G.

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SUPPLEMENTARY MATERIALS:

TABLE S1. List of Landsat-8 OLI optical images used as a function of the season to characterize habitat composition on the east coast of James Bay, Canada.

TABLE S2. List of the Sentinel-1 C-band imagery used as a function of the season, orbit, and polarization to characterize habitat composition on the east coast of James Bay, Canada.

FIGURE S1. Photo and satellite image of Common Eelgrass (*Zostera marina* L.).

FIGURE S2. Photo and satellite image of turbid water.

FIGURE S3. Photo and satellite image of shallow water.

FIGURE S4. Photo and satellite image of tidal flat.

FIGURE S5. Photo and satellite image of cobble beach.

FIGURE S6. Photo and satellite image of salt marsh.

FIGURE S7. Photo and satellite image of freshwater wetlands.

FIGURE S8. Photo and satellite image of tundra.

FIGURE S9. Photo and satellite image of deep water.

FIGURE S10. Photo and satellite image of peatland.

FIGURE S11. Coefficient of variation of Canada Goose (*Branta canadensis*) density (number of geese/km of helicopter path) calculated for increasing section length for each survey conducted in 2018 along the James Bay east coast.

The Canadian Field-Naturalist

Book Reviews

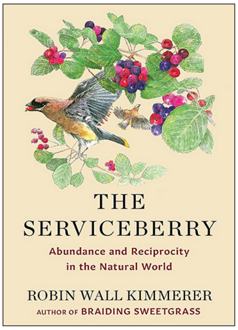
Book Review Editor's Note: The Canadian Field-Naturalist is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those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

The Serviceberry: Abundance and Reciprocity in the Natural World

By Robin Wall Kimmerer. Illustrations by John Burgoyne. 2024. Scribner. 128 pages, 25.00 CAD, Hardcover, 13.99 CAD, E-book. Also available as an Audiobook.



This is the eagerly anticipated third book by the author of *Braiding Sweetgrass* (Milkweed Editions, 2015) and *Gathering Moss* (Oregon State University Press, 2003). It is a treatise on reciprocal gift economies from the perspective of the author and an invitation to explore a mindset of gratitude and abundance instead of scarcity and competition. Serviceberries (*Amelanchier* spp.; other common names include shadbush, Saskatoon berry, juneberry, shadblow, sugarplum, and sarvis) serve as connecting threads in this exploration of how the current market economy contrasts with the reciprocal exchange evident in ecosystems. As a serviceberry tree distributes its wealth of berries to meet the needs of its natural community and in so doing ensures its own survival, a reciprocal gift economy provides wealth and security through the quality of its relationships. Expanding on some of the themes in *Braiding Sweetgrass*, this work more directly critiques the ills of capitalism and resource accumulation and advocates for "a kind of biomimicry to design systems of exchange which benefit human people and non-human people at the same time" (p. 73).

At 109 pages of body text and only 12.7 cm × 17.8 cm in size, with a relatively large font and widely spaced lines, this is a small book. You could finish reading it cover to cover, with some time to ponder, within a few rainy-day hours. In terms of aesthetics, nothing about this book is stark; for the hardcover version, the overall effect of the design choices is one of warmth, with deckle edges and an off-white linen finish and beautiful colour illustrations on the cover. Thematic black and white line illustrations also pepper the text and are lovely additions.

Kimmerer touches on various topics, including Little Free Libraries, YouTube tutorials, repair cafés, ecological economics, and rethinking Garrett Hardin's (1968) article in *Science,* "The Tragedy of the Commons". This book is a good jumping-off point for further reading and reflection. Key authors and theorists are mentioned in the text, making it easy to follow up on ideas or research areas that spark your interest. Those looking for the plant or essay-centred storytelling of the author's previous works will not find it here; instead, *The Serviceberry* is a call for reciprocity, community, gratitude, and acts of care both large and small. This little book would make an excellent gift, and when you are done reading it, pass it on to a friend.

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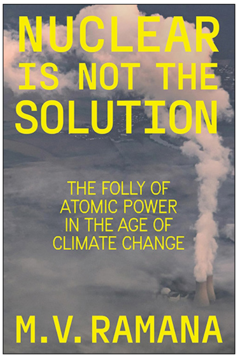
Conservation and Climate Change

COPOUT: How Governments Have Failed the People on Climate—an Insider's View of Climate Change Conferences, from Paris to Dubai

By Nick Breeze. 2024. Gemini Books. 240 pages, 22.99 CAD, Paper.

Nuclear is Not the Solution: the Folly of Atomic Power in the Age of Climate Change

By M.V. Ramana. 2024. Verso Books. 272 pages, 39.95 CAD, Hardcover, 11.99 CAD, E-book.



In two recent books addressing responses to climate change, readers learn about the unwieldly international policy process as well as technological options—in particular nuclear energy—that may or may not effectively mitigate the global crisis.

A COP, or Conference of the Parties, is an annual United Nations meeting on climate change with official and unofficial representatives from countries around the world. Author Nick Breeze attended eight COPs, beginning with the Paris Agreement event at COP 21 (in 2015) where 196 governments agreed on a baseline limit of 1.5°C global temperature rise above pre-industrial levels. His book, *COPOUT*, reviews the progress of those conferences. From COP to COP, there is a growing malaise as emissions increase faster than mitigation. An early focus on planting trees and carbon capture drawdown technologies was missing the mark (p. 248).

Breeze finds some courage among younger COP delegates. At COP 25 in Madrid, in 2019, he felt that the youth climate movement had won significant attention with projects like Fridays for Future and Extinction Rebellion. Yet, climate change as a conflict threat multiplier was being recognized by NATO (North Atlantic Treaty Organization) officials (pp. 190, 202). Breeze writes about double accounting by "dodgy" countries buying and selling authorized carbon offsets (pp. 107, 151–154). Indigenous peoples from the Marshall Islands and Samoa spoke about illnesses linked to climate change, but they were told that migration was the solution (p. 141).

The acceleration of planetary warming (Hansen *et al.* 2025) speeds the loss of both Greenland and Antarctic ice sheets and will result in a sea level rise of 65 m (Hansen *et al.* 2023). Just 10% of that rise would annually flood 630 million people, causing unthinkable levels of global conflict. But, despite a growing popular consensus, leaders are not behaving as if there is an emergency nor that tipping points are irreversible (pp. 172, 194).

Climate scientists like James Hansen are warning of biosphere collapse (p. 157). Breeze writes sparingly about biodiversity challenges. He mentions the Okavango Delta in northern Botswana, home to "elephant, lion, leopard, cheetah, buffalo, hippopotamus, crocodile and hundreds of species of birds", which is at-risk because of fossil fuel company deals with corrupt governments (p. 195). He also cites the destruction of the Great Barrier Reef (due to coral bleaching from ocean warming) on which a wide range of organisms depend (p. 245). The COP 28, where a record 100 000 participants gathered in the United Arab Emirates in 2023, was Breeze's last conference covered in *COPOUT*. That same year, 10 000 young Emperor Penguins perished in Antarctica because of melting sea ice, with the species expected to become extinct by the end of century (p. 242). Also in 2023, 150 000 km^2 of Canadian forests burned, releasing about 640 million tonnes of CO and CO_2, the equivalent of India's annual fossil fuel emissions (Byrne *et al.* 2024).

Breeze calls the Athabasca tar sands in northern Alberta (larger than the size of England) the "most destructive oil-extraction site on the planet", now producing over three million barrels of oil per day (p. 4). Breeze's prognosis is that until we halt supply, the COPs "will continue to be a charade" (p. 255).

He does a good job outlining the mitigation controversies. Solar Radiation Modification (SRM), or geoengineering, has critics and fans. Some critics demand continuing the "rapid, equitable transition to clean energy" and reject all SRM research (pp. 91–92), which they see as a conspiratorial diversion by fossil fuel interests. But the COP 27 Climate Overshoot Commission considered measures that address adaptation and CO_2 removal, including SRM. Breeze is skeptical about this "techno-optimism" pushed by what he calls a determined "geoclique" (pp. 230–231), and he worries whether SRM might change weather systems, disrupt the Indian monsoon, or thin the ozone layer (p. 236). Others are more optimistic.

A young Honduran insisted that research "might help save lives and infrastructure at home" and therefore must be scaled up. Failing to do so would be "nothing short of a human-rights violation" (p. 252). Paul Beckwith, a Canadian climate scientist who supports SRM research, thinks we must buy time because we will face abrupt change soon (p. 39). This will require authority and planning at the level of the United Nations Security Council (pp. 237–238). In a recent article, Hansen argues that "Humanmade climate forcings are already geoengineering the planet at an unprecedented, dangerous, rate" (Hansen *et al.* 2025).

The other controversial technology Breeze discusses is nuclear energy. Engineers like Mark Jacobson at Stanford University believe that 100% renewable energy will be ready in 25 years (Jacobson and Delucci 2009). For Breeze, this is a key argument for switching entirely to renewables, without nuclear. The claim, however, is much contested (p. 46). At COP 21 in Paris, a group of scientists, including Hansen, argued that no energy, transportation, and industrial transition was possible by 2050 without nuclear energy. Hansen believes we "now know how to burn the nuclear fuel in ways which are much safer, in ways where you cannot have the kinds of accidents you had at Fukushima" (p. 133).

In *Nuclear is Not the Solution*, M.V. Ramana would beg to differ. He makes four core arguments against nuclear power: high cost and slow build time, weapons proliferation risk, contamination risk, and the spent fuel disposal problem. Early in the book, he says: "Although climate change scares me, I am even more scared of a future with more nuclear plants" (p. 2). While his book reiterates the standard complaints about nuclear power, it is framed in the context of addressing the climate crisis. Nuclear power plants emit almost no greenhouse gases while operating, and through their full life cycle they currently emit a third of the CO_2 as does solar energy (Jawerth 2020).

Accidents

A familiar quarrel with nuclear power is the possibility of Chernobyl-type reactor accidents. As *Nuclear is Not the Solution* makes clear, there continue to be disagreements over the number of casualties caused by severe radiation contamination and exposure. Japanese officials dispute whether increased cases of thyroid cancers can be attributed to the nuclear accident in Fukushima, claiming that overdiagnosis would explain them (p. 19). The immensity of the disaster—an earthquake and then a tsunami wiping out reactors, the release of radioactive contaminants, and the evacuation of 150 000 people—is not at issue (pp. 21–23). About 22 000 people died, almost all from the tsunami, but also some from suicide, stress, and medical care disruptions. Ramana mocks the International Atomic Energy Agency (IAEA) claim that "no one died from radiation at Fukushima" (p. 40).

The debate is mostly over future deaths from low-level radiation exposure. Ramana defends the widely supported Linear-Non-Threshold (LNT) hypothesis that asserts there is no level of exposure below which radiation is harmless (let alone beneficial). Using official estimates from the Committee on the Biological Effects of Ionizing Radiation (BEIR), 'up to' 1800 people could eventually die from Fukushima radiation effects (p. 42). However, there are credible challenges to the LNT hypothesis (Tubiana *et al.* 2009; Cardarelli and Ulsh 2018; Calabrese 2022; Calabrese *et al.* 2022). According to the Canadian Nuclear Safety Commission, "there is little scientific evidence of adverse health effects from radiation doses below 100 millisieverts (mSv)" (CNSC 2013). For comparison, the global average dose from natural background radiation is ~2.4 mSv a year; a computed tomography (CT) scan dose is about 7 mSv (CNSC 2023). This contest within the scientific literature is not mentioned by Ramana. With apparent certainty he writes that "since radiation, even at very low levels, is harmful to people, the expansion of nuclear energy will necessarily result in increased risk to public health and the environment" (p. 20).

The effects of the explosion or meltdown of a nuclear power reactor need to be compared to failings of other technologies, such as fossil fuel pollution or hydroelectric dam destruction. For example, the destruction of the Kakhovka Dam in Ukraine in 2023 caused the deaths of 59 people, thousands were evacuated, and widespread flooding occurred (BBC 2023; EOS Data Analytics 2024).

The worst nuclear power contamination accident was at the Chernobyl plant in Ukraine in 1986, and Ramana spends significant time on this subject. Experts generally agree that the frequency of childhood thyroid cancers increased, but Ramana challenges those who defend the lower casualty estimates, what he sees as a "mismatch between reality and wishful thinking—or perhaps even deliberate lying" (p. 20; IAEA 2006). The Chernobyl Forum "soberly" listed 50 emergency workers as having died at the accident scene, 4000 young people contracting thyroid cancer (15 of whom died), and that 4000 probable deaths may "eventually be attributable to the Chernobyl accident", although there is uncertainty (IAEA 2008: 4, 134–140). Ramana claims that "nuclear energy advocates assert that future accidents are impossible" (p. 20), but this seems like a generalization.

Energy choices must be made by evaluating which options will provide the required baseload and stored power capacity, in time, given our pressing climate obligations. Here Ramana reveals his preference for continued use of oil and gas-fired power plants over nuclear to cover peak electricity demand (p. 237). The nuclear energy renaissance, the existence of which he appears to doubt (pp. 62–67), may not need to be part of the energy mix in the future. But Ramana also thinks it "inappropriate" to keep existing plants running (pp. 15, 74–80).

Economics

In two of his five chapters, Ramana delves into the political economy of nuclear power. He usefully outlines the significant institutional connectedness between various nuclear streams (power, weapons, research, and medicine; pp. 170–193). The book doesn't explore whether energy nationalization could address the private profit and public subsidy problems raised by Ramana (pp. 143–149), who sees nuclear energy subsidies as "corporate welfare" (p. 144). He doesn't dwell on similar subsidies going to competing sustainable energy companies, a concern raised by Hansen *et al.* (2025). Left-libertarian Noam Chomsky is quoted twice, including regarding the problem of "socialization of cost and risk, privatization of profits" (p. 154). Chomsky is not speaking specifically of nuclear power where he is mentioned. When Chomsky has reflected on it (elsewhere), he has deferred to Hansen or offered tentative support for nuclear energy in the context of climate change until renewable substitutes can be depended on. Chomsky is clear he doesn't think the nuclear option can be foreclosed just yet (McNeill 2014; YouTube 2015: 25:59 min; Chomsky and Pollin 2020; Roberts 2020).

Weapons Proliferation

"Nuclear energy does have one virtue … its innate and inseparable connection to nuclear weapons" (p. 7). As a member of the Canadian Pugwash Group (as is the author of this review), Ramana's credentials in support of nuclear weapon abolition are not in question (Ramana 2024). But *Nuclear is Not the Solution* highlights only interdependence between power generation and weapons production. It also portrays as disingenuous those who emphasize their dissimilarities (p. 168). What is missed is that states wishing to produce a nuclear weapon do not require power generating reactors to do it. There are two sources of weapons-usable fissile material: plutonium produced in any reactor (there currently exist 227 operational non-power research reactors in 54 countries; IAEA 2025); or highly enriched uranium (HEU), which can be produced using (most commonly) centrifuges. Both plutonium and HEU production facilities can be concealed, but by engaging with IAEA oversight and safeguards, it becomes more difficult to build nuclear weapons clandestinely (Rockwood 2013). This important argument is not addressed in Ramana's book. It should also be acknowledged that a government determined to build bombs will likely find a way, with or without a nuclear power plant, as history has shown.

Nuclear Waste

Nuclear is Not the Solution is skeptical of deep burial of radioactive waste—material that needs to be sequestered for hundreds of thousands of years, long after current governments and states have come and gone. Even the most stable geological formations are potentially subject to distant-future seismic disruptions, vessel corrosion, and leakage, although burial sites are engineered to sit far below the water table. As Ramana points out, the other options available (securing spent fuel at the surface, reprocessing, or burning plutonium in reactors) also have risks. While discounting deep burial projects in progress in Finland, Sweden, and Canada (pp. 54–55), he does not appear to have an alternative proposal, even if all nuclear power plants were shut down. This seems a case of the perfect solution being the enemy of a good one.

Ramana is right that advocates of nuclear power want to settle the burial question, make nuclear cost-effective, and disentangle the technology from the legacy of the 1945 atomic bombs. This is particularly the case now, given the revival of power plant construction. As Hansen and co-authors have written:

> The world is finally beginning to realize that nuclear power is needed to address climate change. At the United Nations COP 29 meeting in Baku, 31 nations, including the United States, pledged to work together toward tripling nuclear power capacity by 2050. (Hansen *et al.* 2025: 39)

There may have been a time when non-nuclear sustainable energy options alone could have entirely displaced fossil fuels. But because we sit a scant few years from climate tipping points, this position is now less compelling (Hansen *et al.* 2023, 2025). *Nuclear is Not the Solution* provides a strong and polemical judgement against nuclear power. My caveats above notwithstanding, it is a concise primer, uses non-technical language, and is worth reading together with other viewpoints. The question remains though: if nuclear energy is not the (ultimate) solution to the climate crisis, might it still be a necessary part of it?

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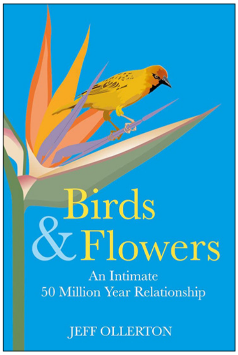
ORNITHOLOGY

Birds and Flowers: an Intimate 50 Million Year Relationship

By Jeff Ollerton. 2024. Pelagic Publishing. 336 pages and 28 colour illustrations, 39.00 CAD, Hardcover, 25.99 CAD, E-book.



While hummingbirds are the most recognized bird family to visit flowers for nectar or insects (at least in the Western Hemisphere), they are just a fraction of the avian species that do so: researchers have documented at least 1390 species (or 12.5% of known bird species) that visit flowers in ways that suggest they might be pollinators (p. 20). The list includes parrots, pigeons, doves, warblers, and even woodpeckers. Sunbirds are common pollinators in Asia, Africa, and Australia, but for no obvious reason, bird pollination of native plants in Europe is rare. Scientist and author Jeff Ollerton estimates that about 20 000 plant species (or 6 to 7% of known plant species) are likely to be bird-pollinated, wholly or in part (p. 46). In *Birds and Flowers*, he touches on three themes: the evolution and subsequent diversification of the bird–flower relationship, the details and intricacies of the ecology of these interactions, and how humans have influenced these interactions.

As suggested in the book's subtitle, the relationship between birds and flowers goes back at least 50 million years. Nectar feeding (nectarivory) evolved at least three times, while flower pollination as an outcome of that lifestyle has evolved in different species much more frequently. Ollerton is particularly interested in the question of how effective some of the non-specialist nectar-feeding birds are at depositing pollen on the stigma of specific plants. If that doesn't happen, then they are just nectar robbers. Observation alone can't always confirm whether pollination occurs when a bird visits a plant. More recent experiments involve covering flowers with netting to only allow certain flowers to be visited, counting the pollen grains before and after each visit, and then counting the seeds that are produced. This provides confirmation of pollination but is very time-consuming and done for very few species.

Ollerton describes collaborating with bird banders to collect pollen from the beaks of birds. In 2019 I was a volunteer bander at Un poco del Chocó, a private nature reserve in Ecuador. One of our projects was capturing hummingbirds for a graduate student, who used a gel syringe to collect pollen from beaks and feathers and spread it on a microscope slide. Back in the lab, she identified the pollen grains to species, a step towards understanding the bird–flower relationship in that area.

Researchers have identified some general characteristics of bird-pollinated flowers: they are often red, orange, magenta, or rose-coloured; they often have larger amounts of more dilute nectar than insect-pollinated flowers; and their sexual parts usually extend farther beyond the mouth of the flower tube, leaving no place for insects to land. But Ollerton questions whether an over-reliance on this set of flower traits (a pollination syndrome) results in a partial and/or oversimplified understanding of flower evolution, thus missing out on important aspects of this ecological relationship.

While we tend to assume that it is the preferences of pollinators that apply evolutionary pressure on flowers to look a certain way and provide certain rewards, the author points out that plants are not passive in this relationship: "they possess behaviours that can manipulate their floral guests in ways that are more advantageous for plant than animal" (p. 92). Interactions between pollinators and their flowers can also vary geographically and over time. A flower's lifespan is negatively correlated with the rate of visitation by pollinators—ones that are infrequently visited must stay open longer. More specialisation (e.g., one species of hummingbird pollinating one species of flower) occurs when there are lots of resources, but generalisation occurs when resources are scarce.

Ollerton looks at the human connection to the birds and flowers relationship in a few ways. He chronicles ancient and Indigenous peoples' representation of bird–flower interactions in pottery, paintings, and stories, and later European explorers' colonial observations and writings. Pollinators enhance the health of human populations by increasing crop production, but on a global scale birds play a minor role in the pollination of food plants. However, at a local scale, and for wild plants that are harvested, birds can play a very important role. In the final two chapters, Ollerton discusses conservation challenges facing pollinating birds (about 15% of hummingbird species are declining in population or distribution [p. 223]) and highlights a few success stories.

There are 19 relatively short chapters in *Birds and Flowers*. Some have provocative and attention-grabbing titles, such as Hitchhikers, Drunks and Killers

(Chapter 10), and Bad Birds and Feral Flowers (Chapter 17). There is an appendix of common and scientific names of species mentioned in the book and 38 pages of references by chapter.

This book stimulates the reader to consider more than superficial relationships in the natural world, to look below the surface of our observations. As Ollerton says, there are “more questions than birds, more puzzles than plants” (p. 245).

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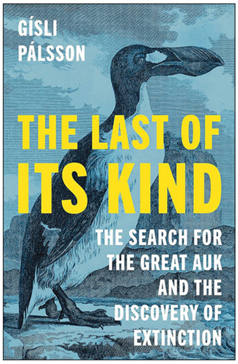
The Last of its Kind: the Search for the Great Auk and the Discovery of Extinction

By Gísli Pálsson. 2024. Princeton University Press. 328 pages, 16 colour illustrations, and 37 black and white illustrations, 38.00 CAD, Hardcover, 31.99 CAD, E-book.



The author of *The Last of its Kind* is not an ornithologist, although he collected bird eggs as a youth. As a result, this is a book primarily about the people of Pálsson's native Iceland, the locals who hunted Great Auk (*Pinguinus impennis*), and the foreigners who came looking for the birds. Pálsson conducted anthropological research in the mainland village nearest to Eldey, a small island off the southwest coast of Iceland where the last Great Auks were hunted in the 1840s. To be fair, because Great Auk lived most of the year at sea and only came ashore briefly to breed on inaccessible and often remote islands, little is known about its biology.

The main thread of the book is an 1858 expedition to Iceland, undertaken by English scientists John Wolley and Alfred Newton, in search of Great Auk. Wolley came from the Victorian tradition of studying medicine but became a naturalist rather than a doctor. He was an avid and experienced oologist with a collection of over 10 000 eggs … but no egg of Great Auk. Newton was a zoologist who studied at Cambridge University and later became a prominent professor there.

Wolley and Newton chose Eldey as their destination because it was more accessible than other known breeding sites in Iceland and Newfoundland. They hired locals who had hunted Great Auks previously to help them achieve their goals, which were to observe breeding behaviour and collect birds and eggs. Icelanders had always hunted seabirds and their eggs for food, but from the mid-1700s onwards hunting supplied the feather market, and skins and bones were also sold to public museums and private collectors. Similarly, the population breeding on Funk Island, off the northeast coast of Newfoundland, was hunted for food and later feathers, which led to its extermination.

The plan was to get to Eldey for the breeding season at the end of May. But the waters around Eldey are treacherous, and 1858 was marked by particularly harsh weather, including a cold and stormy spring. While waiting for calm weather, Wolley and Newton, with the help of an interpreter, undertook extensive interviews with any locals who had knowledge of Great Auks. Wolley compiled five handwritten notebooks, the Gare-Fowl Books (which were never published), written in English, Icelandic, Danish, and German. ('Gare-fowl' was an antiquated English name for Great Auk, which was called *geirfugl* in Icelandic.) In a sense, they became anthropologists, recording everything told to them, not just information related to the birds. Meanwhile, the man they had contracted to collect birds and eggs at another breeding island in southeast Iceland did not find any evidence of living Great Auks, only butchered bones. By mid-July, it was obvious they had missed the breeding season and any hope of seeing Great Auks. They returned to England, not knowing if Great Auk was extinct.

The default explanation suggested when a species has gone missing from a known location is usually that it has gone somewhere else for unknown reasons. That is no different today than it was in the 18th century. There was no mention of the possibility that Great Auk was extinct in the Gare-Fowl Books, but in 1861 Newton (Wolley had died unexpectedly in 1859 of a brain infection) refers to "the last Gare-fowls known to have occurred in Iceland" in a paper in the journal *Ibis* (p. 157; for the article, see Newton 1861). The concept of the extinction of a species had been established in the early 1800s through the study of fossilized bones; Newton added the concept of unnatural extinction, "the loss of a species as a result of human activities" (p. 4), which was "a phenomenon to be subjected to scientific inquiry and political action" (p. 181). Wolley had stressed how important it was to document the relative abundance of a species, which was a new idea at the time and critical to determining whether a species was on its way to extinction.

While emphasizing Newton's achievements in conservation (e.g., enacting game laws in England, including a restriction on hunting seabirds during the breeding season), Pálsson points out Newton's hypocrisy: his purpose in going to Iceland was to procure the skins and eggs of Greak Auks for his personal collection. And even after lobbying for new game laws, he continued to collect birds during the breeding season.

This book tells an interesting story of the individuals who contributed to changing ideas about animal populations and extinction, but I found it difficult to read. Pálsson casts a wide net in his research and appears to have wanted to include most of it in this book, whether directly relevant or not. One example is in Chapter 4 (Arriving), where the author makes a two-and-a-half-page digression into how aquariums came into use in the 1850s, with no connection to Great Auk or the central characters of the book. The author frequently skips back and forth in chronology, an example being his description of Wolley and Newton riding out of Reykjavík, followed by pages of detail about Newton's role in enacting game laws a decade later. Readers that persevere will gain a better understanding of the extinction of a species. The book will also appeal to readers interested in Icelandic history.

The Last of its Kind has a 22-page Bibliography and 15 pages of Notes by chapter, if the reader wants to dig deeper into any of Pálsson's topics. There is also a three-page timeline that starts in 1534 with Jacques Cartier's report of slaughtering many Great Auks for food at Funk Island. Estimates put the population there at over 100 000 breeding pairs at its peak (Montevecchi and Kirk 2020). The last living Great Auk may have been seen off Newfoundland in 1852.

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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

Principles of Animal Behavior. Fifth Edition. By Lee Alan Dugatkin. 2025. University of Chicago Press. 576 pages, 526 colour plates, and 40 halftones, 102.00 USD, Paper. Also available as an E-book.

Seven Challenges for the Science of Animal Minds. By Mike Dacey. 2025. Oxford University Press. 256 pages, 100.00 USD, Hardcover. Also available as an E-book.

Symbiosis: a Very Short Introduction. Very Short Introductions Series. By Nancy A. Moran. 2025. Oxford University Press. 192 pages, 16.95 CAD, Paper, 6.99 CAD, E-book.

BOTANY

Cannabis: a Natural History. By Rob DeSalle. Illustrations by Patricia J. Wynne. 2025. Yale University Press. 352 pages and 76 black and white illustrations, 42.50 CAD, Hardcover.

In the Circle of Ancient Trees: Our Oldest Trees and the Stories They Tell. By Valerie Trouet. Illustrations by Blaze Cyan. 2025. Greystone Books. 224 pages, 42.00 CAD, Hardcover.

Field Guide to the Grasses of Oregon and Washington. Second Edition. By Cindy Talbott Roché, Richard E. Brainerd, Barbara L. Wilson, Nick Otting, and Robert C. Korfhage. 2025. Oregon State University Press. 496 pages, colour photos, illustrations, and maps, 45.00 USD, Paper.

The Genius of Trees: How They Mastered the Elements and Shaped the World. By Harriet Rix. 2025. Knopf Canada. 304 pages, 36.00 CAD, Hardcover, 16.99 CAD, E-book.

Moss Safari: Exploring the Secret Life in Moss. By Andrew Chandler-Grevatt. 2025. Pelagic Publishing. 192 pages and colour illustrations, 47.00 CAD, Paper, 40.99 CAD, E-book.

Mosses, Liverworts, and Hornworts of the World: a Guide to Every Order. By Joanna Wilbraham. 2025. Princeton University Press. 240 pages, 44.00 CAD, Hardcover. Also available as an E-book.

The Princeton Field Guide to Mesozoic Plants. By Nan Crystal Arens. Illustrations by Julius Csotonyl, Sante Mazzei, and Shuyu Hsu. 2025. Princeton University Press. 208 pages, 48.00 CAD, Hardcover. Also available as an E-book.

Silm Da'axk / to Revive and Heal Again: Historical Ecology and Ethnobotany in Laxyuubm Gitselasu. By Chelsey Geralda Armstrong. 2025. Athabasca University Press. Distributed by University of Chicago Press. 376 pages and 80 colour plates, 49.99 CAD, Paper.

Tree Day: a Story of 24 Hours and 24 Arboreal Lives. By Meg Lowman. Illustrations by Thibaud Hérem. 2025. University of Chicago Press. 160 pages and 48 halftones, 18.00 USD, Hardcover. Also available as an E-book.

Vanishing Landscapes: the Story of Plants and How We Lost Them. By Bonnie Lander Johnson. 2025. Hodder & Stoughton. 320 pages, 22.00 GBP, Paper. Also available as an E-book.

World Atlas of Freshwater Macrophytes: Dicotyledonous Species II (Molluginaceae–Tetrachondraceae)—Volume 2. Wetlands: Ecology, Conservation and Management Series (Volume 11). By Tatiana Lobato-de Magalhães, Kevin Murphy, Marinus L. Otte, and Eugenio Molina-Navarro. 2025. Springer Nature. 872 pages, colour illustrations, and black and white illustrations, 321.50 CAD, Hardcover.

CONSERVATION AND CLIMATE CHANGE

†Arctic Passages: Ice, Exploration, and the Battle for Power at the Top of the World. By Kieran Mulvaney. 2025. Island Press. 200 pages, 37.95 CAD, Hardcover.

†The Beaver Manifesto: Conservation, Conflict, and the Future of Wetlands. Edition, Revised and Updated. By Glynnis Hood. 2025. Rocky Mountain Books (RMB). 152 pages, 20.00 CAD, Paper.

Black Gold: the Rise, Reign, and Fall of American Coal. By Bob Wyss. 2025. University of California Press. 312 pages, 36.95 CAD, Hardcover.

The Cinema of Extractions: Film Materials and Their Forms. By Brian Jacobson. 2025. Columbia University Press. 240 pages, 156.00 CAD, Hardcover, 39.00 CAD, Paper. Also available as an E-book.

A Climate of Truth: Why We Need It and How to Get It. By Mike Berners-Lee. 2025. Cambridge University Press. 386 pages, 22.95 CAD, Paper. Also available as an E-book.

Conservation Confidential: a Biologist Investigates the Clash Between Progress and Nature. By Lorne Fitch. 2025. Rocky Mountain Books (RMB). 320 pages, 25.00 CAD, Paper.

Drifting North: Finding the Future in Scotland's Past. By Dominic Hinde. 2025. Manchester University Press. 256 pages, 39.99 CAD, Hardcover.

How to Save the Amazon: a Journalist's Fatal Quest for Answers. By Dom Phillips. 2025. Chelsea Green. 304 pages, 37.95 CAD, Hardcover, 30.99 CAD, E-book.

Just Earth: How a Fairer World Will Save the Planet. By Tony Juniper. 2025. Bloomsbury USA. 368 pages, 37.00 CAD, Hardcover, 20.99 CAD, E-book.

The Lobster Trap: the Global Fight for a Seafood on the Brink. By Greg Mercer. 2025. McClelland & Stewart. 320 pages, 36.99 CAD, Hardcover, 16.99 CAD, E-book.

Ocean: Earth's Last Wilderness. By David Attenborough and Colin Butfield. 2025. Grand Central Publishing. 400 pages, 45.00 CAD, Hardcover, 19.99 CAD, E-book.

A Reverence for Rivers: Imagining an Ethic for Running Waters. By Kurt D. Fausch. Illustrations by Nora Sherwood. 2025. Oregon State University Press. 290 pages, 12 black and white illustrations, and 13 black and white figures, 30.95 CAD, Paper.

Riverine Dreams: Away to the Glorious and Forgotten Grassland Rivers of America. By George Frazier. 2025. University of Chicago Press. 296 pages and 24 halftones, 26.00 USD, Hardcover. Also available as an E-book.

Saving the Big Sky: a Chronicle of Land Conservation in Montana. By Bruce A. Bugbee, Robert J. Kiesling, and John B. Wright. Contributions by the Confederated Salish and Kootenai Tribes, Shane Doyle (Apsáalooke), Steve Running, and Todd Wilkinson. Photography by Kevin League. 2025. Oregon State University Press. 240 pages, 94 colour photos, and 30 colour maps, 61.95, CAD, Hardcover.

Undammed: Freeing Rivers and Bringing Communities to Life. By Tara Lohan. 2025. Island Press. 288 pages, 41.95 CAD, Hardcover.

A Variability Quantifier. By Liam Gillick. Edited by Josée Drouin Brisebois, Liam Gillick, Nicolaus Schafhausen, and Claire Shea. 2025. Sternberg Press, in association with Fogo Island Arts and National Gallery of Canada. 200 pages and 100 colour illustrations, 37.99 CAD, Paper.

Waters of Life: Fighting for Scotland's Beavers. By Tom Bowser. 2025. Birlinn Limited. 272 pages, 24.99 CAD, Paper.

ECOLOGY

†Beyond Equilibria: Historical Approaches to Ecology and Evolution. Oxford Series in Ecology and Evolution. By Hamish G. Spencer. 2025. Oxford University Press. 160 pages, 115.00 USD, Hardcover, 45.00 USD, Paper. Also available as an E-book.

†The Ecology and Evolution of Invasive Populations. By Ben Phillips. 2025. Oxford University Press. 288 pages and 76 figures, 135.00 USD, Hardcover, 50.00 USD, Paper. Also available as an E-book.

Field Ecology: Concepts, Issues and Practice. By Michael Mühlenberg and Thomas Waßmer. 2025. Springer Nature. 798 pages, 323 colour illustrations, and 57 black and white illustrations, 217.95 CAD, Hardcover.

Indigenous Critical Reflections on Traditional Ecological Knowledge. By Lara A. Jacobs. 2025. Oregon State University Press. 440 pages and 21 black and white photos, 51.50 CAD, Hardcover.

†Mysterious Ways: Contingency, Emergence, and Selection in Nature. By Jonathan D. Phillips. 2025. Oxford University Press. 416 pages, 39.99 USD, Hardcover. Also available as an E-book.

ENTOMOLOGY

Butterflies of the World: a Guide to Every Subfamily. A Guide to Every Family Series. By Blanca Huertas and Shinichi Nakahara. 2025. Princeton University Press. 240 pages, 44.00 CAD, Hardcover. Also available as an E-book.

Dragonflies and Damselflies of the World: a Guide to Their Diversity. A Guide to Every Family Series. By Klaas-Douwe B. Dijkstra. 2025. Princeton University Press. 256 pages and 250 colour illustrations, 44.00 CAD, Hardcover. Also available as an E-book.

Insect Architecture: How Insects Build, Engineer, and Shape Their World. By Michael S. Engel and Tom Jackson. 2025. Princeton University Press. 176 pages and 150 colour illustrations, 41.00 CAD, Hardcover.

Insect Ecomorphology: Linking Functional Insect Morphology to Ecology and Evolution. Edited by Oliver Betz. 2025. Academic Press. 586 pages, 296.50 CAD, Paper. Also available as an E-book.

Insectopolis: a Natural History. By Peter Kuper. 2025. W.W. Norton. 256 pages and colour illustrations, 47.00 CAD, Hardcover, 35.99 CAD, E-book.

HERPETOLOGY

The Book of Frogs: a Life-Size Guide to Six Hundred Species from around the World. Second Edition. By Mark O'Shea and Tim Halliday. 2025. University of Chicago Press. 656 pages and 1230 colour plates, 60.00 USD, Hardcover. Also available as an E-book.

ORNITHOLOGY

Bird Photographer of the Year: Collection 10. Edited by Bird Photographer of the Year Limited. 2025. Princeton University Press. 256 pages, 54.00 CAD, Hardcover. Also available as an E-book.

Birds of the Great Lakes. Best Little Books of Birds Series. By Dexter Patterson. 2025. Timber Press. 360 pages, 24.99 CAD, Paper, 15.99 CAD, E-book.

Field Guide to the Birds of North America. By Miles McMullen. 2025. Pelagic Publishing. 372 pages and colour illustrations, 39.99 CAD, Paper, 34.99 CAD, E-book.

A Field Guide to Birds of Ontario. By Mark Peck and Emily Rondel. 2025. Royal Ontario Museum Press. 512 pages, 29.99 CAD, Paper.

New Brunswick Birds: a Field Guide. Second Edition. By Jeffrey C. Domm. 2025. Formac Publishing Company Limited. 224 pages, 27.95 CAD, Paper.

The Physics of Birds and Birding: the Sounds, Colors and Movements of Birds, and Our Tools for Watching Them. By Michael Hurben. 2025. Pelagic Publishing. 240 pages and colour illustrations, 55.00 CAD, Paper. Also available as an E-book.

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ZOOLOGY

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Hidden Wonders: New Species and Rediscoveries in an Age of Extinction. By David Alderton. 2025. Skyhorse Publishing. 288 pages, 44.99 CAD, Hardcover. Also available as an E-book.

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Whale: the Illustrated Biography. By Asha de Vos. Illustrations by Adam Hook. 2025. Princeton University Press. 224 pages and 100 colour illustrations, 41.00 CAD, Hardcover. Also available as an E-book.

OTHER

Best American Science and Nature Writing 2025. Edited by Susan Orlean. 2025. HarperCollins. 272 pages, 23.99 CAD, Paper, 11.99 CAD, E-book.

The Botanic Age: Planting the Seeds of Human Evolution. By Dean Falk. 2025. University of Toronto Press. 272 pages, 29.95 CAD, Hardcover. Also available as an E-book.

†**The Canadian Rockies: Rediscovered.** By Paul Zizka. 2025. Rocky Mountain Books (RMB). 240 pages, 40.00 CAD, Paper.

Foreign Fruit: a Personal History of the Orange. By Katie Goh. 2025. Penguin Canada. 240 pages, 26.95 CAD, Paper, 14.99 CAD, E-book.

Funga Obscura: Photo Journeys among Fungi. By Alison Pouliot. 2025. University of Chicago Press. 192 pages and 122 colour plates, 28.00 USD, Hardcover. Also available as an E-book.

Ghosts Behind Glass: Encountering Extinction in Museums. By Dolly Jørgensen. 2025. University of Chicago Press. 320 pages and 80 colour plates, 149.50 CAD, Hardcover, 26.00 CAD, Paper. Also available as an E-book.

Listening to Beauty: Rhetorics of Science in Sea and Sound. By Megan Poole. 2025. University of Chicago Press. 208 pages, 115.00 USD, Hardcover, 30.00 USD, Paper. Also available as an E-book.

Mythopedia: a Brief Compendium of Natural History Lore. Pedia Books. By Adrienne Mayor. Illustrations by Michele M. Angel. 2025. Princeton University Press. 216 pages and 50 black and white illustrations, 24.99 CAD, Hardcover. Also available as an E-book.

Raising Hare: a Memoir. By Chloe Dalton. 2025. Pantheon. 304 pages, 36.95 CAD, Hardcover, 18.49 CAD, E-book.

A Season in the Okanagan. By Bill Arnott. 2025. Rocky Mountain Books (RMB). 216 pages, 20.00 CAD, Paper.

Of Slash Pines and Manatees: a Highly Selective Field Guide to My Suburban Wilderness. By Andrew Furman. 2025. University Press of Florida. 224 pages, 34.95 CAD, Paper.

Theory of Water: Nishnaabe Maps to the Times Ahead. By Leanne Betasamosake Simpson. 2025. Knopf Canada. 224 pages, 35.00 CAD, Hardcover, 16.99 CAD, E-book.

Waterfalls of Newfoundland and Labrador: a Guide. By Steve Faulkner. 2025. Goose Lane Editions. 296 pages, 29.95 CAD, Paper.

The Whispers of Rock: the Stories that Stone Tells about Our World and Our Lives. By Dr. Anjana Khatwa. 2025. Basic Books. 336 pages, 40.00 CAD, Hardcover, 24.99 CAD, E-book.

Wild Land: a Journey into the Earth's Last Wilds. By Peter Pickford and Beverly Pickford. 2025. W.W. Norton. 400 pages, 60.00 CAD, Hardcover.

Wild Ocean: a Journey to the Earth's Last Wild Coasts. By Peter Pickford and Beverly Pickford. 2025. W.W. Norton. 400 pages, 86.00 CAD, Hardcover.

Wildlife in the Natural Garden: a Journey of Discovery. By Heiko K. Voss. 2025. Springer Nature. 215 pages and colour photos, 48.50 CAD, Hardcover.

Wolverine Tracks: on the Trail of Memory and Meaning in the Wild. By Dag O. Hessen. Translated by Lucy Moffatt. 2025. Greystone Books. 272 pages, 39.95 CAD, Hardcover.

The Canadian Field-Naturalist

News and Comment

Compiled by Amanda E. Martin

Upcoming Meetings and Workshops

International Urban Wildlife Conference

The International Urban Wildlife Conference to be held 1–5 June 2025 at the Crown Plaza Atlanta–Midtown, Atlanta, Georgia. Registration is currently open. The theme of the conference is: 'Urban Reflections: What We've Learned About Nature, Our Communities and Ourselves'. More information is available at https://www.urban-wildlife.org/.

Annual Conference on Great Lakes Research

The 68th Annual Conference on Great Lakes Research to be held 2–6 June 2025 as a hybrid event, with online content and an in-person meeting at the Baird Center, Milwaukee, Michigan. The theme of the conference is: 'Creating Great Lakes Resilience'. Registration is currently open. More information is available at https://iaglr.org/iaglr2025/.

International Conference on Fish Telemetry

The 7th International Conference on Fish Telemetry, hosted by the Great Lakes Acoustic Telemetry Observation System, to be held 8–13 June 2025 at the Park Place Hotel and Conference Center, Traverse City, Michigan. The theme of the conference is: 'Unraveling the Mysteries of Fish to Inform Management and Conservation Decisions'. Registration is currently open. More information is available at https://event.fourwaves.com/7thicft/pages.

Canadian Botanical Association Annual Meeting

The annual meeting of the Canadian Botanical Association/L'Association Botanique du Canada to be held 10–14 June 2025 at Memorial University of Newfoundland, St. John's, Newfoundland. The theme of the conference is: 'Botany on the Rock for Conservation and Sustainability'. Registration is currently open. More information is available at https://www.cba-abc.ca/annual-meetings/.

Wilson Ornithological Society 2025 Meeting

The Wilson Ornithological Society 2025 Meeting to be held 23–25 June 2025 at Loyola Marymount University, Los Angeles, California. Registration is currently open. More information is available at https://wos2025.org/.

American Society of Mammalogists Annual Meeting

The 104th annual meeting of the American Society of Mammalogists to be held 27 June–1 July 2025 at Purdue University, West Lafayette, Indiana. Registration is currently open. More information is available at https://mammalmeetings.org/.

Canadian Society for Ecology and Evolution Annual Conference

The annual conference of the Canadian Society for Ecology and Evolution to be held 6–9 July 2025 at the Delta Hotel Sherbrooke Conference Centre, Sherbrooke, Quebec. Registration is currently open. More information is available at https://event.fourwaves.com/scee2025/pages.

Society of Wetland Scientists Annual Meeting

The annual meeting of the Society of Wetland Scientists to be held 15–18 July 2025 at the Rhode Island Convention Center, Providence, Rhode Island. Registration is currently open. More information is available at https://members.sws.org/event-calendar/Details/2025-sws-annual-meeting-1256452?sourceTypeId=Hub.

Mothapalooza

Mothapalooza to be held 18–20 July 2025 at the Highlands Nature Sanctuary, Bainbridge, Ohio. Registration is currently open. More information is available at https://www.arcofappalachia.org/mothapalooza.

Annual Symposium on the Conservation and Biology of Tortoises and Freshwater Turtles

The 23rd Annual Symposium on the Conservation and Biology of Tortoises and Freshwater Turtles, hosted by Turtle Survival Alliance and the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, to be held 20–25 July 2025 in Chattanooga, Tennessee. Registration is currently open. More information is available at https://turtlesurvival.org/annual-symposium-2025/.

Botany 2025

Botany 2025 to be held 26–30 July 2025 at the Palm Springs Convention Center and Renaissance Hotel, Palm Springs, California. The theme of the conference is: ‘Botany without Barriers’. Registration is currently open. More information is available at https://2025.botanyconference.org/.

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