The CANADIAN FIELD-NATURALIST

A JOURNAL OF FIELD BIOLOGY AND ECOLOGY

Promoting the study and conservation of northern biodiversity since 1880

Volume 135, Number 3 • July–September 2021

Ottawa Field-Naturalists' Club
Club des naturalistes d'Ottawa

The Ottawa Field-Naturalists' Club

FOUNDED 1863 (CURRENT INCORPORATION 1879)

The objectives of this Club shall be to promote the appreciation, preservation, and conservation of Canada's natural heritage; to encourage investigation and publish the results of research in all fields of natural history and to diffuse information on these fields as widely as possible; to support and cooperate with organizations engaged in preserving, maintaining, or restoring environments of high quality for living things.

To communicate with the Club, address postal correspondence to: The Ottawa Field-Naturalists' Club, P.O. Box 35069, Westgate P.O., Ottawa, ON, K1Z 1A2, or e-mail: ofnc@ofnc.ca. For information on club activities, go to www.ofnc.ca.

The Canadian Field-Naturalist

The Canadian Field-Naturalist is published quarterly by The Ottawa Field-Naturalists' Club. Opinions and ideas expressed in this journal do not necessarily reflect those of The Ottawa Field-Naturalists' Club or any other agency.

Website: www.canadianfieldnaturalist.ca/index.php/cfn

All manuscripts intended for publication—except Book Reviews—should be submitted through the online submission system at the CFN website: http://www.canadianfieldnaturalist.ca/index.php/cfn/user. Click the "New Submission" link on the right side of the webpage and follow the prompts. Authors must register for a cfn account at http://www.canadianfieldnaturalist.ca/index.php/cfn/user/register in order to submit a manuscript. Please contact the Online Journal Manager (info@canadianfieldnaturalist.ca) if you have any questions or issues with the online submission process. In only rare, exceptional circumstances will submissions other than online be considered and, in these cases, authors must contact the Editor-in-Chief (editor@canadianfieldnaturalist.ca) prior to submission. Instructions for Authors are found at https://www.canadianfieldnaturalist.ca/public/journals/1/CFN-author-instructions20Sept2019.pdf.

The Thomas H. Manning fund, a special fund of the OFNC, established in 2000 from the bequest of northern biologist Thomas H. Manning (1911–1998), provides financial assistance for the publication of papers in the CFN by independent (non-institutional) authors, with particular priority given to those addressing Arctic and boreal issues. Qualifying authors should make their application for assistance from the fund at the time of their initial submission.

Book-review correspondence, including arranging for delivery of review copies of books, should be sent to the Book Review Editor by e-mail: bookrevieweditor@canadianfieldnaturalist.ca.

Subscriptions and Membership: Subscription rates for individuals are $40 (online only), $50 (print only), or $60 (print + online). Libraries and other institutions may subscribe for $120 (online only or print only) or $180 (print + online). All foreign print subscribers and members (including USA) must add $10 to cover postage. The Ottawa Field-Naturalists' Club annual membership fee of $40 (individual), $45 (family), or $20 (student) includes an online subscription to *The Canadian Field-Naturalist*. Members can receive printed issues of CFN for an additional $30 per volume (four issues). For further details, see http://ofnc.ca/membership-and-donations. The club's regional journal, *Trail & Landscape*, covers the Ottawa District and regional Club events and field trips. It is mailed to all club members. It is available to libraries at $40 per year. Subscriptions, applications for membership, notices of changes of address, and undeliverable copies should be sent to subscriptions@canadianfieldnaturalist.ca or mailed to: The Ottawa Field-Naturalists' Club, P.O. Box 35069, Westgate P.O., Ottawa, ON, K1Z 1A2 Canada. Canada Post Publications Mail Agreement number 40012317. Return postage guaranteed.

Cover: Flower of Swamp Dodder (*Cuscuta gronovii*), an obligate parasitic plant. See Burt *et al.* (pages 250–261) for detailed species descriptions and discussion about ecology and distribution of three other rare, under-collected species in the genus *Cuscuta* newly identified from Quebec; an identification key is provided for all *Cuscuta* spp. now known from the province. Scale bar is 1 mm. Photo: M. Costea.

The Canadian Field-Naturalist

Eighteenth census of seabirds breeding in the sanctuaries of the North Shore of the Gulf of St. Lawrence, 2015

Jean-François Rail

Canadian Wildlife Service, 801 – 1550, ave d'Estimauville, Québec, Quebec G1J 0C3 Canada; email: jean-francois.rail@ec.gc.ca

Rail, J.-F. 2021. Eighteenth census of seabirds breeding in the sanctuaries of the North Shore of the Gulf of St. Lawrence, 2015. Canadian Field-Naturalist 135(3): 221–233. https://doi.org/10.22621/cfn.v135i3.2675

Abstract

In 1925, ten migratory bird sanctuaries were created on the North Shore of the Gulf of St. Lawrence, and their breeding seabird populations have been censused every five years since. Between 2010 and 2015, only three alcid species exhibited positive population trends (Razorbill [*Alca torda*], Common Murre [*Uria aalge*], and Atlantic Puffin [*Fratercula arctica*]), while the remaining 13 species showed declining trends. Leach's Storm-Petrel (*Hydrobates leucorhous*) and Caspian Tern (*Hydroprogne caspia*) are on the verge of disappearing from the sanctuaries, and the prolonged and rapid decline in Black-legged Kittiwake (*Rissa tridactyla*) is worrisome. Based on historical records since 1925, it appears that seabird communities are faring well in some sanctuaries (e.g., Baie de Brador, Îles aux Perroquets, and Îles Sainte-Marie), while numbers are at low levels in others (e.g., Île à la Brume, Baie des Loups, and Saint-Augustin). Human disturbance, harvest of seabirds (eggs and birds), and predation are among the issues potentially most affecting seabird populations on the North Shore of the Gulf of St. Lawrence.

Key words: Seabirds; populations; North Shore; sanctuaries; Gulf of St. Lawrence; larids; alcids

Résumé

En 1925, dix refuges d'oiseaux migrateurs ont été créés sur la Côte-Nord du golfe Saint-Laurent, et depuis les populations d'oiseaux marins qui y nichent ont été recensées à tous les cinq ans. De 2010 à 2015, seulement trois espèces d'alcidés ont montré des tendances positives (le Petit Pingouin [*Alca torda*], le Guillemot marmette [*Uria aalge*], et le Macareux moine [*Fratercula arctica*]), tandis que les treize autres espèces présentaient des déclins à divers degrés. L'Océanite cul-blanc (*Hydrobates leucorhous*) et la Sterne caspienne (*Hydroprogne caspia*) sont à risque de disparaître des refuges, alors que le déclin prolongé et rapide de la Mouette tridactyle (*Rissa tridactyla*) est inquiétant. En comparant avec les données historiques depuis 1925, il apparaît que les communautés d'oiseaux de mer sont en assez bonne santé dans certains refuges (ceux de Baie de Brador, des Îles aux Perroquets et des Îles Sainte-Marie), tandis qu'ils sont à de bas niveaux à d'autres (i.e., ceux de l'Île à la Brume, Baie des Loups et Saint-Augustin). Le dérangement, la consommation (d'œufs et d'oiseaux) par l'homme, ainsi que la prédation, sont parmi les problématiques qui affectent potentiellement le plus la conservation des oiseaux marins de la Côte-Nord du golfe du Saint-Laurent.

Mots clefs: Oiseaux marins; populations; Côte-Nord; refuges; golfe du Saint-Laurent; laridés; alcidés

Introduction

In 1925, when Harrison Flint Lewis succeeded in creating ten migratory bird sanctuaries (MBSs) along the North Shore of the Gulf of St. Lawrence, he also conducted a census of all seabird colonies in those sanctuaries (Lewis 1925). An ornithologist and true pioneer in wildlife conservation, Lewis was a chief migratory bird officer for Ontario and Quebec, and later became the first chief of the Canadian Wildlife Service. His duties were broad: educating local residents about the new conservation laws (i.e., the *Migratory Bird Convention Act*), patrolling the North Shore and charging poachers, investigating potential sites for bird sanctuaries, and issuing scientific and aviculture permits, among other things (Burnett 1999).

Lewis returned in 1930, 1935, and 1940 to monitor seabird populations in the North Shore MBSs and published his findings in *The Canadian Field-Naturalist* (Lewis 1931, 1937, 1942). Many other naturalists continued Lewis' legacy by censusing the seabirds in the MBSs at intervals of approximately five years (Hewitt 1950; Tener 1951; Lemieux 1956; Moisan 1962; Moisan and Fyfe 1967; Nettleship and Lock 1973; Chapdelaine 1980, 1995; Chapdelaine and Brousseau 1984, 1991; Rail and Chapdelaine

2004; Rail and Cotter 2007, 2015). In doing so, they contributed to what would become one of the longest continuous data sets for seabirds in North America (Burnett 1999) and a most precious one for tracking the status and trends of seabirds in Quebec.

Ninety-five years later, three sanctuaries have been abandoned and three others created. Although threats to seabirds may seem less obvious than in the early 20th century, when commercial egging and hunting were flourishing, the purpose and importance of the North Shore sanctuaries remain. Seabirds benefit from the protection afforded by the MBSs, where they find some of the best quality habitat for reproduction along the huge North Shore coastline. For many species, the concentrated breeding populations found in those sanctuaries represent a significant proportion of the provincial or even Canadian populations (Rail and Cotter 2015).

Thus, observations and results from the quinquennial censuses provide useful information regarding the management and conservation of our seabirds. This article details the updated population estimates in each of the sanctuaries on the North Shore of the Gulf of St. Lawrence in 2015 (Figure 1), summarizes the current status for each species and sanctuary, and highlights some conservation issues.

Methods

The fieldwork required to obtain the population estimates was considerable: it involved 30 participants visiting ~130 remote islands over five consecutive weeks. Sixteen species of seabirds were censused simultaneously by counting nests and birds from boats or on foot, using binoculars, telescopes, or photographs. Moreover, various extrapolation methods were used, as the total terrestrial area of the ten sanctuaries exceeds 20 km^2. Methods for estimating the number of breeding birds varied depending on the species and habitats. These have been previously described in detail by Rail and Chapdelaine (2002) for the 1998–1999 census and have been followed consistently over time. Here is a short summary of the methods used in 2015.

Whenever possible, complete nest counts (multiplied by two to get the number of breeding individuals) were used to estimate population sizes of all species, except for alcids, but there were some particularities in methods used and species coverage. For

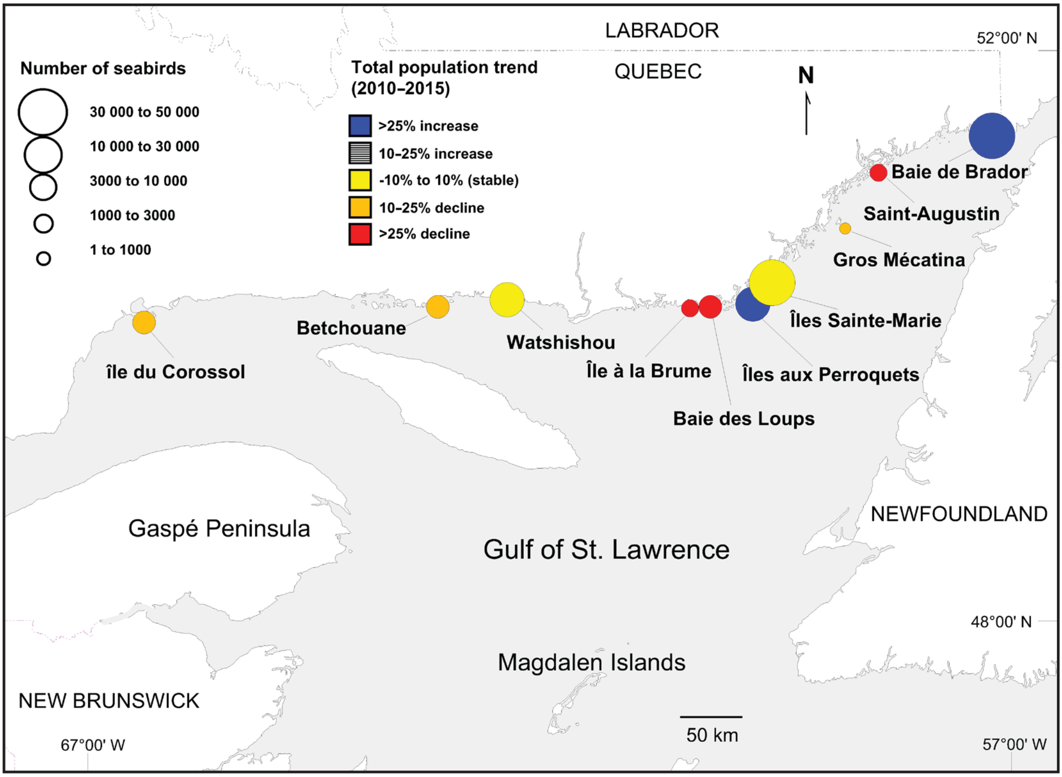


FIGURE 1. Location of the sanctuaries of the North Shore of the Gulf of St. Lawrence. Total breeding population size (all seabird species combined) and recent trend are also indicated for each sanctuary.

example, we looked for Red-throated Loon (*Gavia stellata*) nests by walking around ponds in suitable open habitat. For Leach's Storm-Petrel (*Hydrobates leucorhous*), we searched for apparently occupied burrows in areas known to have been used by the species in past censuses. Evidence of burrow occupation included freshly excavated soil, feathers, and typical musky petrel odour at the burrow entrance.

For Common Eider (*Somateria mollissima*), so ubiquitous in its breeding habitat, different sampling and extrapolation methods were used. In Île du Corossol MBS, five quadrats of 3600 m^2 were used (14% coverage) and mean nest density was extrapolated over the rest of the suitable habitat. In the Betchouane MBS, six 16-m wide transects were used on the main part of Île Innu (where mean nest density was extrapolated), while the rest of the entire sanctuary was searched (total of 45% area coverage). In the Watshishou MBS, mean nest density from a sample of 20 islands visited (representing 12% of the potential habitat of the 201 islands; see Brousseau and Chapdelaine 1990) was extrapolated to the rest of the sanctuary. In Île à la Brume, Baie des Loups, Îles aux Perroquets, and Îles Sainte-Marie MBSs, some of the islands (representing, respectively, 23%, 26%, 19%, and 59% of total land area) was thoroughly searched, and mean nest density was extrapolated to the rest of the sanctuary's area. In the Saint-Augustin MBS, we counted the number of female eiders flushing from the smaller islands (where we did not land), and carried out nest counts on the larger islands.

Because Common and Arctic Terns (*Sterna hirundo* and *Sterna paradisaea*) are physically very similar and often nest in mixed colonies, it would have been time consuming to determine the precise species ratio at each tern colony. Thus, as in previous censuses, we grouped the two species and present the estimated numbers and population trends for "tern spp.". Also, because these species tend to initiate nesting a bit later than other seabirds, we counted individuals when territorial terns were present on an island, even if we found only a few or no nests.

For estimating tern and gull populations in large MBSs (e.g., Watshishou, Baie des Loups, Saint-Augustin), we combined nest counts on larger islands with bird counts on the smaller islands where we did not land. Because nests of Great Black-backed Gull (*Larus marinus*) and Herring Gull (*Larus argentatus*) are difficult to identify to species, after counting the nests of large gulls in a given colony, nests were attributed to each species using the observed species ratio of adults on site.

Population estimates for alcids, namely Common Murre (*Uria aalge*), Razorbill (*Alca torda*), Black Guillemot (*Cepphus grylle*), and Atlantic Puffin (*Fratercula arctica*), were made by counting adult birds visible around the colonies to minimize observer disturbance in large and vulnerable colonies and also because nests are often inaccessible (e.g., in cliffs, under large boulders) or well concealed (e.g., Black Guillemots). In rare circumstances, nest counts were also used: a few Razorbill eggs were found in the Watshishou and Île à la Brume MBSs, and apparently occupied puffin burrows were systematically counted on Île à Calculot (Betchouane MBS). Finally, at Île aux Perroquets (Baie de Brador MBS), a system of transects and quadrats was used to estimate the area of the puffin colony and its mean burrow density (see Rail and Chapdelaine 2002).

Because our alcid breeding population estimates are derived, in large part, from direct counts of individuals, they are probably underestimates. Indeed, a proportion of breeding individuals is usually not visible during a colony census, as they may be hidden at the nest or away from the colony. Thus, correction factors are sometimes used to convert the number of individuals observed into more realistic estimates of the number of breeding pairs (e.g., see Cairns 1979; Harris *et al.* 2015). However, correction factors (k = number of breeding pairs/number of individuals observed) are subject to considerable variation depending on species, site, time of day, breeding phenology, and weather conditions (Rail and Chapdelaine 2002) and, ideally, require field validation. Because we did not have time to obtain such values and our results are mainly used to monitor population trends, we chose not to apply any correction factors to the raw number of individuals counted for the alcids.

Results and Discussion

In 2015, an estimated 146 729 seabirds were breeding in the North Shore sanctuaries. This represents a 13% increase compared with the 2010 total of 130 407 individuals. However, despite this apparent positive overall result, upward population trends were observed for only three alcid species (Razorbill, Common Murre, and Atlantic Puffin), while the remaining 13 species showed various degrees of decline (Table 1). Furthermore, one species was absent in 2015: we could not find any active Leach's Storm-Petrel burrows. Populations showed highly variable trends depending on the species and sanctuary. Below is a short description of the main results for each sanctuary, from west to east, followed by an assessment of the overall situation for each species, from least to highest concern. Trends are based on the data in Table 1.

Sanctuaries (from west to east)

Île du Corossol MBS (visited 30 May to 1 June 2015)—As in 2005, Leach's Storm-Petrel was absent

TABLE 1. Census of seabirds (number of individuals) in the bird sanctuaries of the North Shore of the Gulf of St. Lawrence in 2010 and 2015.

Species	Île du Corossol		Betchouane		Watshishou		Île à la Brume		Baie des Loups	
	2010	2015	2010	2015	2010	2015	2010	2015	2010	2015
Common Eider *Somateria mollissima*	1504	1014	6006	3274	12 958†	14 192†	1610	1208	3436	2302
Red-throated Loon *Gavia stellata*							4	8	12	6
Leach's Storm-Petrel *Hydrobates leucorhous*	72	0								
Double-crested Cormorant *Phalacrocorax auritus*	316	308			1888	1766			40	408
Great Cormorant *Phalacrocorax carbo*										
Ring-billed Gull *Larus delawarensis*					414	12	174	2	128	0
Herring Gull *Larus argentatus*	1040	920	828	464	598	664	422	220	379	230
Great Black-backed Gull *Larus marinus*	420	282	74	26	168	232	82	48	96	91
Black-legged Kittiwake *Rissa tridactyla*	1342	448	58	252						
Caspian Tern Hydroprogne caspia							3	2		
Common and Arctic Terns *Sterna hirundo,* *Sterna paradisaea*			0	12	220	63	35	46	12	14
Common Murre *Uria aalge*	1662	1898	116	724					256	393
Razorbill *Alca torda*	2799	3068	346	1323	0	6	10	8	2984	2329
Black Guillemot *Cepphus grylle*	401	119			1	7	20	49	15	4
Atlantic Puffin‡ *Fratercula arctica*	3	2	540	468					4028	1688
Total	9559	8059	7968	6543	16 247	16 942	2360	1591	11 386	7465

*Totals for 2005 included for comparison purposes.
†The method used to calculate the eider population in Watshishou likely produced a significant overestimation (possibly as much as two to four times; but see Rail and Chapdelaine 2002). However, this method had been used in previous censuses and, thus, allowed better historical comparisons.

in 2015, as we could not find any active burrows (36 had been found in 2010). In addition, Black Guillemot declined sharply (−70%) between 2010 and 2015, as did Black-legged Kittiwake (*Rissa tridactyla*; −66%). The current most abundant species in the sanctuary, Razorbills and Common Murres, increased only marginally (+14% and +10%, respectively). Overall, the estimated number of breeding seabirds decreased by 16% from 2010 to 2015.

Betchouane MBS (visited 6–7 June 2015)—Between 2010 and 2015, numbers of the most abundant and representative species in this sanctuary, Common Eider, decreased by nearly half (−45%). Herring Gull (−44%) and Great Black-backed Gull (−65%) also showed substantial declines. Conversely, the relatively small numbers of Common Murre, Black-legged Kittiwake, and Razorbill increased over sixfold (+524%), fourfold (+334%), and nearly fourfold (+282%), respectively, from 2010 to 2015. The total number of seabirds showed an 18% decline.

Watshishou MBS (visited 3–5 June 2015)—The populations of the most abundant species locally, Common Eider, Double-crested Cormorant (*Phalacrocorax auritus*), and Herring Gull, remained quite stable between 2010 and 2015, as did the total number of breeding seabirds. Razorbill made a small but notable reappearance (three eggs found on one island), after not being detected in the sanctuary during the

Îles aux Perroquets		Îles Sainte-Marie		Gros Mécatina		Saint-Augustin		Baie de Brador		Total		
2010	2015	2010	2015	2010	2015	2010	2015	2010	2015	2005*	2010	2015
986	824	1152	1940	4	14	94	192			25 716	27 750	24 960
30	34	52	44	4	4		2			92	102	98
										0	72	0
		3245	286							3346	5489	2768
0	34	156	30	78	32					48	234	96
0	28	2	0			216	178			1893	934	220
204	167	154	89	93	71	1793	1240	558	543	5914	6069	4608
71	95	182	214	81	51	123	112	348	386	1956	1645	1537
		820	644							3994	2220	1344
										3	3	2
91	48	12	0	8	0	645	220			3311	1023	403
2811	7898	20 078	20 821	12	34			1402	2170	14 877	26 337	33 938
6864	14 945	16 547	20 396	280	401			6283	9305	22 472	36 113	51 781
90	36	103	157	192	37	6	3	3	15	928	831	427
400	391	837	2126	59	29			15 718	19 843	25 335	21 585	24 547
11 547	24 500	43 340	46 747	811	673	28 77	1947	24 312	32 262	109 885	130 407	146 729

‡In 2005, the use of a burrow probe at a few sites at Baie des Loups, Îles aux Perroquets, and Baie de Brador verified that apparently occupied burrows were actually used at a fairly constant rate of 71–76%. Therefore, the puffin population estimates presented here for these sanctuaries, as well as for the Betchouane and Îles Sainte-Marie Sanctuaries, are overestimates because apparently occupied burrow counts were used. We did not apply a correction factor to these estimates to allow better comparison with data from previous censuses.

2005 and 2010 censuses. The declines in Ring-billed Gull (*Larus delawarensis*; −97%) and Common and Arctic Terns (−71%) seem severe, but may be mainly caused by colonies moving outside the sanctuary, rather than an overall population decline. Colonies of those species on the North Shore rarely persist from one census to another and, consequently, numbers have been extremely variable in the past.

Île à la Brume MBS (visited 14–15 June 2015)—Six of the nine breeding species here declined, including the three most abundant species in 2010: Common Eider (−25%), Herring Gull (−49%), and Ring-billed Gull (−99%; only one pair found in 2015). Overall, the sanctuary lost a third (−33%) of its breeding seabirds, and seabird density (579/km^2 of land) is the second lowest among the North Shore sanctuaries. A significant increase (+145%) in the number of Black Guillemot observed is perhaps the only positive trend here, along with the four nests of Red-throated Loon (compared with two in 2010). The sighting of a pair of Caspian Tern (*Hydroprogne caspia*) and their nest confirmed that there is still a breeding population, although a small one.

Baie des Loups MBS (visited 15, 17, and 20 June 2015)—Overall, populations of eight of the 11 breeding species declined between 2010 and 2015, and the total number of seabirds decreased by a third (−34%). Common Eider, one of the most abundant species at this site, declined by 33% from 2010 to 2015. Furthermore, local populations of Atlantic Puffin, Black Guillemot, and Great Black-backed and Herring Gulls, reached their lowest levels observed since 1925–1930. On the positive side, the small number of Double-crested Cormorant grew ten-fold in five years, and the small Common Murre population increased notably (+54%).

Îles aux Perroquets MBS (visited 18–20 June 2015)—Razorbill and Common Murre, by far the two most abundant species in this sanctuary, showed spectacular increases between 2010 and 2015 (+118% and +181%, respectively). The increase in these two species is responsible for the more than doubling (+112%) of the overall number of seabirds in the sanctuary. The density of breeding seabirds here (25 868/km^2 of land) is now the second highest among the North Shore sanctuaries. Also worthy of note is the reappearance of two breeding species, Great Cormorant (*Phalacrocorax carbo*, 17 pairs) and Ring-billed Gull (14 pairs). Other species' numbers remained relatively stable, except for Black Guillemot (60% decline).

Îles Sainte-Marie MBS (visited 16, 21, and 22 June 2015)—In contrast with the adjacent Îles aux Perroquets MBS, the populations of Razorbill and Common Murre here remained stable between the last two censuses (increases of 23% and 4%, respectively). The other alcids (Black Guillemot, +52%; Atlantic Puffin, +154%) fared well from 2010 to 2015, as did Common Eider (+68%). One striking result is the 91% decline in Double-crested Cormorant, resulting from the near abandonment of the large colony on Île de l'Est (1290 nests in 2010), because of the presence of Red Fox (*Vulpes vulpes*). The size of the Great Cormorant colony (on Île Cliff) also declined severely (−81%). Furthermore, for the first time since 1950, no breeding terns were found. Overall, the total number of breeding seabirds remained quite stable (+8%).

Gros Mécatina MBS (visited 23 June 2015)—We did not observe any breeding terns in this sanctuary in 2015. Trends in the small populations of the other species varied considerably, but, overall, the number of breeding seabirds declined only slightly (−17%). Numbers of Common Murre almost tripled (+183%), those of Razorbill increased (+43%), while those of Black Guillemot and Atlantic Puffin declined (−81% and −51%, respectively). Only 16 nests remained in the colony of Great Cormorants on Île aux Trois Collines (−59%).

Saint-Augustin MBS (visited 1 July 2015)—Compared with the other North Shore sanctuaries, Saint-Augustin MBS has the largest land area, but, again in 2015, the density of seabirds was lowest (354/km^2). In fact, the sanctuary lost a third (−32%) of its seabirds, as its most abundant species underwent serious declines between 2010 and 2015 (−31% for the Herring Gull and −66% for the Common and Arctic Terns). On the positive side, the Red-throated Loon nest found in 2015 represents the first breeding record of the species here since 1977. The number of eider nests found in 2015 (96) was double that of 2010 (+104%).

Baie de Brador MBS (visited 27–29 June 2015)—Between 2010 and 2015, marked increases were noted in the numbers of all breeding alcids, namely Common Murre (+55%), Razorbill (+48%), Atlantic Puffin (+26%), and even Black Guillemot (from three to 15 individuals). Meanwhile, populations of Herring Gull and Great Black-backed Gull remained stable (−3% and +11%, respectively). With its total number of seabirds growing 33% since 2010, this MBS now has the highest density of seabirds by far (31 754/km^2). The Atlantic Puffin population has rebounded to about 20 000 individuals (following a 22% decline between 2005 and 2010) and is particularly important for the conservation of the species in Quebec, as this colony holds over 70% of the puffins in the province.

Species accounts (from least to highest concern)

Razorbill—Once again, this species comes first on our list (Rail and Cotter 2015). The population has been growing steadily since 1977 (Figure 2a) and the 43% increase in numbers between 2010 and 2015 (over 7% annually) is still high for a bird laying a single egg. Razorbill is now, by far, the most numerous seabird in the North Shore sanctuaries, and its situation appears positive throughout its range in Quebec (Cotter and Rail 2007; Rail 2009, 2018) and North America (Chapdelaine *et al.* 2001; Lavers *et al.* 2020).

Common Murre—The population increased 29% between 2010 and 2015, reaching its highest level on record (Figure 2b). Numbers rose everywhere, but especially rapidly in recently established colonies, such as those in Betchouane and Baie de Brador MBSs (Table 1). This seabird ranks second in abundance in North Shore sanctuaries. It has been generally increasing and expanding in the province for the past 20 years (Rail 2009, 2018; Canadian Wildlife Service unpubl. data), as well as in most of its global range (BirdLife International 2018a).

Common Eider—With little variation in total numbers observed over the last three censuses (+8% between 2005 and 2010; −10% from 2010 to 2015), the population seems to have stabilized around its highest level on record (Figure 2c). Declines were noted in five MBSs and increases in four (Table 1). The situation of Common Eider on the North Shore (see also Troutet and Samson 2015) contrasts with the significant declining trend (−5%/year) observed in the St. Lawrence Estuary since 2003 (Lepage 2019).

Red-throated Loon—The total number of breeding pairs levelled off close to the high count in 2010 (−4% between 2010 and 2015; Figure 2d). When the presence of Red Fox prevented loons from breeding on an island in the Îles Sainte-Marie MBS, pairs appeared to relocate to adjacent islands. Most nests (80%) are concentrated in the Îles Sainte-Marie and Îles aux Perroquets MBSs. From 1935 to 1955, fairly large numbers (24–70 individuals) of Red-throated Loon were also found in the Mécatina MBS, which was abolished in 1974.

Double-crested Cormorant—The 50% decrease from 2010 to 2015 may seem striking; however, Double-crested Cormorant numbers in the MBSs may vary considerably between quinquennial censuses, and the actual population is still relatively large compared with historical levels since 1925 (Figure 2e). Note also that the recent decline (−93% from 2010 to 2015) is a result of the near abandonment of the largest colony (1290 nests in 2010) on Île de l'Est (Îles Sainte-Marie MBS; Table 1). This in turn is likely the consequence of Red Fox repeatedly accessing the island; as cormorant nests there are built in low krummolz bushes or directly on the ground, they are vulnerable to mammalian predation.

Great Black-backed Gull—A population decline was observed for the third consecutive census. However, the recent decrease is rather marginal (−7% from 2010 to 2015), and numbers rose at four MBSs and fell at six others (Table 1). The actual population size is very close to the average number of Great Black-backed Gulls observed in the sanctuaries since 1925 (Figure 2f). Since the end of the 1980s, however, populations have shown major declines in most parts of southeastern Canada (Wilhelm *et al.* 2016). These declines have been associated with reduced groundfish fisheries, which had been providing abundant discards for gulls in the preceding decades (Wilhelm *et al.* 2016).

Atlantic Puffin—After a large decrease (−54%) between 1993 and 2010, the population now appears to have stabilized, as the recent slight increase in numbers (14% from 2010 to 2015) brought the population close to the level observed in 2005 (Figure 2g). Although the latest increase at the largest colony (+26% at Baie de Brador MBS from 2010 to 2015) may appear reassuring, over 80% of the puffins are now concentrated in this sanctuary, and numbers dwindled (−58%; Table 1) to a record low at Baie des Loups MBS, where the species used to be nearly as abundant. From 1925 to 1955, breeding puffins were twice as abundant as they now are in North Shore MBSs (Figure 2g). Globally, since 2015, the species has been listed as Vulnerable by the International Union for the Conservation of Nature (IUCN; BirdLife International 2018b) because of rapid declines across most of its European range. Factors affecting the species here are unknown, but Fayet *et al.* (2017) found that distance to wintering area was negatively linked with population productivity. Their study used geolocators, but unfortunately did not include birds from Quebec, and, as the species winters far offshore, little is known about its wintering range from banding data (Gaston *et al.* 2008).

Black Guillemot—Population trends were extremely variable among sanctuaries, but large declines were observed where the species was most abundant (−70% and −81% at Île du Corossol and Gros Mécatina MBSs, respectively), so that the total number of individuals in all sanctuaries was halved (−49%) between 2010 and 2015 (Table 1). Although we recognize that estimates from counts of individuals may be subject to substantial variations (e.g., daily, seasonally, weather related; see Cairns 1979), such large declines are nonetheless enigmatic. The species is known to be particularly vulnerable to mammalian predators (Butler *et al.* 2020) and may be outcompeted by increasing numbers of Razorbill and Common Murre at mixed colonies. The highest counts of Black Guillemot were recorded from 1940 to 1950 (Figure 2h), when about half of these birds (600–840) were found in the Mécatina MBS alone. However, seabird populations in this sanctuary declined so much afterwards that it was abolished in 1974.

Herring Gull—Marginal to moderate declines were observed in nine of the ten MBSs (Table 1). In 2015, the estimated total number of Herring Gulls breeding in the MBSs represents a 24% decrease from 2010. On the other hand, it is only 15% lower than the average estimate from the previous four censuses (1993 to 2010; Figure 2i). This still suggests a stabilization of the population, after the large-scale decline that occurred in the late 1980s to early 1990s on the North Shore (−70%; see Chapdelaine 1995; Chapdelaine and Rail 1997) and elsewhere in Atlantic Canada (Cotter *et al*. 2012; Wilhelm *et al.* 2016).

Great Cormorant—The two medium-sized colonies noted in 2010 (78 and 39 nests at the Îles Sainte-Marie and Gros Mécatina MBSs, respectively) were markedly smaller in 2015 (−81% and −59%, respectively). However, a new colony of 17 pairs was found at the Îles aux Perroquets MBS, for an overall decline of −59% between 2010 and 2015 (Table 1). The species was found breeding in three sanctuaries, but in such small numbers that its persistence in the North Shore MBSs now appears rather fragile. In 1930, it was found breeding in the Îles Sainte-Marie MBS, and the size of this colony peaked at 339 pairs in 1955 (Figure 2j).

Arctic and Common Terns and Ring-billed Gull—The total number of terns and Ring-billed Gulls in

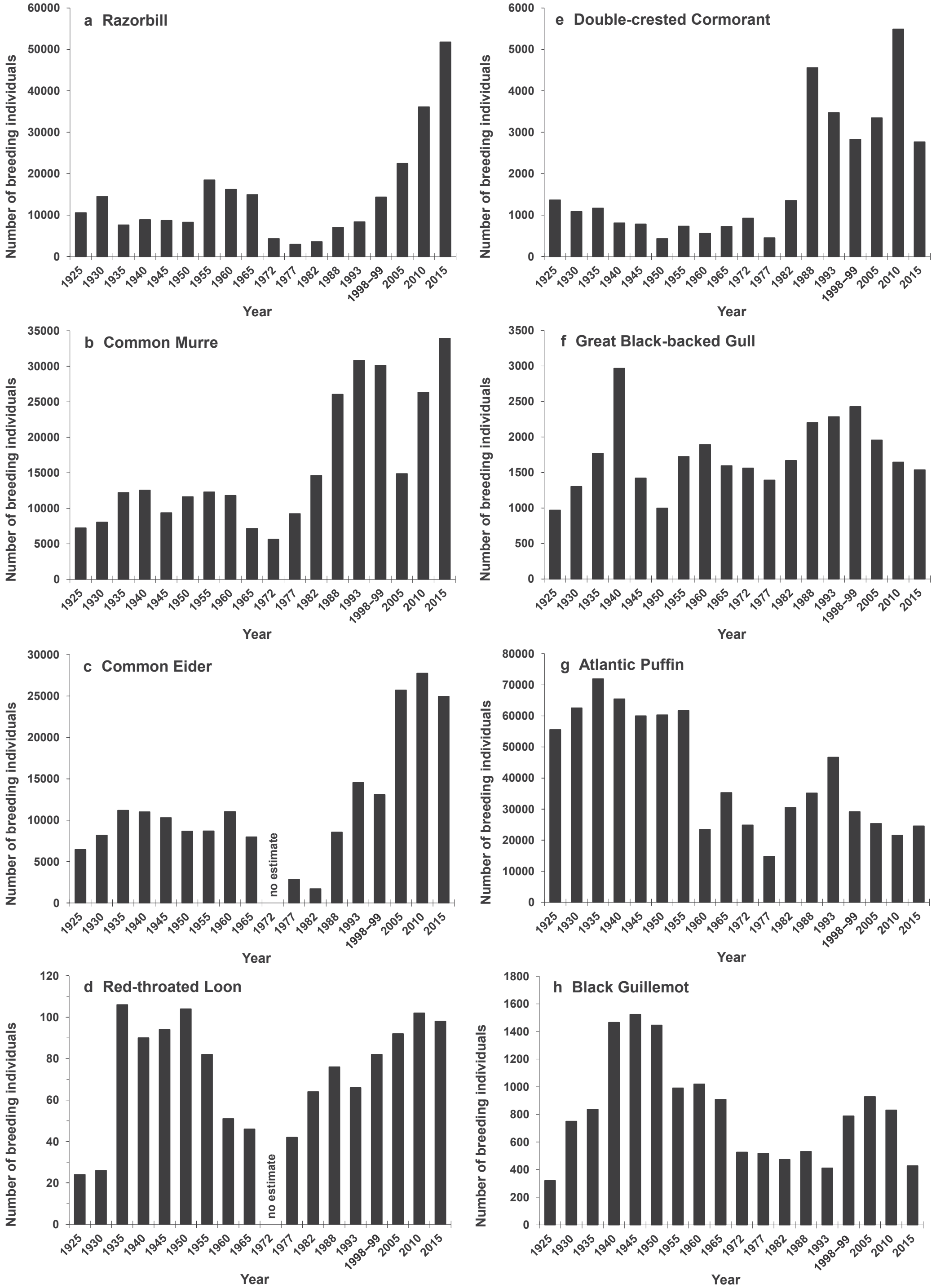


FIGURE 2. Population trends among seabirds breeding in the migratory bird sanctuaries of the North Shore of the Gulf of St. Lawrence, 1925–2015, in order from least to most concern.

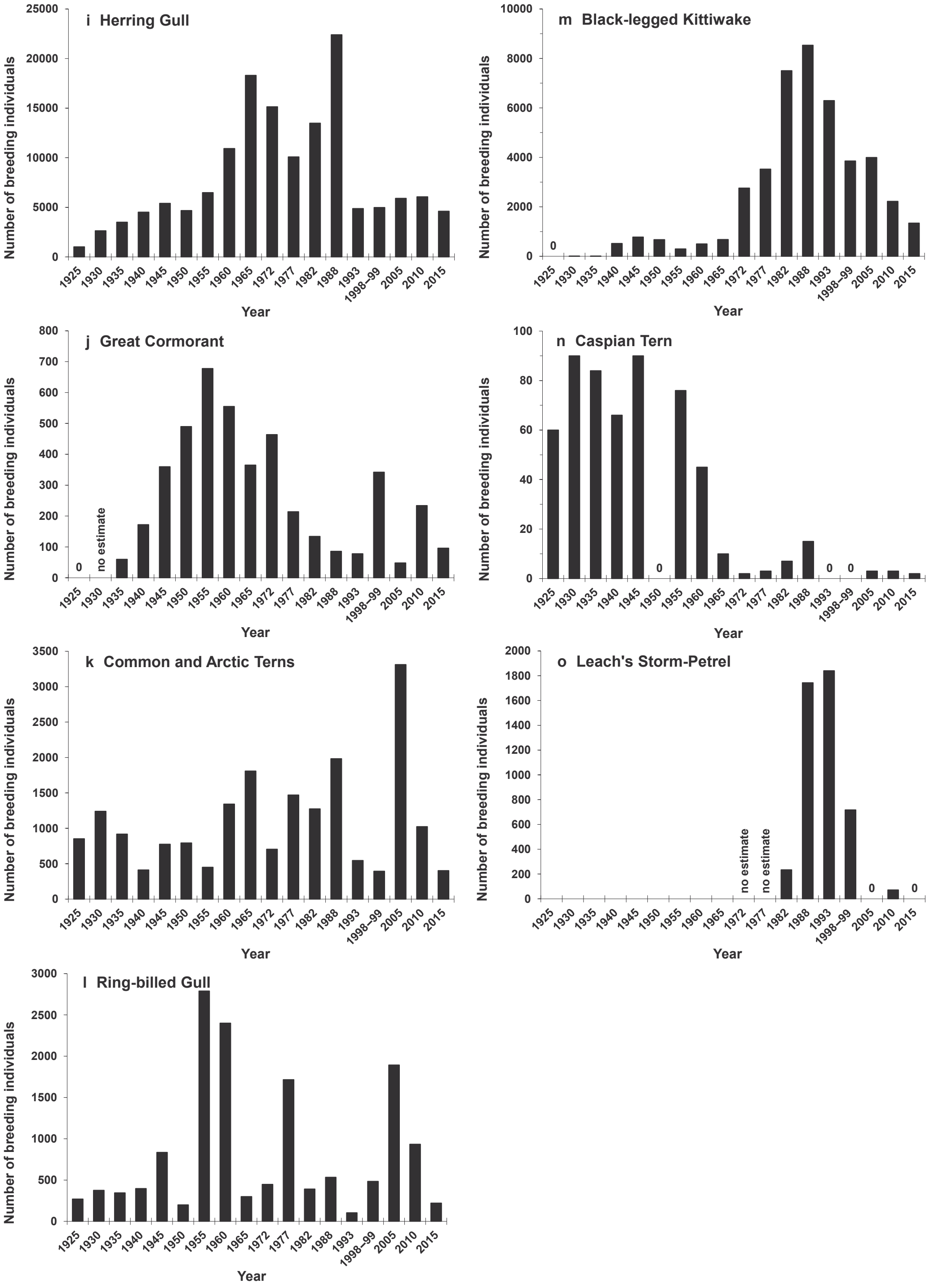


FIGURE 2. *Continued.*

the North Shore MBSs decreased by 61% and 76%, respectively, between 2010 and 2015 (Table 1). The abundance of these species is characterized by extreme fluctuations between censuses (Figure 2k–l), as colonies of all sizes move in and out of the MBSs and new colonies are found while others are abandoned. Thus, such small population levels as those of 2015 have been observed in the past and are not necessarily indicative of a longer-term decline. The Mingan Archipelago National Park Reserve, a much wider area that includes the Betchouane and Watshishou MBSs, stretches along 152 km of coastline and encompasses over 1000 islands; it provides the most representative results for terns on the North Shore of the Gulf of St. Lawrence. Yet, the park's large tern population remained quite stable from 2009 to 2019, at around 4500 pairs, and shows a 20% increase since 1999 (Abgrall and Langlois 2019).

Black-legged Kittiwake—The Île du Corossol MBS has always been the stronghold for Black-legged Kittiwake on the North Shore. However, with a fifth consecutive decrease (−67% between 2010 and 2015), for the first time since this MBS was created in 1937, it no longer holds the largest kittiwake colony. The only positive trend was observed in the Betchouane MBS where a small colony (126 pairs in 2015) is doing well (+334%; Table 1). The overall decline of 84% in the MBSs since 1988 is troubling, as there is no indication of it slowing down, and there are only a few hundred (n = 672) pairs left (Figure 2m). Long-term large-scale declines are also occurring elsewhere in the species' core breeding distribution in eastern Canada, i.e., Gaspé Peninsula (−52% between 1989 and 2018; Canadian Wildlife Service unpubl. data), Anticosti Island (−90% from 1985 to 2019; Canadian Wildlife Service unpubl. data), and Newfoundland (Cotter *et al.* 2012). The species, which has been listed as Vulnerable by the IUCN since 2017 (BirdLife International 2018c) because of continuing declines in large parts of its global range, appears affected by ocean warming rates and trophic shifts in the Atlantic (Descamps *et al.* 2017).

Caspian Tern—Two adults and one nest were found in 2015, confirming that the species still breeds, sporadically, at the Île à la Brume MBS. In 2005 and 2010, three birds, presumably breeders (but no nest), had been observed after no detection of the species in 1999 and 1993. The Îles à la Brume MBS is the only site where the species breeds regularly in Quebec. Between 1925 and 1945, 60–90 birds were observed during the quinquennial censuses (Figure 2n). This tiny and isolated colony appears fragile, especially as Caspian Terns are particularly vulnerable to human disturbance (Cuthbert and Wires 2020), and the site is probably visited by people from local communities. Moreover, as Caspian Terns often nest among Ring-billed Gulls, the near disappearance of the latter species on Île à la Brume MBS may represent a lost opportunity for Caspian Terns to breed.

Leach's Storm-Petrel—No active nests were found in 2015, as in 2005. However, given the small size of the entrance to this species' burrows, which can be easily missed in vegetation, it may still breed on Île du Corossol MBS, because 36 occupied burrows were counted there in 2010. However, the species is obviously less abundant now than in the 1980s and early 1990s, when with minimal effort, up to 900 active burrows were found in colonies at four MBSs: Île du Corossol, Baie des Loups, Îles aux Perroquets, and Îles Sainte-Marie. Burrows were noted in 1972 and their number first estimated in 1982 (Figure 2o), but breeding storm-petrels have probably been present since the sanctuaries were created. The species was globally listed as Vulnerable in 2018, because of worldwide declines (BirdLife International 2018d). In November 2020, the Atlantic population in Canada was assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (SARA Registry 2021). It is known to be particularly vulnerable to mammalian predation, and American Mink (*Neovison vison*) and Red Fox have been seen for the first time on Île du Corossol in recent years. On a brighter note, audio recordings from Île aux Perroquets, in the Baie de Brador MBS, suggest that storm-petrels might breed there (e.g., 74 chatter calls [see Pollet *et al.* 2020] between 0100 and 0200 on 28 June 2015). There is no previous breeding record for this species there, but again, Leach's Storm-Petrel burrows may be difficult to detect and identify through the vegetation, especially among nearly 10 000 puffin burrows.

Conclusions

Our results highlight, once again, the precariousness of the status of Caspian Tern and Leach's Storm-Petrel breeding populations in North Shore MBSs. The main threats they potentially face (disturbance and egg harvest for the former, invading American Mink and Red Fox for the latter) should be addressed before these species vanish permanently from the sanctuaries. Black-legged Kittiwake is another species of concern, showing a fast and steady decline since 1988. Compared with historical levels since 1925, the seabird community appears generally healthy in some MBSs (e.g., Baie de Brador, Îles aux Perroquets, and Îles Sainte-Marie). However, seabird numbers are obviously declining and not recovering at others, particularly alcids at Île à la Brume and Baie des Loups MBSs, and Common Eider at Saint-Augustin MBS. We found some evidence and reported facts suggesting that human disturbance and harvest of seabirds (eggs and birds) could still be the main limiting factors in these areas. Seabird population monitoring, wildlife law enforcement, and raising public awareness all remain important challenges to ensure the conservation of seabird populations in such a huge and remote area as the North Shore.

Acknowledgements

Our hosts André and Antoinette Gallienne made our stay most enjoyable on Île du Corossol. Field assistance was provided by colleagues Richard Cotter, Laurie Isabel, Bruno Drolet, Myriam Drolet-Lambany, and Pierre Brousseau, and also by Environment and Climate Change Canada's wildlife enforcement officers, Wilson Evans and Paul Rowsell. For the Betchouane and Watshishou migratory bird sanctuaries (MBSs), Parks Canada personnel at Havre Saint-Pierre, and the volunteers they recruited (coordinated by Nancy Dénommée), gave us much help. I also thank volunteer Christine Vatcher (Baie des Loups and Îles aux Perroquets MBSs) and Glenn McKinnon, our local boatman for the Saint-Augustin MBS. At the Baie de Brador MBS, we were assisted by Kathleen Blanchard (Intervale Associates Inc.) and Mégane Déziel (Quebec-Labrador Foundation) and safe travel to the islands was ensured by boatman Jean-Marie Jones. Finally, I'm grateful to Shirley Orichefsky and François Bolduc for reviewing the first draft of this manuscript.

Literature Cited

Abgrall, M.-J., and J. Langlois. 2019. Surveillance de la population nicheuse de Sternes pierregarin et arctique du milieu côtier de la réserve de parc national de l'Archipel-de-Mingan en 2019. Parks Canada, Mingan Field Unit, Havre-Saint-Pierre, Quebec, Canada.

BirdLife International. 2018a. Common Murre: *Uria aalge*. *In* IUCN Red List of Threatened Species 2018. International Union for the Conservation of Nature, Gland, Switzerland. https://doi.org/10.2305/iucn.uk.2018-2.rlts.t22694841a132577296.en

BirdLife International. 2018b. Atlantic Puffin: *Fratercula arctica*. *In* IUCN Red List of Threatened Species 2018. International Union for the Conservation of Nature, Gland, Switzerland. https://doi.org/10.2305/iucn.uk.2018-2.rlts.t22694927a132581443.en

BirdLife International. 2018c. Black-legged Kittiwake: *Rissa tridactyla*. *In* IUCN Red List of Threatened Species 2018. International Union for the Conservation of Nature, Gland, Switzerland. https://doi.org/10.2305/iucn.uk.2018-2.rlts.t22694497a155617539.en

BirdLife International. 2018d. Leach's Storm-petrel: *Hydrobates leucorhous*. *In* IUCN Red List of Threatened Species 2018. International Union for the Conservation of Nature, Gland, Switzerland. https://doi.org/10.2305/iucn.uk.2018-2.rlts.t132438298a132438484.en

Brousseau, P., and G. Chapdelaine. 1990. Treizième inventaire des oiseaux marins dans les refuges de la Côte-Nord: techniques et résultats détaillés. Technical report 96. Canadian Wildlife Service, Environment Canada, Sainte-Foy, Quebec, Canada. Accessed 29 September 2020. https://publications.gc.ca/collections/collection_2018/eccc/cw69-5/CW69-5-96-fra.pdf.

Burnett, J.A. 1999. Chapter 1. Exercising dominion: the genesis of Canadian wildlife policy. Canadian Field-Naturalist 113: 4–15. Accessed 20 September 2020. https://biodiversitylibrary.org/page/34234910.

Butler, R.G., D.E. Buckley, D.N. Nettleship, P.F.D. Boesman, and E. Garcia. 2020. Black Guillemot: *Cepphus grylle*, version 1.0. *In* Birds of the World. *Edited by* S.M. Billerman. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.blkgui.01

Cairns, D. 1979. Censusing hole-nesting auks by visual counts. Bird Banding 50: 358–364. https://doi.org/10.2307/4512487

Chapdelaine, G. 1980. Onzième inventaire et analyse des fluctuations des populations d'oiseaux marins dans les refuges de la Côte Nord du Golfe Saint-Laurent. Canadian Field-Naturalist 94: 34–42. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28088915.

Chapdelaine, G. 1995. Fourteenth census of seabird populations in the sanctuaries of the North Shore of the Gulf of St. Lawrence, 1993. Canadian Field-Naturalist 109: 220–226. Accessed 20 September 2020. https://biodiversitylibrary.org/page/35457068.

Chapdelaine, G., and P. Brousseau. 1984. Douzième inventaire des populations d'oiseaux marins dans les refuges de la Côte-Nord du golfe du Saint-Laurent. Canadian Field-Naturalist 98: 178–183. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28064009.

Chapdelaine, G., and P. Brousseau. 1991. Thirteenth census of seabird populations in the sanctuaries of the North Shore of the Gulf of St. Lawrence, 1982–1988. Canadian Field-Naturalist 105: 60–66. Accessed 20 September 2020. https://biodiversitylibrary.org/page/34348566.

Chapdelaine, G., A.W. Diamond, R.D. Elliot, and G.J. Robertson. 2001. Status and population trends of the Razorbill in eastern North America. Occasional paper 105. Canadian Wildlife Service, Ottawa, Ontario, Canada. Accessed 20 September 2020. https://publications.gc.ca/collections/collection_2011/ec/CW69-1-105-eng.pdf.

Chapdelaine, G., and J.-F. Rail. 1997. Relationship between cod fishery activities and the population of herring gulls on the North Shore of the Gulf of St Lawrence, Quebec, Canada. ICES Journal of Marine Science 54: 708–713. https://doi.org/10.1006/jmsc.1997.0248

Cotter, R., and J.-F. Rail. 2007. Third census of seabird populations of the Gaspé Peninsula, Québec, 2002. Canadian Field-Naturalist 121: 274–286. https://doi.org/10.22621/cfn.v121i3.475

Cotter, R.C., J.-F. Rail, A.W. Boyne, G.J. Robertson, D.V.C. Weseloh, and K.G. Chaulk. 2012. Population status, distribution, and trends of gulls and kittiwakes breeding in eastern Canada, 1998–2007. Occasional paper 120. Canadian Wildlife Service, Ottawa, Ontario, Canada. Accessed 20 September 2020. https://publications.gc.ca/collections/collection_2013/ec/CW69-1-120-eng.pdf.

Cuthbert, F.J., and L.R. Wires. 2020. Caspian Tern: *Hydroprogne caspia*, version 1.0. *In* Birds of the World. *Edited by* S.M. Billerman. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.caster1.01

Descamps, S., T. Anker-Nilssen, R.T. Barrett, D.B. Irons, F. Merkel, G.J. Robertson, N.G. Yoccoz, M.L. Mallory, W.A. Montevecchi, D. Boertmann, Y. Artukhin, S. Christensen-Dalsgaard, K.-E. Erikstad, H.G. Gilchrist, A.L. Labansen, S.-H. Lorentsen, A. Mosbech, B. Olsen, A. Petersen, J.-F. Rail, H.M. Renner, H. Strøm, G.H. Systad, S.I. Wilhelm, and L. Zelenskaya. 2017. Circumpolar dynamics of a marine top-predator track ocean warming rates. Global Change Biology 23: 3770–3780. https://doi.org/10.1111/gcb.13715

Fayet, A.L., R. Freeman, T. Anker-Nilssen, A. Diamond, K.E. Erikstad, D. Fifield, M.G. Fitzsimmons, E.S. Hansen, M.P. Harris, M. Jessopp, A.-L. Kouwenberg, S. Kress, S. Mowat, C.M. Perrins, A. Petersen, I.K. Petersen, T.K Reiertsen, G.J. Robertson, P. Shannon, I.A. Sigurõsson, A. Shoji, S. Wanless, and T. Guilford. 2017. Ocean-wide drivers of migration strategies and their influence on population breeding performance in a declining seabird. Current Biology 27: 3871–3878. https://doi.org/10.1016/j.cub.2017.11.009

Gaston, A.J., D. Brewer, A.W. Diamond, E.J. Woodsworth, and B.T. Collins. 2008. Canadian Atlas of Bird Banding, Volume 2: Seabirds, 1921–1995. Special publication. Canadian Wildlife Service, Ottawa, Ontario, Canada. Accessed 20 September 2020. https://publications.gc.ca/collections/collection_2011/ec/CW69-20-2-2-2008-eng.pdf.

Harris, M.P., M.A. Newell, and S. Wanless. 2015. The use of k values to convert counts of individual Razorbills *Alca torda* to breeding pairs. Seabird 28: 30–36.

Hewitt, O.H. 1950. Fifth census of non-passerine birds in the bird sanctuaries of the North Shore of the Gulf of St. Lawrence. Canadian Field-Naturalist 64: 73–76. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28088686.

Lavers, J., J.M. Hipfner, and G. Chapdelaine. 2020. Razorbill: *Alca torda*, version 1.0. *In* Birds of the World. *Edited by* S.M. Billerman. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.razorb.01

Lemieux, L. 1956. Seventh census of nonpasserine birds in the bird sanctuaries of the North Shore of the Gulf of St. Lawrence. Canadian Field-Naturalist 70: 183–185. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28387105.

Lepage, C. 2019. Common Eider. Pages 126–127 *in* Second Atlas of the Breeding Birds of Southern Québec. *Edited by* M. Robert, M.-H. Hachey, D. Lepage, and A.R. Couturier. Regroupement QuébecOiseaux, Environment and Climate Change Canada, and Bird Studies Canada, Montréal, Quebec, Canada.

Lewis, H.F. 1925. The new bird sanctuaries in the Gulf of St. Lawrence. Canadian Field-Naturalist 39: 177–179. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28091940.

Lewis, H.F. 1931. Five years' progress in the bird sanctuaries of the North Shore of the Gulf of St. Lawrence. Canadian Field-Naturalist 45: 73–78. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28008491.

Lewis, H.F. 1937. A decade of progress in the bird sanctuaries of the North Shore of the Gulf of St. Lawrence. Canadian Field-Naturalist 51: 51–55. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28113555.

Lewis, H.F. 1942. Fourth census of non-passerine birds in the bird sanctuaries of the North Shore of the Gulf of St. Lawrence. Canadian Field-Naturalist 56: 5–8. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28023103.

Moisan, G. 1962. Eighth census of non-passerine birds in the bird sanctuaries on the North Shore of the Gulf of St. Lawrence. Canadian Field-Naturalist 76: 78–82. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28112390.

Moisan, G., and R.W. Fyfe. 1967. Ninth census of non-passerine birds in the sanctuaries of the North Shore of the Gulf of St. Lawrence. Canadian-Field-Naturalist 81: 67–70. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28370745.

Nettleship, D.N., and A.R. Lock. 1973. Tenth census of seabirds in the sanctuaries of the North Shore of the Gulf of St. Lawrence. Canadian Field-Naturalist 87: 395–402. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28059120.

Pollet, I.L., A.L. Bond, A. Hedd, C.E. Huntington, R.G. Butler, and R. Mauck. 2020. Leach's Storm-Petrel: *Oceanodroma leucorhoa*, version 1.0. *In* Birds of the World. *Edited by* S.M. Billerman, B.K. Keeney, P.G. Rodewald, and T.S. Schulenberg. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.lcspet.01

Rail, J.-F. 2009. Seabirds and colonial waterbirds of the Magdalen Islands: statuses and population trends. Technical report 502. Canadian Wildlife Service, Quebec region, Sainte-Foy, Quebec, Canada. Accessed 29 September 2020. https://publications.gc.ca/collections/collection_2018/eccc/cw69-5/CW69-5-502-eng.pdf.

Rail, J.-F. 2018. Les oiseaux marins nicheurs dans l'aire de coordination du parc marin du Saguenay–Saint-Laurent. Le Naturaliste canadien 142(2): 47–54. https://doi.org/10.7202/1047148ar

Rail, J.-F., and G. Chapdelaine. 2002. Quinzième inventaire des oiseaux marins dans les refuges de la Côte-Nord: techniques et résultats détaillés. Technical report 392. Canadian Wildlife Service, Quebec region, Sainte-Foy, Quebec, Canada. Accessed 29 September 2020. https://publications.gc.ca/collections/collection_2018/eccc/cw69-5/CW69-5-392-fra.pdf.

Rail, J.-F., and G. Chapdelaine. 2004. Fifteenth census of seabird populations in the sanctuaries of the North Shore of the Gulf of St. Lawrence, 1998–99. Canadian Field-Naturalist 118: 256–263. https://doi.org/10.22621/cfn.v118i2.924

Rail, J.-F., and R. Cotter. 2007. Sixteenth census of seabird populations in the sanctuaries of the North Shore of the Gulf of St. Lawrence, 2005. Canadian Field-Naturalist 121: 287–294. https://doi.org/10.22621/cfn.v121i3.476

Rail, J.-F., and R. Cotter. 2015. Seventeenth census of seabird populations in the sanctuaries of the North Shore of the Gulf of St. Lawrence, 2010. Canadian Field-Naturalist 129: 152–158. https://doi.org/10.22621/cfn.v129i2.1695

SARA (*Species at Risk Act*) Registry. 2021. Species summary: Leach's Storm-Petrel (*Oceanodroma leucorhoa*), Atlantic population. Government of Canada, Ottawa, Ontario, Canada. Accessed 20 May 2021. https://species-registry.canada.ca/index-en.html#/species/1496-1084.

Tener, J.S. 1951. Sixth census of non-passerine birds in the bird sanctuaries of the North Shore of the Gulf of St. Lawrence. Canadian Field-Naturalist 65: 65–68. Accessed 20 September 2020. https://biodiversitylibrary.org/page/28386143.

Troutet, Y., and C. Samson. 2015. Situation de la population nicheuse d'Eiders à duvet dans les forêts de la réserve de parc national de l'Archipel-de-Mingan en 2008. Parks Canada, Mingan Field Unit, Havre-Saint-Pierre, Quebec, Canada.

Wilhelm, S.I., J.-F. Rail, P.M. Regular, C. Gjerdrum, and G.J. Robertson. 2016. Large-scale changes in abundance of breeding Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*Larus marinus*) relative to reduced fishing activities in southeastern Canada. Waterbirds 39(sp1): 136–142. https://doi.org/10.1675/063.039.sp104

Received 7 December 2020
Accepted 27 July 2021
Associate Editor: D.C. Tozer

The Canadian Field-Naturalist

Introduced earthworms (Lumbricidae) in restored and remnant tallgrass prairies of southern Ontario

Heather A. Cray[1, 2], **Justin M. Gaudon**[1, 3,*], and **Stephen D. Murphy**[1]

[1]School of Environment, Resources and Sustainability, University of Waterloo, 200 University Avenue West, Waterloo, Ontario N2L 3G1 Canada
[2]School for Resource and Environmental Studies, Dalhousie University, 6100 University Avenue, Halifax, Nova Scotia B3H 4R2 Canada
[3]*rare* Charitable Research Reserve, 1679 Blair Road, Cambridge, Ontario N3H 4R8 Canada
[*]Corresponding author: justin.gaudon@uwaterloo.ca

Cray, H.A., J.M. Gaudon, and S.D. Murphy. 2021. Introduced earthworms (Lumbricidae) in restored and remnant tallgrass prairies of southern Ontario. Canadian Field-Naturalist 135(3): 234–244. https://doi.org/10.22621/cfn.v135i3.2721

Abstract

Introduced earthworms alter the trajectory and composition of plant communities, for example, through their feeding, burrowing behaviour, and interactions with seeds. High densities of several earthworm species may decrease native biodiversity and disrupt restoration efforts in tallgrass prairies. This affects efforts to conserve and restore such habitat, which is of high conservation and restoration priority in eastern North America and typically restored through seeding events. To date, *Lumbricus terrestris* (Lumbricidae) and other species have remained largely undocumented in tallgrass prairies. We surveyed 22 tallgrass prairie sites in southern Ontario, Canada, to document earthworm density and species. *Lumbricus terrestris* was found at all sites. The average density was 66 ± 91 (SD) earthworms/m^2 across our sampling plots, mostly juveniles (~94%). The number of all earthworms per plot significantly increased with the number of earthworm middens in each plot ($\chi^2_1 = 4.50$, $P = 0.034$). Prairies with a large number of middens had high earthworm density, but middens alone appear to explain little variation in our data (linear mixed-effects model, marginal $R^2 = 0.12$) meaning there are other biologically important factors that affect their density. However, we found no effects of soil pH, organic matter content, or texture on the number earthworms per plot suggesting that earthworms can invade a range of tallgrass prairie soils with pH values between 5.27 and 7.67.

Key words: Earthworm invasion; invasive species; *Lumbricus terrestris*; restoration ecology; tallgrass prairie restoration

Introduction

Agriculture, urban development, and woody encroachment have reduced the tallgrass prairie ecosystem in North America to less than 1% of its historical area (Bakowsky and Riley 1994; Samson and Knopf 1994). In southern Ontario, Canada, tallgrass prairie likely once covered 800–2000 km^2, but now typically exists as small, isolated parcels (Bakowsky and Riley 1994; Rodger 1998). These parcels are composed of plants that are unique to the tallgrass prairie ecosystem and provide rare habitat for native biodiversity (Morgan *et al.* 1995). Active restoration of tallgrass prairie is ongoing, often on former croplands, with the aim of re-establishing native vegetation communities through seeding (Kindscher and Tieszen 1998). Restoration sites vary in size and connectivity, but most are <0.03 km^2 and isolated (Bakowsky and Riley 1994). The success of tallgrass prairie restoration efforts has been mixed, as restoring historical, highly diverse vegetation communities may take a long time (Kindscher and Tieszen 1998). The richness of native plant species in restored tallgrass prairie is usually lower than in remnant parcels and often declines over time, whereas the richness of exotic plants is higher and increases with time (Leach and Givnish 1996; Sluis 2002; Camill *et al.* 2004; Martin *et al.* 2005; McLachlan and Knispel 2005).

Earthworms (Oligochaeta: Lumbricidae) are influential soil macro-organisms. As a result of their high consumption rates, burrowing activity, and large body sizes, they alter fundamental ecosystem processes, such as nutrient cycling, water infiltration, rates of decomposition, and seedbank conditions; this affects the availability of resources for other soil biota and influences vegetative communities (Brown 1995; Edwards and Bohlen 1996; Forey *et al.* 2011). In the context of tallgrass prairie restoration, which is typically initiated by a single seeding event, the impact of introduced earthworms on seed dispersal and consumption may be exacerbated. Earthworms are

---

A contribution towards the cost of this publication has been provided by the Thomas Manning Memorial Fund of the Ottawa Field-Naturalists' Club.

increasingly recognized as important and under-studied seed predators (Eisenhauer *et al*. 2010; Forey *et al*. 2011; Drouin *et al*. 2014) that affect the dispersal, survival, and establishment of seeds through selection pressure (Forey *et al*. 2011; Clause *et al*. 2016). This pressure includes selective ingestion as well as digestion and egestion (Shumway and Koide 1994; Eisenhauer *et al*. 2009; Clause *et al*. 2016; McTavish and Murphy 2019), accelerated or inhibited germination (Decaëns *et al*. 2003; Clause *et al.* 2011), and transport of seeds (McRill and Sagar 1973; Thompson *et al.* 1994). Thus, earthworms have direct effects on the composition and function of plant communities, but these vary by ecosystem, and species–specific interactions are common (Shumway and Koide 1994; Eisenhauer *et al.* 2009; Clause *et al.* 2016; Craven *et al.* 2016). These effects compound other post-dispersal challenges to seed establishment, e.g., granivory by birds, rodents, and insects; competition with ruderal weeds; and water availability (Moles and Westoby 2006; Eisenhauer and Scheu 2008; Forey *et al.* 2011). Thus, it is critical to understand the distribution and density of earthworms to effectively manage and restore invaded ecosystems.

Although earthworms did not survive the Wisconsin glaciation that receded approximately 11 000 years ago in Canada and the northern United States (Gates 1982; Reynolds 1994; Edwards and Bohlen 1996), 21 species have been recorded in Ontario. Of these, 19 are introductions from Europe and Asia, while the other two suspected native species, *Bimastos parvus* Eisen and *Sparganophilus tamesis* Benham, are provincially rare and known exclusively from arboreta and aquatic or semi-aquatic mud, respectively (Reynolds 2014). Introduced earthworms can expand their range naturally by only 5–10 m/year (Marinissen and van den Bosch 1992); consistent with their origin, most introduced earthworms expand their range because humans move them (soil and bait movement; Callaham *et al.* 2006; Hale 2007). Despite human dispersal (Edwards and Bohlen 1996), the distribution of earthworms is limited by soil pH, texture, and moisture as well as food availability (i.e., leaf litter, vegetation, and consolidated organic matter) and temperature (Guild 1952; Murchie 1958).

Previous work on Ontario earthworms has focussed on compiling individual observations to create a province-wide map of distribution by species (Reynolds 1977, 2011a,b; Reynolds and Reynolds 1992) and earthworm-driven changes in forest ecosystems (Cassin and Kotanen 2016; Jennings and Watmough 2016; Choi *et al.* 2017). Although the negative effects of industrial tillage practices on earthworm populations in agricultural fields are well established (Clapperton *et al.* 1997; VandenBygaart *et al.* 1999; Simonsen *et al.* 2010; Briones and Schmidt 2017), there is neither an estimate of the average biomass of earthworms in Ontario soils nor a comprehensive survey of earthworm species, densities, and biomass. Such surveys can be difficult if earthworms in samples are mostly juveniles (e.g., as in surveys of deadwood in forests; Ashwood *et al.* 2019), which are difficult to identify to species.

Although the establishment and spread of non-native earthworm species in North America has been occurring for centuries, we are only beginning to understand their current distribution (Phillips *et al.* 2019). *Lumbricus terrestris* (Lumbricidae) appears to be widely distributed (Addison 2009), perhaps because it is commonly used as fishing bait (Keller *et al.* 2007). Research conducted in the midwestern United States (e.g., Callaham *et al.* 2001, 2003; Loss *et al.* 2017) can be relevant to Ontario because the two areas are part of the current northern range limit of tallgrass prairie. However, research is still needed in Ontario because Canada and the northern United States had few widespread native earthworm communities following glaciation (Reynolds 2014), the northern tallgrass prairie plant community of Ontario forms a distinct subtype (Rodger 1998), and Ontario tallgrass prairie conservation remnants and restorations occur on a small scale (e.g., <1 ha; Bakowsky and Riley 1994).

Introduced earthworms have severely impacted North American ecosystems and tallgrass prairies in southern Ontario may experience similar effects of earthworm invasion, specifically changes in plant composition and desired trajectory in restored sites. The objectives of this study were (1) to determine the densities of earthworms in tallgrass prairies of southern Ontario, (2) to document the species of earthworms found in tallgrass prairies, and (3) to summarize the relationship between earthworm numbers and soil properties to provide some direction on where and how to focus tallgrass prairie restoration efforts.

Methods

For sampling earthworm populations, we selected 22 tallgrass prairie sites, including five remnant, two restored-remnant, and 15 restored sites in southern Ontario, Canada (Table 1, Figure 1). Restored-remnant sites describe prairie that has re-established unexpectedly from the seedbank following accidental fire or large-scale brush cutting. To represent the diversity of tallgrass prairie sampling sites across southern Ontario, we selected sites that varied in geographic range, management history, restoration age, adjacent land use, parcel size, and soil characteristics. Study site vegetation communities included ruderal weeds,

TABLE 1. Site characteristics and management history of restored and remnant tallgrass prairies sampled for earthworms in southern Ontario, Canada.

Site no.	Location*	Area, ha	Status	Adjacent land use†	Year restoration started	Method of restoration	Most recent burn	Site management practice		
								Herbicide	Removal of woody plants	Grazed
1	Windsor	17.5	Remnant	P, H	—	—	2010	—	—	—
2	Cambridge	1.2	Remnant	P, H, A	—	—	2010	—	Yes	—
3	Windsor	1.3	Remnant	I, P, H	—	—	2012	Yes	Yes	—
4	Windsor	1.9	Remnant	I, P, H	—	—	2014	Yes	Yes	—
5	East Gwillimbury	3.5	Remnant	P, H	—	—	—	—	Yes	—
6	Brantford	3.3	Restored-remnant	P, H	2006	Seeded	2015	—	Yes	—
7	East Gwillimbury	0.6	Restored-remnant	P, H	2015	—	—	Yes	—	—
8	Oakville	3.3	Restored	P, A, H	2015	Seeded	—	Yes	Yes	—
9	Windsor	1.6	Restored	I, H, A, E	2013	Seeded	—	—	—	—
10	Windsor	0.3	Restored	I, H	2013	Planted	—	Yes	—	—
11	Windsor	2.1	Restored	I, H	2013	Seeded + planted	—	Yes	—	—
12	Cambridge	1.2	Restored	P, E, H, A	2006	Seeded + planted	2010	Yes	Yes	—
13	Chatham-Kent	21.5	Restored	A, I	2010	Seeded	—	Yes	Yes	—
14	Middlesex County	2.0	Restored	A, P	2011	Seeded	—	Yes	Yes	Yes
15	Norfolk County	36.0	Restored	P, A	2013	Seeded	—	Yes	Yes	—
16	Norfolk County	14.5	Restored	P, A	2012	Seeded	—	Yes	Yes	—
17	Norfolk County	14.0	Restored	P, A	2011	Seeded	—	Yes	Yes	—
18	Oakville	6.1	Restored	P, I, H	2012	Seeded	—	Yes	—	—
19	Oakville	6.0	Restored	P, I, H	2013	Seeded	—	Yes	—	—
20	Oakville	6.3	Restored	P, I, H	2014	Seeded	—	Yes	—	—
21	Cambridge	16.0	Restored	P, H	2010	Seeded	2015	—	—	—
22	North Dumfries	23.5	Restored	P, A	2011	Seeded	2015	—	Yes	—

*Specific latitude and longitude of sample sites are not provided because of data sensitivity and research permit requirements.
†H = suburban housing, P = protected area, E = resource extraction, A = agriculture, I = major infrastructure.

invasive plant species, and expected southern Ontario tallgrass prairie plants including grasses (Poaceae), such as Big Bluestem (*Andropogon gerardi* Vitman), Yellow Indiangrass (*Sorghastrum nutans* (L.) Nash), Switchgrass (*Panicum virgatum* L.), Little Bluestem (*Schizachyrium scoparium* (Michaux) Nash), and Canada Wildrye (*Elymus canadensis* L.) as well as forbs, such as Wild Bergamot (*Monarda fistulosa* L.; Lamiaceae), Virginia Mountain-mint (*Pycnanthemum virginianum* (L.) B.L. Robinson & Fernald; Lamiaceae), Black-eyed Susan (*Rudbeckia hirta* L; Asteraceae), Grey-headed Prairie Coneflower (*Ratibida pinnata* (Ventenat) Barnhart; Asteraceae), *Asclepias* spp. L. (Apocynaceae), Beardtongue (*Penstemon* spp. Schmidel; Plantaginaceae), Round-headed Bush-clover (*Lespedeza capitata* Michaux; Fabaceae), Dense Blazing-start (*Liatris spicata* (L.) Willdenow; Asteraceae), *Symphyotrichum* spp. Nees (Asteraceae), *Solidago* spp. L. (Asteraceae), and *Desmodium* spp. Desvaux (Fabaceae).

Fieldwork was conducted 10–25 October in 2015 and 3–30 October in 2016. Five plots per site in 2015 and ten plots per site in 2016 were pre-assigned using satellite imagery to distribute sampling plots evenly across the entire prairie area and not within 10 m of any edge. Because of a severe flooding event that led to standing water on the sampling area at six sites (three restored, three remnant) in 2016, the data presented for these sites are from 2015 only. Field sampling was conducted during the day when soil temperatures were above 10°C and no rain had fallen in the previous 24 h.

At each site, earthworms were collected from one 20 × 20 cm plot using a mustard liquid extraction technique (Lawrence and Bowers 2002). Plot boundaries were marked with a plastic frame. At plots

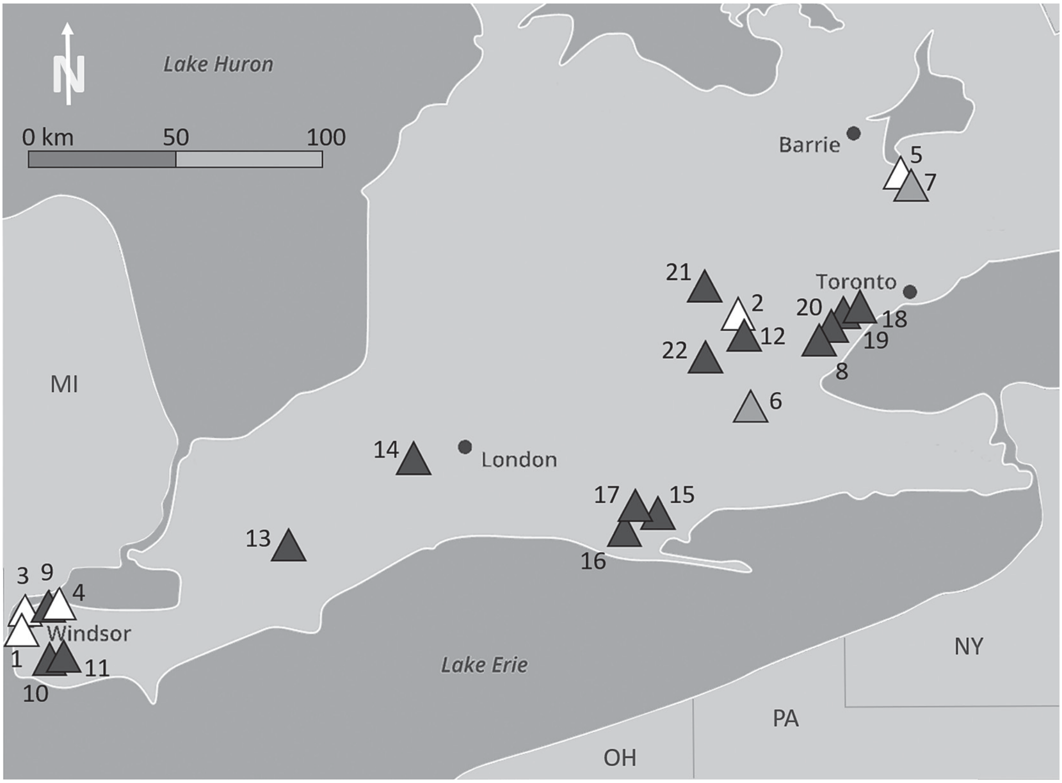


Figure 1. Earthworm sampling locations in restored (▲), remnant (△), and restored-remnant (▲) tallgrass prairies in southern Ontario, Canada.

with litter cover, the surface litter was first removed and searched for earthworms. Then, 2 L of mustard solution (10 g of hot mustard powder [Weston Inc., Bulk Barn, Aurora, Ontario, Canada] per litre of distilled water) was applied to the plot over 10 min, and emerging earthworms were collected for the following 15 min. As we were unable to reliably identify juveniles (i.e., sub-adult but ≥2 cm long) to species level based on physical traits alone, body length and counts were used to characterize the earthworm populations. Each earthworm was allowed to become active in a collection container before its length was measured. We assumed that annelids <2 cm long and white were not earthworms but rather Enchytraeidae (i.e., microdriles, Oligochaeta: Annelida) and, thus, they were not counted.

Adult earthworms were identified by the presence of the clitellum. At each sampling site, a voucher specimen of any adult earthworm that could not be identified in the field was collected and immediately placed in a 75% isopropyl alcohol solution to obtain minimum species counts (i.e., the number of identifiable species) for each site. After being identified using physical attributes (Hale 2007), adult specimens were donated to The Barcode of Life project at the University of Guelph and are curated at that institution. The adult earthworms identified were used to create a minimum species list, which represents the lowest number of species that have been verified to occur at our sampling sites.

Lumbricus terrestris creates a permanent or semi-permanent vertical burrow system that may extend several metres into the soil profile and is likely to be under-sampled using extraction methods appropriate for most other earthworm species (Hamilton and Sillman 1989; Edwards and Bohlen 1996). To achieve a representative sampling of this species, we counted the number of middens that were contained wholly or in part within each 20 × 20 cm sampling plot. Middens are unique to this species in southern Ontario and occur as distinctive piles of cast, organic, and inorganic materials that an individual *L. terrestris* creates around the opening to its vertical burrow (Butt and Grigoropoulou 2010; Stroud *et al.* 2016).

To quantify soil characteristics at each site, three soil samples were collected within 20 cm of each sampling plot using a 3-cm diameter soil corer to a depth of 20 cm after the application of 2 L of mustard solution. Soil samples were stored in a sample bag (Whirl-Pak, Madison, Wisconsin, USA) and frozen until processing. Soil cores from each plot were homogenized and subsampled for analysis of pH, organic matter content, and texture following protocols by McKeague (1978).

Data were analyzed using R version 4.0.3 (R Core Development Team 2020). We tested the effects of soil pH, soil texture, soil organic matter content, and midden area on the number of all earthworms per plot (i.e., density, including juveniles) using a linear mixed-effects model (LMM). In the LMM, soil pH, soil texture, soil organic matter content, and midden area were fixed effects, and site was used as a random effect to account for the repeated measures within each tallgrass prairie site. Model fit was determined by assessing constancy of variance and normality of residuals using graphical methods. This model did not meet our assumptions of constancy of variance and normal residuals, so we $\log(x + 1)$ transformed the number of all earthworms (including juveniles) per plot, which accounted for heteroscedastic and non-normal residuals. Marginal and conditional R^2 values were calculated using the *r.squaredGLMM* function in the "MuMIn" package (Bartoń 2020). We used the *ggpredict* function in the "ggeffects" package (Lüdecke 2018) to compute marginal effects of the number of middens per plot on the number of all earthworms per plot. Data were then back-transformed for graphical representation and graphed using the package "ggplot2" (Wickham 2016). All means are presented with ± 1 SD.

Results

Soil properties varied across the sampling plots: soil pH 5.27–7.67, mean 6.27 ± 0.68. Soil textures across our study sites ranged from sand to silty clay. Organic matter content was 1.7–4.3% and averaged 3.0 ± 1.0% across our sampling plots. The percentage of sand, clay, or silt had no significant effect on the number of all earthworms (including juveniles) per plot in tallgrass prairie soils (sand: $\chi^2_1 = 1.96$, $P = 0.161$; clay: $\chi^2_1 = 1.95$, $P = 0.163$; silt: $\chi^2_1 = 1.96$, $P = 0.161$). There were also no significant effects of soil pH ($\chi^2_1 = 0.12$, $P = 0.728$) or soil organic matter content on the number of all earthworms per plot ($\chi^2_1 = 2.49$, $P = 0.115$).

Earthworms were found at every tallgrass prairie site in this study. Species included *Allolobophora chlorotica* (process ID: HCOEW026-17, sample ID: BIOUG32056-C02), *Aporrectodea longa* (process ID: HCOEW012-17, sample ID: BIOUG32056-A12), *Aporrectodea rosea* (process ID: HCOEW005-17, sample ID: BIOUG32056-A05), *Aporrectodea tuberculata* (process ID: HCOEW009-17, sample ID: BIOUG32056-A09), *Dendrobaena octaedra* (process ID: HCOEW015-17, sample ID: BIOUG32056-B03), *Lumbricus rubellus* (process ID: HCOEW001-17, sample ID: BIOUG32056-A01), *L. terrestris* (process ID: HCOEW029-17, sample ID: BIOUG32056-C05), *Octolasion tyrtaeum* (process ID: HCOEW003-17, sample ID: BIOUG32056-A03), and the *Aporrectodea caliginosa* species complex (process ID: HCOEW019-17, sample ID: BIOUG32056-B07). DNA barcoding analysis could not distinguish between several species in the *A. caliginosa* species complex, so we list this species here. We consider *A. longa* and *A. tuberculata*, as well as *Aporrectodea turgida*, to be part of the *A. caliginosa* species complex. *Lumbricus terrestris* was the only species observed at every site. We report the first record of *D. octaedra* in Waterloo Region, Ontario, Canada, and *L. rubellus* in Halton Region, Ontario, Canada. Voucher specimens were deposited at the Biodiversity Institute of Ontario, University of Guelph. No native earthworms were identified in this study. Earthworm species richness (based on adults) at each site varied between one and five species per site. On average, we found 3 ± 1 earthworm species in each tallgrass prairie.

The total number of all earthworms per site (including juveniles) varied between five and 108 (Table 2), with a mean count of 37 ± 29 earthworms across all sites. The earthworm density across our tallgrass prairie sites was 8–346 earthworms/m^2 (average 66 ± 91 earthworms/m^2). Most of the earthworms found were juveniles (94.0 ± 6.5%). The highest percentage of adult earthworms (17%) was found in site 11, a restored tallgrass prairie with clay loam soil adjacent to suburban housing and other major infrastructure (Table 1). At eight sites, no adult earthworms were collected (Table 2).

The distribution of earthworm size classes varied considerably among sampling sites. Earthworms 5.0–9.9 cm were the most abundant overall (39.3 ± 15.7%, absent from four sites), followed by 1.0–4.9 cm (32.5 ± 25.0%, absent from one site), 10.0–15.0 cm (23.4 ± 24.6%, absent from three sites), and >15 cm (4.9 ± 6.3%, absent from 10 sites; Figure 2).

The number of middens per plot varied from zero to 10, with an average of 3 ± 2 middens per plot. The number of all earthworms per plot (including juveniles) significantly increased with the number of middens ($\chi^2_1 = 4.50$, $P = 0.034$; Figure 3). However, fixed effects in the LMM, such as the number of middens per plot, explained little variation in our data (marginal $R^2 = 0.12$). Most of the variance was explained by the full model (i.e., both fixed and random effects; conditional $R^2 = 0.63$).

TABLE 2. Number of earthworms and species distribution in tallgrass prairies sampled in southern Ontario, Canada.

Site	No. earthworms*		%	Species present†								
no. (plots)	Total	Mean ± SD	adults	*Allobophora chlorotica*	*Allobophora* sp.	*Aporrectodea longa*	*Aporrectodea rosea*	*Aporrectodea tuberculata*	*Dendrobaena octaedra*	*Lumbricus rubellus*	*Lumbricus terrestris*	*Octolasion tyrtaeum*
1 (10)	35	4 ± 3	2	—	—	—	—	—	—	P	P	—
2 (10)	28	3 ± 3	5	—	—	—	—	P	P	—	P	—
3 (5)	31	6 ± 2	15	—	—	—	—	—	—	—	P	—
4 (5)	35	7 ± 5	4	—	—	—	—	—	—	—	P	—
5 (10)	9	1 ± 1	0	—	—	—	—	—	—	—	P	—
6 (10)	5	1 ± 1	0	—	P	—	—	—	—	—	P	—
7 (10)	18	2 ± 1	4	—	—	—	—	—	—	—	P	—
8 (10)	9	1 ± 1	0	—	—	—	—	—	—	—	P	—
9 (5)	37	7 ± 6	16	—	—	P	—	—	—	—	P	—
10 (5)	70	14 ± 8	0	—	—	—	—	—	—	—	P	—
11 (5)	108	22 ± 18	17	—	P	—	—	—	—	—	P	—
12 (10)	44	4 ± 3	11	—	—	—	P	P	—	P	P	P
13 (10)	5	1 ± 1	0	—	—	—	—	P	—	—	P	—
14 (10)	7	1 ± 1	0	—	—	—	—	—	—	—	P	—
15 (10)	79	8 ± 5	13	—	P	—	—	—	—	P	P	—
16 (10)	49	5 ± 4	3	—	—	—	—	P	—	—	P	—
17 (10)	7	1 ± 2	0	—	—	—	—	—	—	—	P	—
18 (10)	45	5 ± 3	9	P	—	—	—	P	—	P	P	—
19 (10)	68	7 ± 4	16	P	—	—	—	P	—	P	P	—
20 (10)	81	8 ± 3	15	P	—	—	—	P	—	P	P	—
21 (10)	32	3 ± 1	8	P	—	—	—	—	—	P	P	P
22 (10)	6	1 ± 1	0	—	P	—	—	—	—	P	P	—

*Includes juveniles $\geq$2 cm long.

†Only presence (P) or not detected (—) is available at the species level.

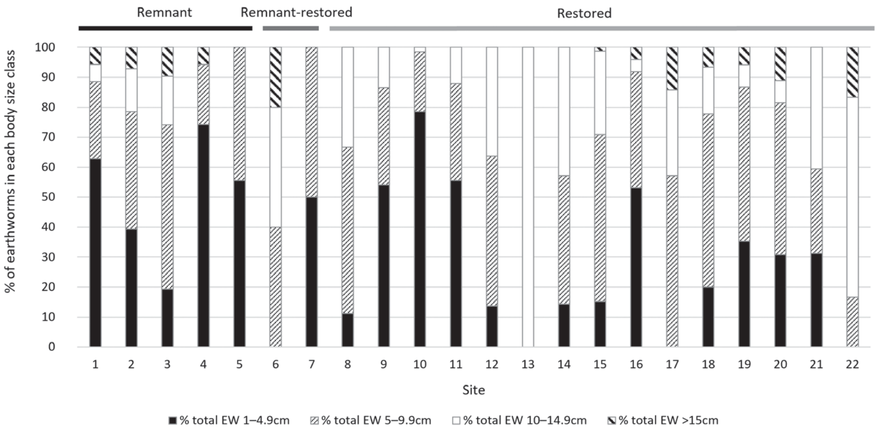


FIGURE 2. Percentage of earthworms (EW) in each body size class in tallgrass prairies sampled across southern Ontario, Canada.

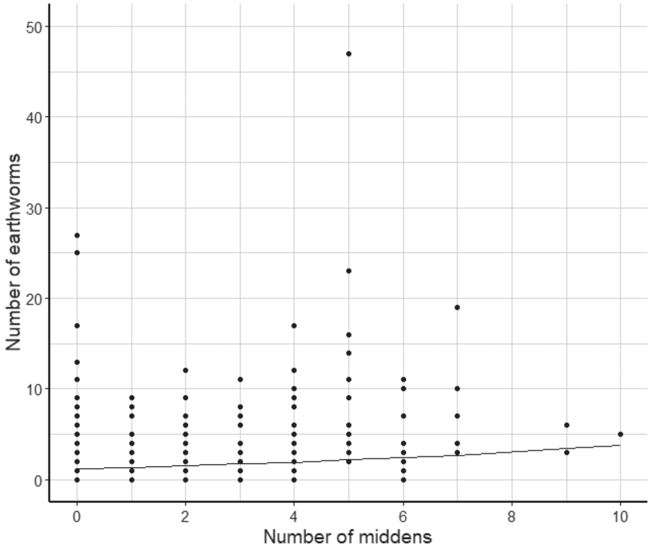


FIGURE 3. Relationship between the number of all earthworms (including juveniles ≥2 cm long) per plot and number of middens per plot in tallgrass prairies in southern Ontario. The solid line shows the predicted values computed using the R function *ggpredict*.

Discussion

Introduced earthworms were found in all the tallgrass prairie sites that we examined in southern Ontario, Canada. The earthworms we found likely underrepresent the number of endogeic and anecic species in particular because of the vertical stratification of earthworm communities, their phenology, and our choice of sampling method (Edwards and Bohlen 1996). Because we found earthworms at all sites and in all plots at an average density of 66 ± 91 earthworms/m^2, we suspect that earthworms are now important macrofauna in southern Ontario tallgrass prairie soils compared to before their introduction (Forey *et al.* 2011).

Comparisons among studies of earthworm populations are complicated by variations in timing, method of collection, and their uneven distribution. Hand sorting is usually considered superior to other methods for quantifying earthworm populations; in comparison, the mustard extraction method will tend to underestimate numbers (Pelosi *et al.* 2009). The main argument against hand extraction is that it necessitates digging up, breaking apart, and sieving an entire column of soil for each sampling plot (Nordström and Rundgren 1972). This has consequences for the sampling plot, including homogenization of the soil profile and disturbance of plant root networks, fungal hyphae, and soil-dwelling organisms. In contrast, mustard extraction is a low-disturbance method particularly suitable for use in sensitive, conservation-focussed habitats. Although we anticipated low earthworm densities as a result of using the mustard solution extraction method, we found densities similar to those documented in other ecosystems (Shakir and Dindal 1997; Price and Gordon 1998; Bohlen *et al.* 2004).

It was not surprising to find that the number of middens was related to the number of all earthworms per plot (including juveniles). Although the number of earthworms was poorly correlated with the number of middens in our tallgrass prairie plots (i.e., little variation in our data was explained), middens may be centres of activity for other earthworm species, meaning that the invasion of *L. terrestris* may facilitate introductions of other species (Butt and Lowe 2007). Therefore, plots with more middens could be expected to contain higher numbers of earthworms, including species other than *L. terrestris*. Middens may provide some indication of earthworm density in tallgrass prairies as observed in forests ecosystems (Loss *et al.* 2013); thus, assessing midden prevalence may be a cost-effective and low-impact approach to determining whether an alternative planting method is needed for tallgrass prairie restoration (e.g., plugging in addition to seeding).

If there was temporal bias from sampling only in October, we would have expected to see earthworms that were similar in size and of the same species. The high percentage of juvenile earthworms of varying size recorded in this study suggests that the populations we sampled are persistent and successfully reproducing. Whereas some species can only breed sexually (e.g., earthworms in the genera *Lumbricus*), many others can reproduce parthenogenetically (e.g., *Octolasion* and *Dendrobaena* spp.; Edwards and Bohlen 1996). With this reproductive flexibility, we suspect that the earthworm populations we found are either resilient to stochastic disturbances, such as the prolonged flooding or fire events that have occurred in our tallgrass prairie sites (e.g., by escaping flooded or burned areas), and/or have recolonized from nearby areas post-disturbance. If this is the case, earthworms now represent a persistent and dominant soil fauna in tallgrass prairies in southern Ontario, which complicates our capacity to manage and restore these ecosystems, especially because of earthworms' potential to damage seeds.

We found that *L. terrestris* density was similar across a range of tallgrass prairie sites. Although we specifically analyzed site history (i.e., remnant versus restored tallgrass prairie), that does not appear to influence susceptibility to invasion based on our data. As such, restoration efforts in all sites may require high-density broadcasting of seeds to account for the relatively high density of earthworms that will ingest and transport seeds. Because we did not observe effects of soil texture or soil pH on earthworm density, our work suggests that ecosystems previously considered resistant to earthworm invasion (e.g., sandy and acidic soils; Frelich *et al.* 2006) should be monitored for earthworm introductions, and proactive planning may be a necessary component of restoration efforts in ecosystem management plans.

New research using nested polymerase chain reaction to improve detection of earthworm DNA is promising for early detection and rapid response to introduced earthworms, but has yet to be widely implemented (Jackson *et al.* 2017). If viable, this approach would be effective in generating a comprehensive survey of earthworm distribution and anticipating future earthworm spread. This is particularly important in the context of tallgrass prairie restoration because plant community trajectory and composition are affected by earthworm species-specific interactions with seeds, including ingestion and digestion, accelerated or inhibited germination, and seed transport through the soil profile (McRill and Sagar 1973; Shumway and Koide 1994; Thompson *et al.* 1994; Decaëns *et al.* 2003; Eisenhauer *et al.* 2009; Clause *et al.* 2011, 2016).

Author Contributions

Conceptualization and Design: H.A.C. and S.D.M.; Investigation: H.A.C.; Formal Analysis: H.A.C. and J.M.G.; Writing: H.A.C., J.M.G., and S.D.M.

Acknowledgements

We thank the *rare* Charitable Research Reserve, Conservation Halton, the Fadden family, Ontario Parks, the Ministry of Natural Resources and Forestry, the Ministry of Transportation, AMEC Foster Wheeler, Wayneo, the Nature Conservancy of Canada, the Grand River Conservation Authority, and the Lower Thames Valley Conservation Authority for permitting for site access. We also thank John W. Reynolds for sharing his extensive knowledge of North America's earthworms, Michael J. McTavish for lending his expertise on earthworm identification, and three anonymous reviewers for their helpful comments on an earlier draft of this manuscript. Financial support was provided by Natural Sciences and Engineering Research Council (scholarship to H.A.C. and funding to S.D.M.) and the *rare* Charitable Research Reserve.

Literature Cited

Addison, J.A. 2009. Distribution and impacts of invasive earthworms in Canadian forest ecosystems. Biological Invasions 11: 59–79. https://doi.org/10.1007/s10530-008-9320-4

Ashwood, F., E.I. Venguelova, S. Benham, and K.R. Butt. 2019. Developing a systematic sampling method for earthworms in and around deadwood. Forest Ecosystems 6: 33. https://doi.org/10.1186/s40663-019-0193-z

Bakowsky, W., and J. Riley. 1994. A survey of the prairies and savannas of southern Ontario. Pages 7–16 *in* Proceedings of the Thirteenth North American Prairie Conference: Spirit of the Land, Our Prairie Legacy. *Edited by* P.D. Lewis, A. Woodliffer, and P. Pratt. Corporation of the City of Windsor, Windsor, Ontario, Canada.

Bartoń, K. 2019. MuMIn: multi-model inference. R package version 1.43.17. Accessed 17 January 2021. https://CRAN.R-project.org/package=MuMIn.

Bohlen, P.J., P.M. Groffman, T.J. Fahey, M.C. Fisk, E. Suarez, D.M. Pelletier, and R.T. Fahey. 2004. Ecosystem consequences of exotic earthworm invasion of north temperate forests. Ecosystems 7: 1–12. https://doi.org/10.1007/s10021-003-0126-z

Briones, M.J.I., and O. Schmidt. 2017. Conventional tillage decreases the abundance and biomass of earthworms and alters their community structure in a global meta-analysis. Global Change Biology 23: 4396–4419. https://doi.org/10.1111/gcb.13744

Brown, G.G. 1995. How do earthworms affect microfloral and faunal community diversity? Plant and Soil 170: 209–231. https://doi.org/10.1007/bf02183068

Butt, K.R., and N. Grigoropoulou. 2010. Basic research tools for earthworm ecology. Applied and Environmental Soil Science 2010: 562816. https://doi.org/10.1155/2010/562816

Butt, K.R., and C.N. Lowe. 2007. Presence of earthworm species within and beneath *Lumbricus terrestris* (L.) middens. European Journal of Soil Biology 43: S57–S60. https://doi.org/10.1016/j.ejsobi.2007.08.002

Callaham, M.A., J.M. Blair, and P.F. Hendrix. 2001. Different behavioral patterns of the earthworms *Octolasion tyrtaeum* and *Diplocardia* spp. in tallgrass prairie soils: potential influences on plant growth. Biology and Fertility of Soils 34: 49–56. https://doi.org/10.1007/s003740100370

Callaham, M.A., J.M. Blair, T.C. Todd, D.J. Kitchen, and M.R. Whiles. 2003. Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass. Soil Biology and Biochemistry 35: 1079–1093. https://doi.org/10.1016/s0038-0717(03)00153-6

Callaham, M.A., G. González, C.M. Hale, L. Heneghan, S.L. Lachnicht, and X. Zou. 2006. Policy and management responses to earthworm invasions in North America. Pages 117–129 *in* Biological Invasions Belowground: Earthworms as Invasive Species. *Edited by* P.F. Henrix. Springer, Dordrecht, Netherlands. https://doi.org/10.1007/978-1-4020-5429-7_11

Camill, P., M.J. McKone, S.T. Sturges, W.J. Severud, E. Ellis, J. Limmer, C.B. Martin, R.T. Navratil, A.J. Purdie, B.S. Sandel, S. Talukder, and A. Trout. 2004. Community- and ecosystem-level changes in a species-rich tallgrass prairie restoration. Ecological Applications 14: 1680–1694. https://doi.org/10.1890/03-5273

Cassin, C.M., and P.M. Kotanen. 2016. Invasive earthworms as seed predators of temperate forest plants. Biological Invasions 18: 1567–1580. https://doi.org/10.1007/s10530-016-1101-x

Choi, A., T.E. Sackett, S.M. Smith, and M. Bellocq. 2017. Exotic earthworm (Oligochaeta: Lumbricidae) assemblages on a landscape-scale in central Canadian woodlands: importance of region and vegetation type. Canadian Journal of Forest Research 47: 935–945. https://doi.org/10.1139/cjfr-2016-0337

Clapperton, M.J., J.J. Miller, F.J. Larney, and C.W. Lindwall. 1997. Earthworm populations as affected by long-term tillage practices in southern Alberta, Canada. Soil Biology and Biochemistry 29: 631–633. https://doi.org/10.1016/s0038-0717(96)00189-7

Clause, J., E. Forey, N. Eisenhauer, C.E. Seal, A. Soudey, L. Colville, and S. Barot. 2016. Seed selection by earthworms: chemical seed properties matter more than morphological traits. Plant and Soil 413: 97–110. https://doi.org/10.1007/s11104-016-3085-9

Clause, J., P. Margerie, E. Langlois, T. Decaëns, and E. Forey. 2011. Fat but slim: criteria of seed attractiveness for earthworms. Pedobiologia 54: S159–S165. https://doi.org/10.1016/j.pedobi.2011.08.007

Craven, D., M.P. Thakur, E.K. Cameron, L.E. Frelich, R. Beauséjour, R.B. Blair, B. Blossey, J. Burtis, A. Choi, A. Dávalos, T.J. Fahey, N.A. Fisichelli, K. Gibson, I.T. Handa, K. Hopfensperger, S.R. Loss, V. Nuzzo, J.C. Maerz, T. Sackett, B.C. Scharenbroch, S.M. Smith, M. Vellend, L.G. Umek, and N. Eisenhauer. 2016. The unseen invaders: introduced earthworms as drivers of change in plant communities in North American forests (a meta-analysis). Global Change Biology 23: 1065–1074. https://doi.org/10.1111/gcb.13446

Decaëns, T., L. Mariani, N. Betancourt, and J.J. Jiménez. 2003. Seed dispersion by surface casting activities of earthworms in Colombian grasslands. Acta Oecologica 24: 175–185. https://doi.org/10.1016/s1146-609x(03)00083-3

Drouin, M., R. Bradley, L. Lapointe, and J. Whalen. 2014. Non-native anecic earthworms (*Lumbricus terrestris* L.) reduce seed germination and seedling survival of temperate and boreal trees species. Applied Soil Ecology 75: 145–149. https://doi.org/10.1016/j.apsoil.2013.11.006

Edwards, C.A., and P.J. Bohlen. 1996. Biology and Ecology of Earthworms. Third Edition. Chapman and Hall, London, United Kingdom.

Eisenhauer, N., O. Butenschoen, S. Radsick, and S. Scheu. 2010. Earthworms as seedling predators: importance of seeds and seedlings for earthworm nutrition. Soil Biology and Biochemistry 42: 1245–1252. https://doi.org/10.1016/j.soilbio.2010.04.012

Eisenhauer, N., and S. Scheu. 2008. Invasibility of experimental grassland communities: the role of earthworms, plant functional group identity and seed size. Oikos 117: 1026–1036. https://doi.org/10.1111/j.0030-1299.2008.16812.x

Eisenhauer, N., D. Straube, E.A. Johnson, D. Parkinson, and S. Scheu. 2009. Exotic ecosystem engineers change the emergence of plants from the seed bank of a deciduous forest. Ecosystems 12: 1008–1016. https://doi.org/10.1007/s10021-009-9275-z

Forey, E., S. Barot, T. Decaëns, E. Langlois, K.-R. Laossi, P. Margerie, S. Scheu, and N. Eisenhauer. 2011. Importance of earthworm–seed interactions for the composition and structure of plant communities: a review. Acta Oecologica 37: 594–603. https://doi.org/10.1016/j.actao.2011.03.001

Frelich, L.E., C.M. Hale, S. Scheu, A.R. Holdsworth, L. Heneghan, P.J. Bohlen, and P.B. Reich. 2006. Earthworm invasion into previously earthworm-free temperate and boreal forests. Biological Invasions 8: 1235–1245. https://doi.org/10.1007/978-1-4020-5429-7_5

Gates, G.E. 1982. Farewell to North American megadriles. Megadrilogica 4(1–2): 12–77.

Guild, W.J. 1952. Variation in earthworm numbers within field populations. Journal of Animal Ecology 21: 169–183. https://doi.org/10.2307/1956

Hale, C. 2007. Earthworms of the Great Lakes. Kollath and Stensaas, Duluth, Minnesota, USA.

Hamilton, W.E., and D.Y. Sillman. 1989. Influence of earthworm middens on the distribution of soil microarthropods. Biology and Fertility of Soils 8: 279–284. https://doi.org/10.1007/bf00266491

Jackson, M., C. Myrholm, C. Shaw, and T. Ramsfield. 2017. Using nested PCR to improve detection of earthworm eDNA in Canada. Soil Biology and Biochemistry 113: 215–218. https://doi.org/10.1016/j.soilbio.2017.06.009

Jennings, B.W., and S.A. Watmough. 2016. The impact of invasive earthworms on soil respiration and soil carbon within temperate hardwood forests. Ecosystems 19: 942–954. https://doi.org/10.1007/s10021-016-9977-y

Keller, R.P., A.N. Cox, C. Van Loon, D.M. Lodge, L.-M. Herborg, and J. Rothlisberger. 2007. From bait shops to the forest floor: earthworm use and disposal by anglers. American Midland Naturalist 158: 321–328. https://doi.org/10.1674/0003-0031(2007)158[321:fbsttf]2.0.co;2

Kindscher, K., and L.L. Tieszen. 1998. Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. Restoration Ecology 6: 181–196. https://doi.org/10.1111/j.1526-100x.1998.06210.x

Lawrence, A.P., and M.A. Bowers. 2002. A test of the 'hot' mustard extraction method of sampling earthworms. Soil Biology and Biochemistry 34: 549–552. https://doi.org/10.1016/s0038-0717(01)00211-5

Leach, M.K., and T.J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. Science 273: 1555–1558. https://doi.org/10.1126/science.273.5281.1555

Loss, S.R., R.M. Hueffmeier, C.M. Hale, G.E. Host, G. Sjerven, and L.E. Frelich. 2013. Earthworm invasions in northern hardwood forests: a rapid assessment method. Natural Areas Journal 33: 21–30. https://doi.org/10.3375/043.033.0103

Loss, S.R., S. Paudel, C.M. Laughlin, and C. Zou. 2017. Local-scale correlates of native and non-native earthworm distributions in juniper-encroached tallgrass prairie. Biological Invasions 19: 1621–1635. https://doi.org/10.1007/s10530-017-1383-7

Lüdecke, D. 2018. ggeffects: tidy data frames of marginal effects from regression models. Journal of Open Source Software 3: 772. http://doi.org/10.21105/joss.00772

Marinissen, J.C.Y., and F. van den Bosch. 1992. Colonization of new habitats by earthworms. Oecologia 91: 371–376. https://doi.org/10.1007/bf00317626

Martin, L.M., K.A. Moloney, and B.J. Wilsey. 2005. An assessment of grassland restoration success using species diversity components. Journal of Applied Ecology 42: 327–336. https://doi.org/10.1111/j.1365-2664.2005.01019.x

McKeague, J.A. 1978. Manual on Soil Sampling and Methods of Analysis. Second Edition. Canadian Society of Soil Science, Ottawa, Ontario, Canada.

McLachlan, S.M., and A.L. Knispel. 2005. Assessment of long-term tallgrass prairie restoration in Manitoba, Canada. Biological Conservation 124: 75–88. https://doi.org/10.1016/j.biocon.2005.01.014

McRill, M., and G.R. Sagar. 1973. Earthworms and seeds. Nature 243: 482. https://doi.org/10.1038/243482a0

McTavish, M.J., and S.D. Murphy. 2019. Seed density and previous egestion affect earthworm seed ingestion: preliminary observations using granivory of *Alliaria petiolata* by *Lumbricus terrestris*. Applied Soil Ecology 139: 29–31. https://doi.org/10.1016/j.apsoil.2019.01.019

Moles, A.T., and M. Westoby. 2006. Seed size and plant strategy across the whole life cycle. Oikos 113: 91–105. https://doi.org/10.1111/j.0030-1299.2006.14194.x

Morgan, J.P., D.R. Collicutt, and J.D. Thompson. 1995. Restoring Canada's Native Prairies: a Practical Manual. Prairie Habitats, Argyle, Manitoba, Canada.

Murchie, W.R. 1958. Biology of the oligochaete *Eisenia rosea* (Savigny) in an upland forest of southern Michigan. American Midland Naturalist 66: 113–131. https://doi.org/10.2307/2422469

Nordström, S., and S. Rundgren. 1972. Methods of sampling lumbricids. Oikos 23: 344–352. https://doi.org/10.2307/3543173

Pelosi, C., M. Bertrand, Y. Capowiez, H. Boizard, and J. Roger-Estrade. 2009. Earthworm collection from agricultural fields: comparisons of selected expellants in presence/absence of hand-sorting. European Journal of Soil Biology 45: 176–183. https://doi.org/10.1016/j.ejsobi.2008.09.013

Phillips, H.R.P., C.A. Guerra, M.L.C. Bartz, M.J.I. Briones, G. Brown, T.W. Crowther, O. Ferlian, K.B. Gongalsky, J. van den Hoogen, J. Krebs, A. Orgiazzi, D. Routh, B. Schwarz, E.M. Bach, J.M. Bennett, U. Brose, T. Decaëns, B. König-Ries, M. Loreau, J. Mathieu, C. Mulder, W.H. van der Putten, K.S. Ramirez, M.C. Rillig, D. Russell, M. Rutgers, M.P. Thakur, F.T. de Vries, D.H. Wall, D.A. Wardle, M. Arai, F.O. Ayuke, G.H. Baker, R. Beauséjour, J.C. Bedano, K. Birkhofer, E. Blanchart, B. Blossey, T. Bolger, R.L. Bradley, M.A. Callaham, Y. Capowiez, M.E. Caulfield, A. Choi, F.V. Crotty, J.M. Crumsey, A. Dávalos, D.J. Diaz Cosin, A. Dominguez, A.E.

Duhour, N. van Eekeren, C. Emmerling, L.B. Falco, R. Fernández, S.J. Fonte, C. Fragoso, A.L.C. Franco, M. Fugère, A.T. Fusilero, S. Gholami, M.J. Gundale, M.G. López, D.K. Hackenberger, L.M. Hernández, T. Hishi, A.R. Holdsworth, M. Holmstrup, K.N. Hopfensperger, E.H. Lwanga, V. Huhta, T.T. Hurisso, B.V. Iannone III, M. Iordache, M. Joschko, N. Kaneko, R. Kanianska, A.M. Keith, C.A. Kelly, M.L. Kernecker, J. Klaminder, A.W. Koné, Y. Kooch, S.T. Kukkonen, H. Lalthenzara, D.R. Lammel, I.M. Lebedev, Y. Li, J.B. Jesus Lidon, N.K. Lincoln, S.R. Loss, R. Marichal, R. Matula, J. Hendrik Moos, G. Moreno, A. Morón-Ríos, B. Muys, J. Neirynck, L. Norgrove, M. Novo, V. Nuutinen, V. Nuzzo, M. Rahman, P.J. Pansu, S. Paudel, G. Pérès, L. Pérez-Camacho, R. Piñeiro, J.-F. Ponge, M.I. Rashid, S. Rebollo, J. Rodeiro-Iglesias, M.Á. Rodríguez, A.M. Roth, G.X. Rousseau, A. Rozen, E. Sayad, L. van Schaik, B.C. Scharenbroch, M. Schirrmann, O. Schmidt, B. Schröder, J. Seeber, M.P. Shashkov, J. Singh, S.M. Smith, M. Steinwandter, J.A. Talavera, D. Trigo, J. Tsukamoto, A.W. de Valença, S.J. Vanek, I. Virto, A.A. Wackett, M.W. Warren, N.H. Wehr, J.K. Whalen, M.B. Wironen, V. Wolters, I.V. Zenkova, Weixin Zhang, E.K. Cameron, and N. Eisenhauer. 2019. Global distribution of earthworm diversity. Science 366: 480–485. https://doi.org/10.1126/science.aax4851

Price, G.W., and A.M. Gordon. 1998. Spatial and temporal distribution of earthworms in a temperate intercropping system in southern Ontario, Canada. Agroforestry Systems 44: 141–149.

R Core Development Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reynolds, J.W. 1977. The earthworms (Lumbricidae and Sparganophilidae) of Ontario. Life Sciences Miscellaneous Publications, Royal Ontario Museum, Toronto, Ontario, Canada. https://doi.org/10.5962/bhl.title.60740

Reynolds, J.W. 1994. The distribution of the earthworms (Oligochaeta) of Indiana: a case for the post quaternary introduction theory for megadrile migration in North America. Megadrilogica 5(3): 28–32.

Reynolds, J.W. 2011a. Earthworms of the University of Guelph Arboretum. Megadrilogica 15(2): 15–20.

Reynolds, J.W. 2011b. The earthworms (Oligochaeta: Lumbricidae) of Pelee Island, Ontario, Canada. Megadrilogica 15(3): 23–33.

Reynolds, J.W. 2014. A checklist by counties of earthworms (Oligochaeta: Lumbricidae, Megascolecidae and Sparganophilidae) in Ontario, Canada. Megadrilogica 16(10): 111–135.

Reynolds, J.W., and J.W. Reynolds. 1992. Additional Ontario earthworm county records (Lumbricidae). Megadrilogica 4(8): 143–144.

Rodger, L. 1998. Tallgrass Communities of Southern Ontario: a Recovery Plan. World Wildlife Fund Canada and the Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. BioScience 44: 418–421. https://doi.org/10.2307/1312365

Shakir, S.H., and D.L. Dindal. 1997. Density and biomass of earthworms in forest and herbaceous microecosystems in central New York, North America. Soil Biology and Biochemistry 29: 275–285. https://doi.org/10.1016/s0038-0717(96)00051-x

Shumway, D.L., and R.T. Koide. 1994. Seed preferences of *Lumbricus terrestris* L. Applied Soil Ecology 1: 11–15. https://doi.org/10.1016/0929-1393(94)90019-1

Simonsen, J., J. Posner, M. Rosemeyer, and J. Baldock. 2010. Endogeic and anecic earthworm abundance in six midwestern cropping systems. Applied Soil Ecology 44: 147–155. https://doi.org/10.1016/j.apsoil.2009.11.005

Sluis, W.J. 2002. Patterns of species richness and composition in re-created grassland. Restoration Ecology 10: 677–684. https://doi.org/10.1046/j.1526-100x.2002.01048.x

Stroud, J.L., D.E. Irons, J.E. Carter, C.W. Watts, P.J. Murray, S.L. Norris, and A.P. Whitmore. 2016. *Lumbricus terrestris* middens are biological and chemical hotspots in a minimum tillage arable ecosystem. Applied Soil Ecology 105: 31–35. https://doi.org/10.1016/j.apsoil.2016.03.019

Thompson, K., A. Green, and A.M. Jewels. 1994. Seeds in soil and worm casts from a neutral grassland. Functional Ecology 8: 29–35. https://doi.org/10.2307/2390108

VandenBygaart, A.J., R. Protz, and A.D. Tomlin. 1999. Changes in pore structure in a no-till chronosequence of silt loam soils, southern Ontario. Canadian Journal of Soil Science 79: 149–160. https://doi.org/10.4141/s98-034

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, New York, USA. Accessed 17 January 2021. https://ggplot2-book.org/.

Received 10 February 2021
Accepted 13 July 2021
Associate Editor: P.M. Catling

The Canadian Field-Naturalist

Note

First evidence of White-footed Deer Mouse (*Peromyscus leucopus*) on mainland New Brunswick, Canada

Howard M. Huynh[1, 2, 3,*], **Donald F. McAlpine**[2], and **Scott A. Pavey**[1]

[1]Canadian Rivers Institute Genomics Laboratory, University of New Brunswick, Saint John, New Brunswick E2L 4L5 Canada
[2]Department of Natural History, New Brunswick Museum, 277 Douglas Avenue, Saint John, New Brunswick E2K 1E5 Canada
[3]Natural History Campus, Canadian Museum of Nature, Gatineau, Quebec J9J 3N7 Canada
[*]Corresponding author: hmhuynh11@gmail.com

Huynh, H.M., D.F. McAlpine, and S.A. Pavey. 2021. First evidence of White-footed Deer Mouse (*Peromyscus leucopus*) on mainland New Brunswick, Canada. Canadian Field-Naturalist 135(3): 245–249. https://doi.org/10.22621/cfn.v135i3.2625

Abstract

White-footed Deer Mouse (*Peromyscus leucopus*) and the closely related, and more northerly ranging, Deer Mouse (*Peromyscus maniculatus*) broadly overlap in distribution and are often difficult to distinguish from each other. Based on molecular genetic data (cytochrome *b* gene), we report two new distribution records for *P. leucopus* for New Brunswick, Canada, the first mainland localities for this species in the province. Previous sampling of *Peromyscus* in New Brunswick may have overlooked the presence of *P. leucopus*, possibly because the specimens collected were all assumed to be *P. maniculatus*. However, current detection in New Brunswick may be part of a broader recent northward range expansion documented to be underway in *P. leucopus*. Although our use of a single mitochondrial gene to identify *P. leucopus* does not eliminate the possibility that the New Brunswick specimens are of hybrid origin, our results support the presence of *P. leucopus* in New Brunswick and suggest more detailed analyses will be required to determine the nature of any genetic interaction between *P. leucopus* and *P. maniculatus* in the province. Recognition of morphologically cryptic *Peromyscus* in southern New Brunswick also emphasizes the need to incorporate comprehensive methods to ensure the correct identification of specimens of this genus in Maritime Canada. We also note the potential implications of this discovery with respect to the incidence of Lyme disease in New Brunswick.

Key words: Distributional range; *Peromyscus*; White-footed Mouse; New Brunswick distribution; Lyme disease

White-footed Deer Mouse (*Peromyscus leucopus*) is one of several species of Nearctic rodents in the speciose genus *Peromyscus*. The species tolerates variable environmental conditions, but is most abundant in warm, wooded-shrubby habitats (Kaufman *et al.* 1983). Compared with the closely related Deer Mouse (*Peromyscus maniculatus*), *P. leucopus* has a less northward-ranging distribution in eastern Canada; the extent of the species' northern range is believed to occur across southern Ontario and Quebec, with a disjunct Maritime population confined to Nova Scotia (Hall 1981; Forbes *et al.* 2010).

Recent studies have documented *P. leucopus* in new localities in northeastern North America, which suggests the species is undergoing a northward range expansion, perhaps in response to climate warming (Roy-Dufresne *et al.* 2013; Fiset *et al.* 2015; Garcia-Elfring *et al.* 2017). Huynh *et al.* (2021) recently documented the presence of *P. leucopus* on Grand Manan Island, based on specimens taken in 2011 and identified via molecular genetic methods. Those vouchers represented the first New Brunswick reports and emphasized the need to establish whether the species was present on the adjacent mainland. Here we report the first evidence for *P. leucopus* on mainland New Brunswick, likewise supported by molecular genetic data, and discuss wildlife management implications of this information.

In 2013–2014, *Peromyscus* spp. were collected from various localities throughout New Brunswick using museum special snap traps (Woodstream Corporation, Lititz, Pennsylvania, purchased from Forestry Suppliers, Inc., Jackson, Mississippi, USA) and Sherman live traps (BioQuip Products, Inc., Rancho Dominguez, California, USA). Mice were collected from several trap lines of 100–125 traps deployed at ~5-m intervals in microhabitats (e.g., entrance to burrows, runways) that appeared suitable for *Peromyscus*. All specimens (*n* = 92) were prepared as traditional museum vouchers (skin and skull), with tissues extracted and preserved in 95% ethanol and archived in the New Brunswick Museum frozen tissue collection.

Genomic DNA was extracted from subsamples of frozen tissues at the Canadian Rivers Institute Genomics Laboratory using an OMEGA DNA extraction kit (Omega Bio-tek, Inc., Norcross, Georgia, USA). DNA samples were subsequently stored in elution buffer (Tris) and archived at −80°C. The entire cytochrome *b* gene (1143 base pairs) for almost all specimens was amplified via polymerase chain reaction (PCR) using primers MVZ05 (Smith and Patton 1993) and PERO3′ (Tiemann-Boege *et al.* 2000). The PCR thermal profile consisted of the following: initial denaturation at 95°C for 2 min, followed by 35 cycles of denaturation at 95°C for 1 min, annealing at 51°C for 1 min, and extension at 72°C for 2 min, with a final extension at 72°C for 7 min. PCR products were subjected to electrophoresis on a 1% agarose gel and then viewed on a molecular imager (ChemiDoc XRS+ Gel Imaging System, Bio-Rad Laboratories, Montréal, Quebec, Canada) to confirm successful amplification of the target gene.

The PCR products were then shipped to Genome Quebec for Sanger sequencing. Resulting sequences were aligned (using ClustalW, a standard general purpose software program for aligning nucleotide sequences) and proofed using the program MEGAX (Kumar *et al.* 2018); chromatograms were examined to verify all base changes. Sequences were then input into BLAST (Basic Local Alignment Search Tool, developed by the National Center for Biotechnology Information) to ascertain species identity (i.e., *P. maniculatus* or *P. leucopus*) and to compare with other *Peromyscus* sequences. Among the 85 samples sequenced (seven of the original 92 did not produce suitable PCR product), two specimens were identified as *P. leucopus*: an adult, lactating, female, 172 mm in total length, trapped 28 May 2014 at Blacks Harbour, Charlotte County (45.059°N, 66.785°W; NBM-MA-13000) and an adult male with testes 9 mm and total length 159 mm, trapped 6 August 2014 at Lake Utopia, Charlotte County (45.170°N, 66.794°W; NBM-MA-14183; Figure 1). NBM-MA-13000 was collected concurrently with *P. maniculatus,* Red-backed Vole (*Myodes gapperi*)*,* and Masked Shrew (*Sorex cinereus*)*,* while NBM-MA-14183 was the sole specimen collected at the Lake Utopia site. The remaining 83 specimens were determined to be *P. maniculatus*. Sequences for the two vouchers of *P. leucopus* were deposited in GenBank: OK263085 and OK263086, respectively.

Range expansion of *P. leucopus* at the species' northeastern range limit has been reported in the northern Great Lakes (Myers *et al.* 2009; Moscarella 2011), in southern Quebec (Garcia-Elfring *et al.* 2017), and in adjacent Maine (Bennett 2020). Such expansion has been attributed mainly to anthropogenic activity, including habitat modification and climate change (Roy-Dufresne *et al.* 2013; Leo and Millien 2017).

The Blacks Harbour and Lake Utopia specimens are the first evidence that *P. leucopus* is present on mainland New Brunswick. Lake Utopia is ~14.5 km north of Blacks Harbour, suggesting that the species is established, at minimum, in the southwestern region of New Brunswick. Mainland New Brunswick records are about 90 km northeast of coastal Maine reports from Mount Desert Island (Bennett 2020) and about 56 km northeast of Great Wass Island (Rich 1993). Mount Desert Island is just 300 m offshore and connected to the mainland by a causeway; Great Wass Island, although about 5 km offshore, is likewise connected to the mainland by a series of causeways that link adjacent islands. New Brunswick records are about 485 km east of the nearest confirmed Quebec records (Fiset *et al*. 2015) and about 350 km west by land to the nearest Nova Scotia occurrences for *P. leucopus* (Naughton 2012).

Huynh *et al.* (2021) reported *P. leucopus* on Grand Manan Island, but it is unclear how or when the species colonized and established itself there, i.e., historical natural dispersal and (or) recent human transport. Blacks Harbour is the northern terminus for ferries that serve as a daily connection between Grand Manan Island and mainland New Brunswick, ferrying passengers, vehicles, and goods year-round. It is feasible that the ferries are an accessible vector for point of dispersal for *Peromyscus*. However, it is possible that *P. leucopus* has been present on both Grand Manan and the adjacent mainland for some time but has been previously undetected. This could be because the species occurs at very low densities in the region and has not been collected in the past (Rich 1993) or, more likely, because it has been assumed that all specimens encountered are *P. maniculatus* and appropriate methods to identify *P. leucopus* have not been used (see Rich *et al.* 1996). It is also possible that *P. leucopus* has been present on Grand Manan, as in Nova Scotia, as a relict population and has only recently recolonized southwestern mainland New Brunswick as part of an apparently recent and now well-documented northward range expansion (Fiset *et al*. 2015).

Garcia-Elfring *et al.* (2017) noted gene flow between *P. leucopus* and *P. maniculatus* via secondary

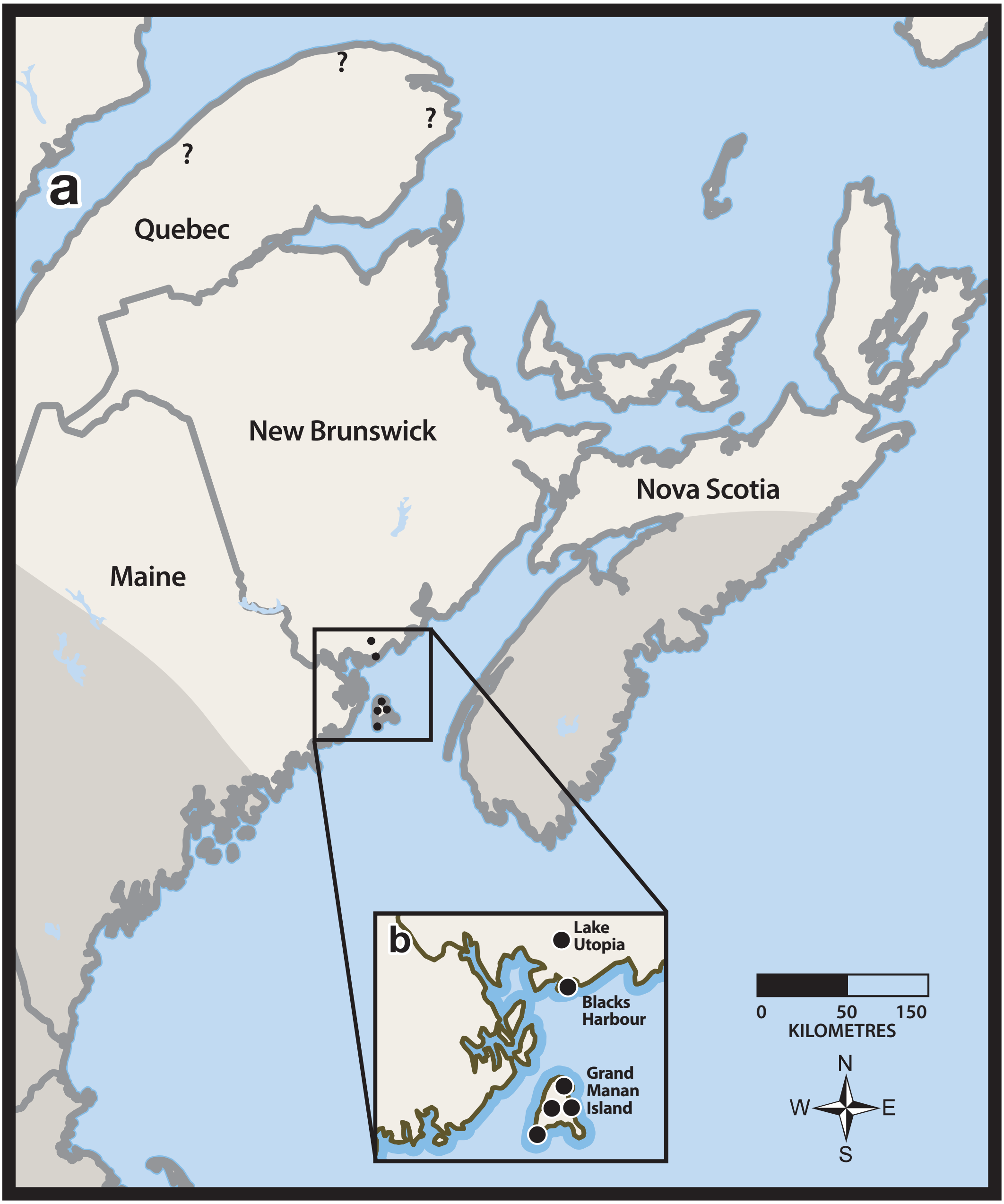


FIGURE 1. a. Range of White-footed Deer Mouse (*Peromyscus leucopus*) in Quebec (?) and Nova Scotia and Maine (shaded area). b. Closed circles mark recent localities for *P. leucopus* in New Brunswick: Grand Manan Island (Huynh *et al.* 2021), Blacks Harbour, and Lake Utopia. Unconfirmed Gaspe localities are from Desrosiers *et al.* (2002).

contact in some populations in southern Quebec, resulting in apparent hybridization and introgression at extremely low frequencies (*n* = 5 in a sample of 238). Likewise, working in the same region, Leo and Millien (2017) report low frequencies of apparent hybridization (*n* = 5–8 out of 153, depending on method of analysis) among *P. leucopus* and *P. maniculatus*. Vrla (2019) used genetic (including sequencing of the cytochrome *b* gene) and morphometric methods to separate *P. leucopus* and *P. maniculatus* in western Oklahoma, identifying a series of *Peromyscus* that are putative hybrids.

Although our use of a single mitochondrial gene to identify *P. leucopus* does not eliminate the possibility that the New Brunswick specimens are of hybrid origin, we believe the probability is low. Previous studies suggest that both pre- and post-zygotic mechanisms ensure that these species are normally well isolated reproductively (e.g., see Leo and Millien 2017 and references therein). Leo and Millen (2017) concluded that the low rate of apparent hybridization appeared to justify their use of the mtDNA COIII gene to separate *P. leucopus* and *P. maniculatus*, but they noted that recorded natural hybridization between these two congeners may warrant more comprehensive identification methods. Evidence is accumulating that where *P. leucopus* is undergoing range expansion (perhaps associated with climate change), pre-zygotic barriers with *P. maniculatus* may be altered, and hybridization at low rates may occur (Garcia-Elfring *et al.* 2017; Vrla 2019). Although our results support the presence of *P. leucopus* in New Brunswick, more detailed analyses will be required to determine the true nature of any genetic interaction between these species in the province.

Regardless of when *P. leucopus* became established in New Brunswick, the occurrence of the species in the province may have relevance to wildlife management and human health. Although both *P. leucopus* and *P. maniculatus* are considered competent host reservoirs for *Borrelia burgdorferi*, the spirochete bacterium that causes Lyme disease, there is evidence that *P. leucopus* may be the more competent of the two (Donahue *et al.* 1987; Garman *et al.* 1994; Fiset *et al.* 2015). *Peromyscus leucopus* also appears to be the preferred host species among rodents for ticks (*Ixodes scapularis*) that transmit *B. burgdorferi* (Schmidt *et al.* 1999). Thus, the apparent geographic expansion of *P. leucopus*, alongside the concurrent range expansion of Lyme disease in Canada (Ogden *et al.* 2008), may have an impact on the health of human communities in New Brunswick, as has been suggested for southern Quebec (Fiset *et al.* 2015).

Acknowledgements

We thank Jagger Watters-Gray and Elise Stevens for their assistance in the Genomics Laboratory at the Canadian Rivers Institute. H.M.H. extends his gratitude to Fenning McAlpine for his kindness during his collecting forays in New Brunswick, Karen Vanderwolf for her assistance in the field, Alfred Gardner for insightful discussions, and Thomas Jung for helpful comments that improved the manuscript. This research was supported by grants from the New Brunswick Wildlife Trust Fund, the Natural Sciences and Engineering Research Council, Canada Research Chairs, the New Brunswick Foundation for Innovation, the Canadian Foundation for Innovation, the New Brunswick Museum, and the University of New Brunswick.

Literature Cited

Bennett, M.R. 2020. Characterizing the range shifts of two *Peromyscus* species in Maine. Honors thesis, Honors College*,* University of Maine, Orono, Maine, USA. Accessed 8 June 2021. https://digitalcommons.library.umaine.edu/honors/580.

Desrosiers, N., R. Morin, and J. Jutras. 2002. Atlas des micromammifères du Québec. Société de la faune et des parcs du Québec, Fondation de la faune du Québec, Québec City, Québec, Canada.

Donahue, J.G., J. Piesman, and A. Spielman. 1987. Reservoir competence of white-footed mice for Lyme disease spirochetes. American Journal of Tropical Medicine and Hygiene 1: 92–96. http://doi.org/10.4269/ajtmh.1987.36.92

Fiset, J., N. Tessier, V. Millien, and F.-J. Lapointe. 2015. Phylogeographic structure of the white-footed mouse and the deer mouse, two Lyme disease reservoir hosts in Quebec. PLoS ONE 10(12): e0144112. https://doi.org/10.1371/journal.pone.0144112

Forbes, G.J., D.F. McAlpine, and F.W. Scott. 2010. Mammals of the Atlantic Maritime Ecozone. Pages 693–718 *in* Assessment of Species Diversity in the Atlantic Maritime Ecozone. *Edited by* D.F. McAlpine and I.M. Smith. NRC Research Press, National Research Council Canada, Ottawa, Ontario, Canada.

Garcia-Elfring, A., R.D.H. Barrett, M. Combs, T.J. Davies, J. Munshi-South, and V. Millien. 2017. Admixture on the northern front: population genomics of range expansion in the white-footed mouse (*Peromyscus leucopus*) and secondary contact with the deer mouse (*Peromyscus maniculatus*). Heredity 119: 447–458. https://doi.org/10.1038/hdy.2017.57

Garman, S.L., A.F. O'Connell, Jr., and J.H. Connery. 1994. Habitat use and distribution of the mice *Peromyscus leucopus* and *P. maniculatus* on Mount Desert Island, Maine. Canadian Field-Naturalist 108: 67–71. Accessed 11 June 2021. https://www.biodiversitylibrary.org/page/34263673.

Hall, E.R. 1981. The Mammals of North America, Volume II. John Wiley & Sons, New York, New York, USA.

Huynh, H.M., J. Norman, K.J. Vanderwolf, R.D. Bradley, R.J. Baker, and D.F. McAlpine. 2021. Detection of white-footed deer mouse (*Peromyscus leucopus*) on Grand Manan Island, New Brunswick, Canada: taxonomic, biogeographic, and human-health implications. Occasional Papers, Museum of Texas Tech University 379: 1–9.

Kaufman, D.W., S.K. Peterson, R. Fristik, and G.A. Kaufman. 1983. Effect of microhabitat features on habitat use by *Peromyscus leucopus*. American Midland Naturalist 110: 177–185. https://doi.org/10.2307/2425223

Kumar, S., G. Stecher, M. Li, C. Knyaz, and K. Tamura. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. Molecular Biology and Evolution 35: 1547–1549. http://doi.org/10.1093/molbev/msy096

Leo, S.S.T., and V. Millien. 2017. Microsatellite markers reveal low frequency of natural hybridization between the white-footed mouse (*Peromyscus leucopus*) and deer mouse (*Peromyscus maniculatus*) in southern Quebec, Canada. Genome 60: 454–463. http://doi.org/10.1139/gen-2016-0163

Moscarella, R.A. 2011. Dissecting the geographical expansion of *Peromyscus leucopus* in the northern Great Lakes: insights from genetics, morphometrics and ecology. Ph.D dissertation, Michigan State University, East Lansing, Michigan, USA. https://doi.org/doi:10.25335/M54192

Myers, P., B.L. Lundrigan, S.M.G. Hoffman, A.P. Haraminac, and S.H. Seto. 2009. Climate-induced changes in the small mammal communities of the Northern Great Lakes Region. Global Change Biology 15: 1434–1454. https://doi.org/10.1111/j.1365-2486.2009.01846.x

Naughton, D. 2012. The Natural History of Canadian Mammals. Canadian Museum of Nature and University of Toronto Press, Toronto, Ontario, Canada.

Ogden, N.H., L. St-Onge, I.K. Barker, S. Brazeau, M. Bigras-Poulin, D.F. Charron, C.M. Francis, A. Heagy, L.R. Lindsay, A. Maarouf, P. Michel, F. Milord, C.J. O'Callaghan, L. Trudel, and R. Thompson. 2008. Risk maps for range expansion of the Lyme disease vector, *Ixodes scapularis*, in Canada now and with climate change. International Journal of Health Geographics 7: 24. https://doi.org/10.1186/1476-072X-7-24

Rich, S.M. 1993. Distribution, biogeography and population genetics of *Peromyscus leucopus* and *Peromyscus maniculatus* in New England and Maritime Canada. M.Sc. thesis, University of Vermont, Burlington, Vermont, USA.

Rich, S.M., C.M. Kilpatrick, J.L. Shippee, and K.L. Crowell. 1996. Morphological differentiation and identification of *Peromyscus leucopus* and *P. maniculatus* in Northeastern North America. Journal of Mammalogy 77: 985–991.

Roy-Dufresne, E., T. Logan, J.A. Simon, G.L. Chmura, and V. Millien. 2013. Poleward expansion of the white-footed mouse (*Peromyscus leucopus*) under climate change: implications for the spread of Lyme disease. PLoS ONE 8(11): e80724. https://doi.org/10.1371/journal.pone.0080724

Schmidt, K.A., R.S. Ostfeld, and E.M. Schauber. 1999. Infestation of *Peromyscus leucopus* and *Tamias striatus* by *Ixodes scapularis* (Acari: Ixodidae) in relation to the abundance of hosts and parasites. Journal of Medical Entomology 36: 749–757. https://doi.org/10.1093/jmedent/36.6.749

Smith, M.F., and J.L. Patton. 1993. The diversification of South American rodents: evidence from mitochondrial sequence data for the akodontine tribe. Biological Journal of the Linnean Society 50: 149–177. https://doi.org/10.1111/j.1095-8312.1993.tb00924.x

Tiemann-Boege, I.C., C.W. Kilpatrick, D.J. Schmidly, and R.D. Bradley. 2000. Molecular phylogenetics of the *Peromyscus boylii* species group (Rodentia: Muridae) based on mitochondrial cytochrome *b* sequences. Molecular Phylogenetics and Evolution 16: 366–378. https://doi.org/10.1006/mpev.2000.0806

Vrla, S.C. 2019. Genetic structure and the potential for hybridization in populations of *Peromyscus* spp. of plateau regions in western Oklahoma. M.Sc. thesis, University of Central Oklahoma, Edmond, Oklahoma, USA. Accessed 8 June 2021. https://shareok.org/bitstream/handle/11244/325125/VrlaSC2019.pdf.

Received 20 September 2020
Accepted 9 June 2021
Associate Editor: T.S. Jung

The Canadian Field-Naturalist

Rare species of dodder (*Cuscuta* L.; Convolvulaceae) in Quebec and a plea for their search in the wild

Corey W. Burt[1,*], **Étienne Léveillé-Bourret**[2], and **Mihai Costea**[1]

[1]Wilfrid Laurier University, 75 University Avenue West, Waterloo, Ontario N2L 3C5 Canada
[2]Institut de recherche en biologie végétale, Département de sciences biologiques, Université de Montréal, 4101 Sherbrooke East, Quebec H1X 2B2 Canada
[*]Corresponding author: burt7030@mylaurier.ca

Burt, C.W., É. Léveillé-Bourret, and M. Costea. 2021. Rare species of dodder (*Cuscuta* L.; Convolvulaceae) in Quebec and a plea for their search in the wild. Canadian Field-Naturalist 135(3): 250–261. https://doi.org/10.22621/cfn.v135i3.2671

Abstract

We report three rare dodders (*Cuscuta* L.) from Quebec: Buttonbush Dodder (*Cuscuta cephalanthi* Engelmann), Hazel Dodder (*Cuscuta coryli* Engelmann), and Smartweed Dodder (*Cuscuta polygonorum* Engelmann). Detailed descriptions of their morphological characteristics, ecology, and host range are discussed. The genus *Cuscuta* is severely under-collected in Quebec and elsewhere, and targetted fieldwork is needed to better assess the distribution and conservation status of the three rare (or overlooked) species reported here. An identification key to all *Cuscuta* species from Quebec is provided to aid botanists in accurately identifying these challenging species.

Key words: Dodder; Convolvulaceae; *Cuscuta*; parasitic plants; phytogeography; Quebec; species of conservation concern

Résumé

La présence de trois cuscutes rares (*Cuscuta* L.) est confirmée au Québec: la cuscute du céphalanthe (*Cuscuta cephalanthi* Engelmann), la cuscute du noisetier (*Cuscuta coryli* Engelmann) et la cuscute des renouées (*Cuscuta polygonorum* Engelmann). Une description détaillée de leurs caractéristiques morphologiques et écologiques, ainsi qu'une liste de leurs hôtes sont incluses. Le genre *Cuscuta* est gravement sous-représenté dans les collections québécoises. Des inventaires ciblés sur le terrain sont nécessaires pour mieux évaluer la répartition et le statut de conservation des trois espèces rares (ou négligé) signalées ici. Une clef d'identification de toutes les espèces de *Cuscuta* du Québec est présentée pour faciliter l'identification de ce genre difficile.

Mots clés: convolvulacées; cuscute; *Cuscuta*; espèce susceptible d'être désignée; plantes parasites; phytogéographie; Québec

Introduction

Dodders (*Cuscuta* L.; Convolvulaceae) are a group of obligate stem parasitic plants with enormous economic and ecological significance. The genus is nearly cosmopolitan and includes close to 200 species, about 70% of which have evolved in the Americas (Yuncker 1932; Stefanović *et al*. 2007; García *et al*. 2014). Some *Cuscuta* species are well-known agricultural pests, and 15–20 species are capable of causing major yield losses in numerous crops worldwide (Parker and Riches 1993; Dawson *et al*. 1994; Costea and Tardif 2006). Non-native species of *Cuscuta* are federally legislated as agricultural/horticultural pests in Canada, the United States, and other countries (e.g., Costea and Tardif 2006), and commercial seed crops (especially legumes) contaminated with *Cuscuta* seeds (Knepper *et al*. 1990; Olszewski *et al*. 2020) discovered at the border are quarantined (Costea and Tardif 2006). However, some native *Cuscuta* are keystone species and, as ecosystem engineers in their natural habitats, can increase plant community diversity (Callaway and Pennings 1998; Press and Phoenix 2005). Other *Cuscuta* species are rare or at-risk worldwide (Costea and Stefanović 2009), but their conservation is challenging because of the stigma created by noxious dodder species.

Herbarium specimens from Canada and the United States were studied and annotated by M.C. during preparation of the taxonomic treatment of *Cuscuta* for Flora of North America. Annotated specimens in the holdings of larger Canadian herbaria have been digitized; the data are mediated by Canadensys

(canadensys.net) and the Global Biodiversity Information Facility (gbif.org), and taxonomic and floristic updates resulting from these data are incorporated into VASCAN, an online database of vascular plants in Canada (Brouillet *et al*. 2010+).

During the process of examining previously collected specimens, we identified three *Cuscuta* species from Quebec: Knotweed Dodder (*Cuscuta polygonorum* Engelmann), Buttonbush Dodder (*Cuscuta cephalanthi* Engelmann), and Hazel Dodder (*Cuscuta coryli* Engelmann). The presence of *C. polygonorum* in Quebec is mentioned in Flore laurentienne (Marie-Victorin 1964, 1995), but we were unable to find a herbarium voucher. Scoggan (1979) also referred to a specimen of *C. polygonorum* from “Lachine, near Montreal” (probably the same one as in Flore laurentienne), supposedly deposited in the Gray Herbarium, Harvard University, and identified by T.G. Yuncker, but we were unable to locate this collection in the Gray Herbarium, the William and Lynda Steere Herbarium—New York Botanical Garden (where Yuncker’s collections are held)—or other North American herbaria. However, M.C. recently annotated several specimens of *C. polygonorum* collected in the Montréal, Quebec, area that had been previously misidentified, and É.L.-B. recently discovered a new site for *C. polygonorum* in the same area. *Cuscuta cephalanthi* and *C. coryli* are known from other Canadian provinces (e.g., Crins and Ford 1988), but no specimens from Quebec have been previously identified.

Our objectives were to provide information about *C. cephalanthi*, *C. coryli*, and *C. polygonorum* in Quebec; to illustrate the morphological traits useful for their identification; to elaborate on their ecology and host range; and to emphasize their rarity in the province. Ultimately, our aim is to stimulate field searches for these species to better assess their distribution, rarity, and conservation status in Quebec.

Methods

Cuscuta specimens from the herbaria listed in Appendix 1 have been analyzed and annotated and their hosts recorded if they had been identified by the collector on the herbarium label or when verifiable host material was attached to the herbarium specimen. Flowering times reported in the results section are based on Ontario and Quebec herbarium specimen phenology.

The species can be separated using qualitative and quantitative characters of the calyx, corolla, infrastaminal scale, gynoecium, and capsule. These characters are based on Yuncker (1932, 1965), three species-level taxonomic studies (Costea *et al*. 2006a,b,c), and several character evolution studies for *Cuscuta* (Wright *et al*. 2011, 2012; Riviere *et al*. 2013; Ho and Costea 2018). Stereomicroscopy images were taken from rehydrated flowers and fruits of herbarium specimens using a Nikon SMZ1500 stereomicroscope (Nikon Corporation, Tokyo, Kantō, Japan), equipped with a PaxCam Arc digital camera (MIS Inc., Villa Park, Illinois, USA) and Pax-it 7.5 software (MIS Inc.). Rehydration was done by steeping the dry plant material in 50% ethanol, which was gradually warmed up to boiling point. Rehydration in a solution of ethanol hardens the tissues, thus protecting the very delicate corolla and infrastaminal scales from disintegration during dissection.

Results

Identification key for Cuscuta species in Quebec

At the vegetative stage, all *Cuscuta* species that occur in Quebec are morphologically indistinguishable, with trailing or twining, yellow or orange filiform stems 0.2–0.4 mm wide. Accurate species identification based on morphology is only possible when flowers are present, from late summer to early fall. With experience, some species may be distinguished in the field using a strong magnifier. However, accurate identification of most species requires dissecting the flowers using a stereomicroscope. If fresh material is unavailable, dried flowers can be easily rehydrated (see Methods). All species included in the following taxonomic key have been recorded in Quebec, except for Large Alfalfa Dodder (*Cuscuta indecora* Choisy var. *indecora*), which we included because it is morphologically similar to *C. coryli* and has been recorded in neighbouring states in the United States. Figures 1–3 compare flower and fruit morphology of *C. cephalanthi*, *C. coryli*, and *C. polygonorum* with morphologically similar species with which they may be easily confused.

1a. Stigmas cylindric, elongated, as wide as the styles; capsules dehiscent **2**

  2a. Calyces and stems often reddish-purple (calyces sometimes creamy white); styles equal or longer than ovary; growing on Fabaceae, especially *Medicago* and *Trifolium* .... ***C. epithymum***

  2b. Calyces and stems not purple (often yellow to orange); styles shorter than ovary; growing primarily on *Linum usitatissimum* (Linaceae) .... ***C. epilinum***

1b. Stigmas capitate, globose, wider than the styles; capsules indehiscent **3**

  3a. Corolla lobe apices acute to acuminate, inflexed **4**

    4a. Calyx lobes more or less carinate, acute; papillae or dome-shaped epidermal cells present on calyx and corolla lobes (requires rehydration of flowers and >40× magnification) **5**

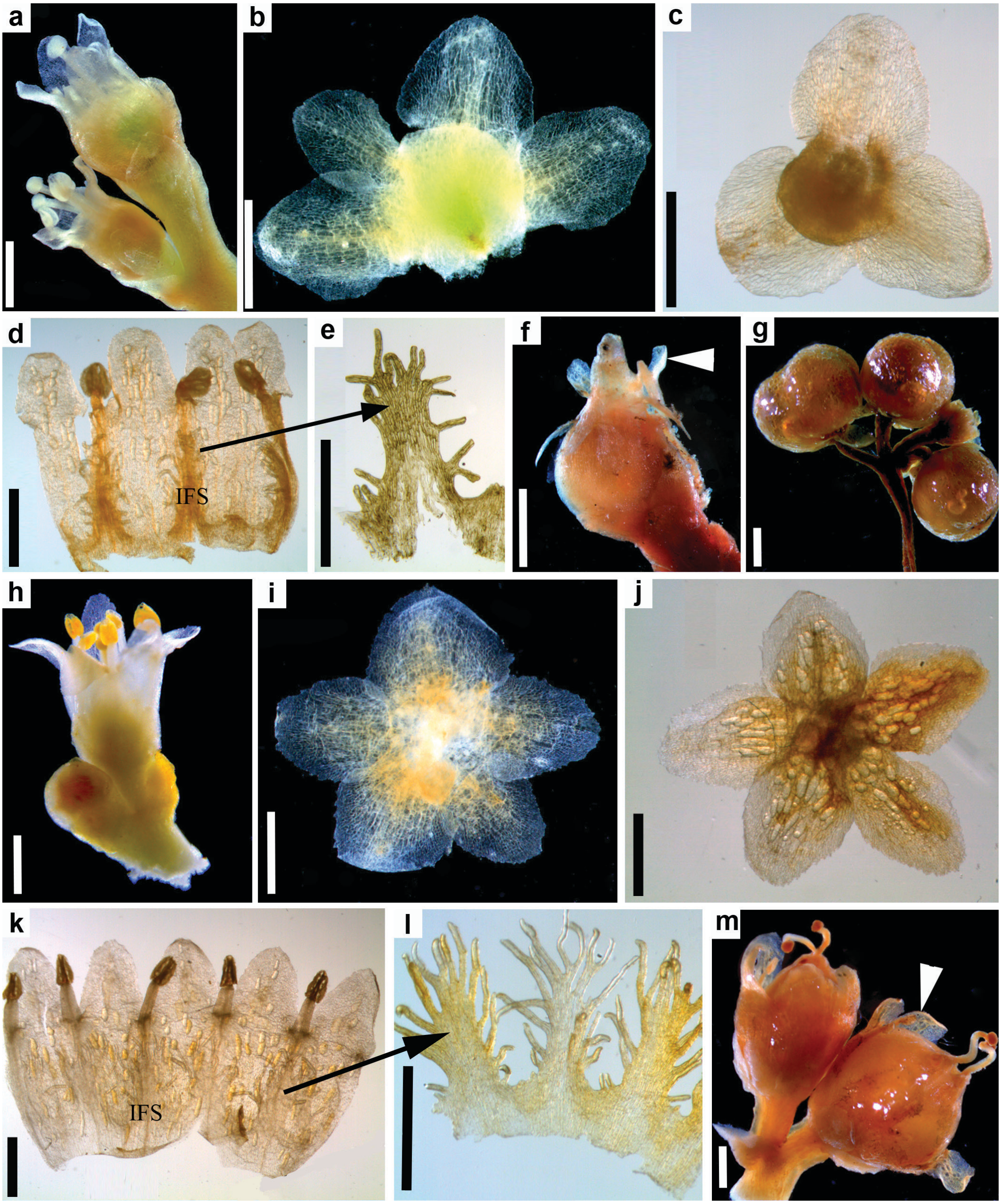


FIGURE 1. Flowers and fruits of Buttonbush Dodder (*Cuscuta cephalanthi*; a–g) and Swamp Dodder (*Cuscuta gronovii*; h–m). *Cuscuta cephalanthi*. a. Flowers. b and c. Variation of calyx (dissected). d. Corolla dissected and opened to show infrastaminal scales (IFS). e. Infrastaminal scales removed from flower to show fimbriae details. Note the 3- or 4-merous, smaller flowers. f. Early stage in development of the capsule capped by persistent corolla (white arrow). g. Mature capsules (corolla was lost because of rehydration in boiling ethanol). *Cuscuta gronovii*. h. Flower. i and j. Variation of calyx (dissected). k. Corolla dissected and opened to show IFSs. l. Note the 5-merous, larger flowers. Detail of IFSs removed from the corolla tube. m. Mature capsules surrounded by persistent corolla (white arrow). Scale bars = 1 mm. Colours as resulted after rehydration. Photos: Mihai Costea.

5a. Flowers mostly 4-merous (sometimes 3- or 5-merous within the same inflorescence); 1.7–2.6 (3.0) mm long; infrastaminal scales oblong, apex bifid, with short dentate wings or sparse 1–3 fimbriae on each side of the filament (rarely truncate with 3–6 fimbriae) .... ***C. coryli***

5b. Flowers mostly 5-merous (sometimes 4-merous within the same inflorescence); flowers 2.0–5.3 mm long; infrastaminal scales subspatulate to spatulate, apex rounded or truncate (rarely lobed), with (6–)20–35(–50) fimbriae .... ***C. indecora* (var. *indecora*)**

4b. Calyx lobes not carinate, rounded to obtuse; papillae or dome-shaped epidermal cells absent (requires rehydration of flowers and >40× magnification) **6**

6a. Flowers 4-merous, 2.0–2.7 mm long; calyx lobes not overlapping at base; infrastaminal scales bifid or with 2–3 irregular lobes, each bearing 1–2 fimbriae .... ***C. polygonorum***

6b. Flowers 5-merous (sometimes 4-merous within the same inflorescence), 1.4–3.6 mm long; calyx lobes overlapping at base; infrastaminal scales oblong-ovate to spatulate, uniformly and densely fimbriate .... ***C. campestris***

3b. Corolla lobe apices rounded or obtuse, straight **7**

7a. Flowers mostly 3- or 4-merous (rarely 5-merous within the same inflorescence), 2.0–3.0 mm long; persistent corolla capping the depressed-globose to globose capsule .... ***C. cephalanthi***

7b. Flowers mostly 5-merous (sometimes 4-merous within the same inflorescence), 3.0–4.0 mm long; persistent corolla surrounding the globose-ovoid capsule .... ***C. gronovii***

Cuscuta cephalanthi Engelmann
Buttonbush Dodder; Cuscute du Céphalanthe

Type—USA, Missouri, St. Louis County, on the margins of ponds and swamps near St. Louis, 1841, *Engelmann s.n.* (lectotype: MO, designated by Yuncker 1932).

Description—**Inflorescences** dense to loose, spiciform or paniculiform; pedicels 0.2–1 mm. **Flowers** 3–4(–5)-merous, 2–3 mm long; dome-like cells on calyx and corolla absent; **calyx** campanulate to shallowly cupulate, ½ length of corolla tube, divided ⅔ its length, lobes not carinate, oblong-ovate, bases slightly overlapping, margins entire or serrulate, apex obtuse; **corolla** white when fresh, becoming creamy to light brown when dry, cylindric-campanulate to cylindric, 1.8–2.8 mm long, lobes spreading to reflexed, ovate, ⅓–½ the tube length, apex obtuse, straight; **infrastaminal scales** oblong, 0.9–1.7 mm long, shorter than or equalling corolla tube length, sparsely fimbriate laterally, more densely fimbriate distally; **styles** (0.6–) 1–2 mm, equalling or longer than ovary; stigmas capitate. **Capsules** depressed-globose to globose, 2.5–3.2(–4) × 2–4 mm, not thickened or raised around relatively small interstylar aperture, capped by the withered corolla. **Seeds** 1–2/capsule, 1.4–2 × 1.3–1.4 mm. **2*n*** = 60.

Distribution in Canada—British Columbia, Manitoba, New Brunswick, Nova Scotia, Ontario, and Quebec. In Quebec, it is known from only one herbarium specimen collected in 1950 on the rocky margins of Saint François River in Drummondville.

Ecology and host range—In Ontario and Quebec, it flowers between July and September. It usually grows in wet habitats, such as lake shores, river, or stream banks, marshes, alluvial or periodically inundated woods, and wet meadows. The most common hosts throughout its range are Eastern Buttonbush (*Cephalanthus occidentalis* L.), willows (*Salix* L., including Sandbar Willow [*Salix interior* Rowlee], Almond Willow [*Salix triandra* L.], and Black Willow [*Salix nigra* Marshall]), goldenrods (*Solidago* L., including Giant Goldenrod [*Solidago gigantea* Aiton] and Spreading Goldenrod [*Solidago patula* Muhlenberg ex Willdenow]), and asters (*Symphyotrichum* Nees, including Heart-leaved Aster [*Symphyotrichum cordifolium* (L.) G.L. Nesom], Calico Aster [*Symphyotrichum lateriflorum* (L.) Á. Löve & D. Löve], Ontario Aster [*Symphyotrichum ontarionis* (Wiegand) G.L. Nesom], and Willow-leaved Aster [*Symphyotrichum praealtum* (Poiret) G.L. Nesom]). It also grows on numerous other woody and herbaceous genera and species, such as yarrow (*Achillea* L.), alder (*Alnus* Miller), Shrubby False Indigo (*Amorpha fruticosa* L.), American Hog Peanut (*Amphicarpaea bracteata* (L.) Fernald), Small-spike False Nettle (*Boehmeria cylindrica* (L.) Swartz), bindweed (*Calystegia* R. Brown), Trumpet Creeper (*Campsis radicans* (L.) Seeman ex Bureau), thistle (*Cirsium* Miller), tickseed (*Coreopsis* L.), Purple-veined Willowherb (*Epilobium coloratum* Biehler), Spotted Joe Pye Weed (*Eutrochium maculatum* (L.) E.E. Lamont), White Wood Aster (*Eurybia divaricata* (L.) G.L. Nesom), Common Sneezeweed (*Helenium autumnale* L.), St. John's Wort (*Hypericum* L.), touch-me-not (*Impatiens* L.), American Water-willow (*Justicia americana* (L.) Vahl), sweet pea (*Lathyrus* L.), water-horehound (*Lycopus* L., including American Water-horehound [*Lycopus americanus* Muhlenberg ex W.P.C. Barton]), loosestrife (*Lysimachia* L., including Lowland Yellow Loosestrife [*Lysimachia hybrida* Michaux]), holly (*Ilex* L.), mints (*Mentha* L., including Peppermint [*Mentha* ×*piperita* L.] and Spearmint [*Mentha spicata* L.]), forget-me-not (*Myosotis* L.), smartweed (*Persicaria* Scopoli, including Dotted Smartweed

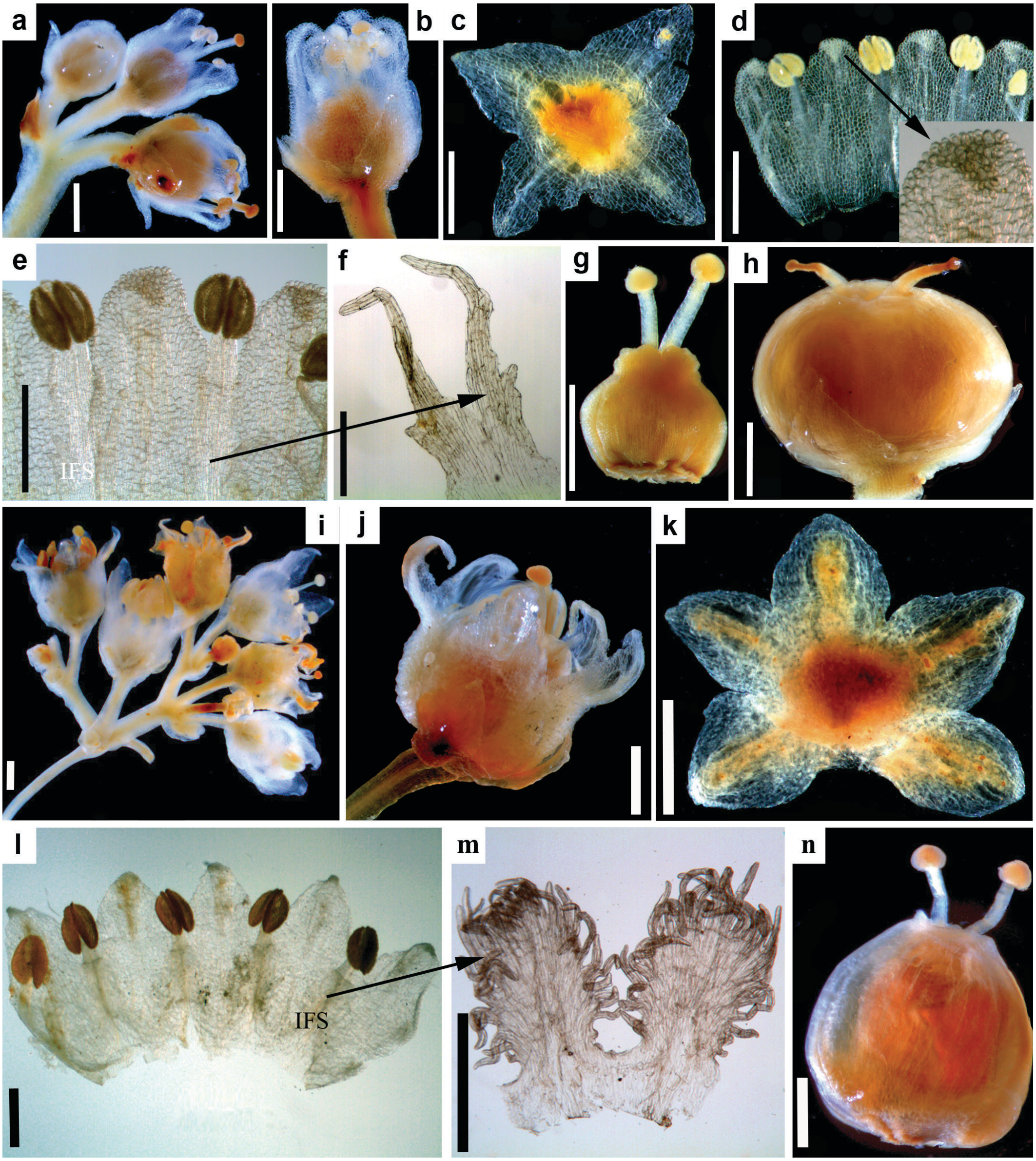


FIGURE 2. Flowers and fruits of Hazel Dodder (*Cuscuta coryli*; a–h) and Large Alfalfa Dodder (*Cuscuta indecora*; i–n). *Cuscuta coryli*. a. Fragment of inflorescence. b. Flower. c. Dissected calyx. d and e. Dissected corolla. f. Infrastaminal scale (IFS) detail. Note the 4-merous flowers with dome-like cells in the calyx and especially the corolla lobes and comparatively reduced scales. g. Gynoecium. h. Mature capsule. *Cuscuta indecora*. i. Inflorescence fragment. j. Flower. k. Dissected calyx. l. Dissected corolla. m. Detail of IFSs. Note the 6-merous, larger flowers with dome-like cells or papillae in the calyx and especially the corolla lobes and large IFSs with numerous fimbriae. n. Mature capsule. Scales bars = 1 mm, except f = 0.25 mm. Photos: Mihai Costea.

[*Persicaria punctata* (Elliott) Small]), American False Turtlehead (*Physostegia americana* (L.) Bentham), currant (*Ribes* L.), elderberry (*Sambucus* L.), Marshy Hedge-nettle (*Stachys palustris* L.), Bittersweet Nightshade (*Solanum dulcamara* L.), skullcaps (*Scutellaria* L., including Marsh Skullcap [*Scutellaria galericulata* L.] and Mad-dog Skullcap [*Scutellaria lateriflora* L.]), Steeplebush (*Spiraea tomentosa* L.), Canada Germander (*Teucrium canadense* L.), Poison Ivy (*Toxicodendron radicans* (L.), Kuntze),

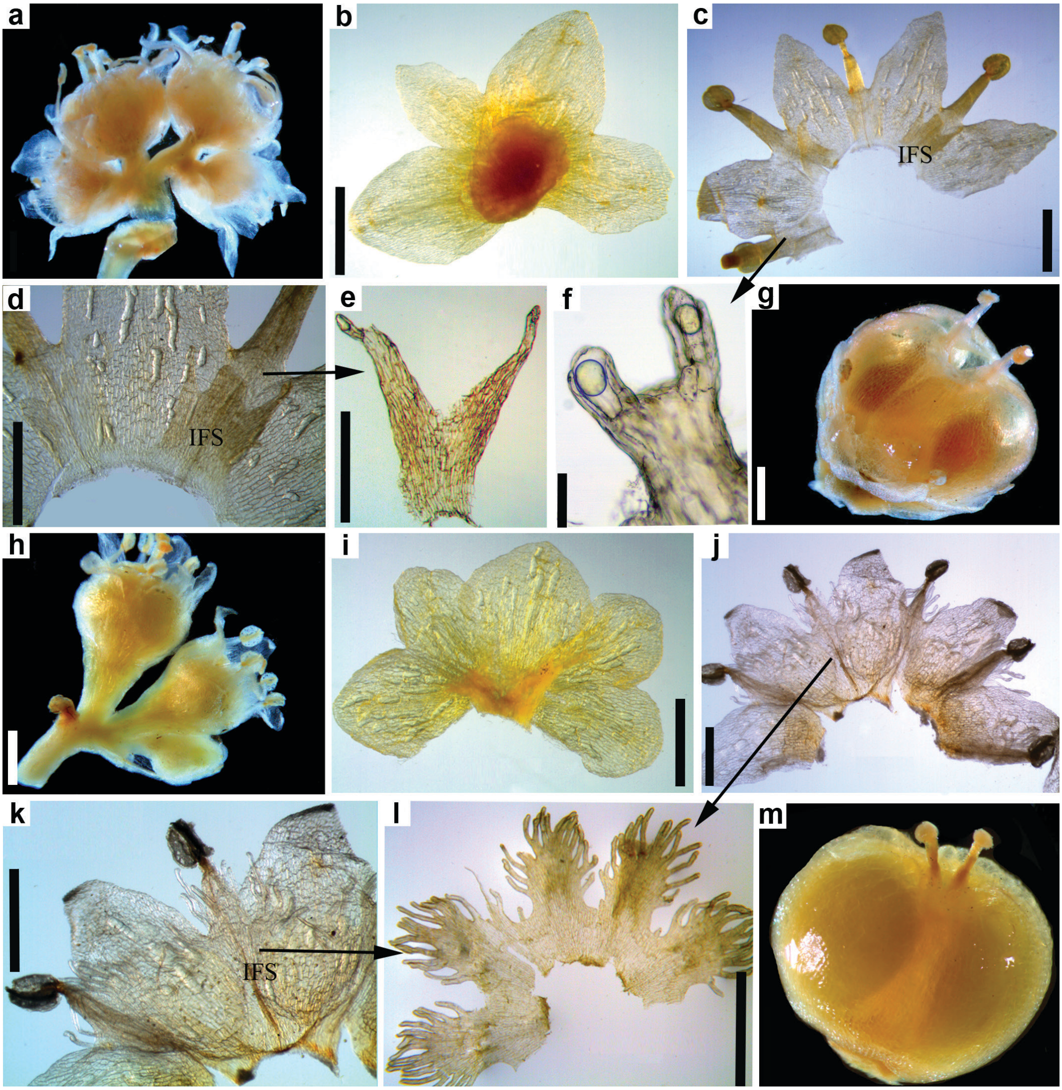


FIGURE 3. Flowers and fruits of Smartweed Dodder (*Cuscuta polygonorum*; a–g) and Field Dodder (*Cuscuta campestris*; h–m). *Cuscuta polygonorum*: a. Inflorescence fragment. b. Dissected calyx. c. Dissected corolla. d and e. Variation of infrastaminal scales (IFSs). Note the 4-merous flowers with non-overlapping calyx lobes and relatively reduced IFSs. g. Mature capsule. *Cuscuta campestris*: h. Inflorescence fragment. i. Dissected calyx. j–l. Dissected corolla and detail of IFSs. Note 5-merous flowers (larger than in *C. polygonorum*) with overlapping calyx lobes, and well-developed IFSs with numerous fimbriae. m. Mature capsule. Scale bars = 1 mm, except e and f = 0.5 mm. Photos: Mihai Costea.

ironweed (*Vernonia* Schreber), vetch (*Vicia* L.), and elm (*Ulmus* L.).

Conservation status—The species is Unrankable (SU) in British Columbia, Critically Imperilled in Manitoba (S1), Vulnerable–Critically Imperilled (S1S3) in New Brunswick, Imperilled (S2) in Ontario, and considered an inexact rank (S2?) in Nova Scotia (NatureServe 2021). In the United States, it is Presumed Extirpated (SX) from the District of Columbia; Critically Imperilled (S1) in New Hampshire, New Jersey, New York, North Carolina, South Carolina, Utah, Vermont, and Virginia; Imperilled (S2) in Pennsylvania and Kansas; and not yet evaluated in the other states where it occurs (NatureServe 2021).

Herbarium voucher—Canada, Quebec, Drummond County, Drummondville, Bords rocheux du Saint-François, 5 September 1950, *L. Cinq-Mars* (QFA 0145549, QUE 0005442).

Cuscuta coryli Engelmann
Hazel Dodder; Cuscute du Noisetier

Type—USA, Missouri: St. Louis County, on hazelnut (*Corylus*) near St. Louis, September 1841, *Engelmann s.n.* (holotype: MO 2524873, isotype: GH 00054310).

Description—**Inflorescences** paniculate-corymbiform to glomerulate; pedicels 0.5–3 mm long. **Flowers** 4-merous (sometimes 3- to 5-merous within the same inflorescence), fleshy, with epidermal cells of calyx and especially of corolla lobes dome-like (if herbarium specimens are examined, flowers need rehydration and at least 40× to discern this trait); **calyx** cupulate, equalling or somewhat longer than corolla tube, divided ½–⅔ of the length, lobes carinate, not or only slightly overlapping at the base, triangular-ovate, margins entire, apex acute; **corolla** white when fresh, becoming dark brown when dry, campanulate to suburceolate, 1.5–2.5 mm long, lobes erect to slightly spreading, triangular-ovate, ⅓ to equalling corolla tube, apex acute, inflexed; **infrastaminal scales** reaching the filament bases, oblong, bifid, with short dentate wings or 1–3 fimbria on each side of filament attachment, rarely truncate with 3–6 fimbriae; **styles** 0.7–1.5 mm long; stigmas capitate. **Capsules** initially globose later becoming depressed, 1.8–2.5 × 3.5–5 mm raised, around relatively large interstylar aperture, usually surrounded by the withered corolla. **Seeds** 1.3–1.6 × 1.2–1.4 mm. **2*n*** = 30.

Distribution in Canada—Saskatchewan, Manitoba, Ontario, and Quebec. In Quebec, it is known only from one herbarium specimen collected from St. Lambert, Chambly County (now Montérégie).

Ecology and host range—In Ontario and Quebec, it flowers between July and September. Found in terrestrial, wetland, and anthropogenic habitats throughout its range. Terrestrial habitats include dry, rocky, upland, hardwood dominated and lowland forest types, wooded ravines, open woodlands, savannahs, thickets, forest clearings, prairies, rocky ground, and sandy old fields. Wet habitats include bottomlands, marshes, sedge marshes, salt marshes, meadow marshes, wet meadows, calcareous mixed swamps, interdunal wetlands, lake shores, pond shores, river, stream, and creek banks, and swales. Also found in agricultural fields of Alfalfa (*Medicago sativa* L.) and occasionally Common Flax (*Linum usitatissimum* L.), cutovers (lands harvested for timber), roadsides, and cemeteries. Parasitizes many herbaceous and woody species, frequently found on ceanothus (including Narrow-leaved New Jersey Tea [*Ceanothus herbaceous* Rafinesque]), hazelnut (*Corylus* L., including American Hazelnut [*Corylus americana* Water]), tick trefoil (*Desmodium* Desvaux, including Paniculate Desmody [*Desmodium paniculatum* (L.) de Candolle]), goldentops (*Euthamia* (Nuttall) Cassini, including Grass-leaved Goldenrod [*Euthamia graminifolia* (L.) Nuttall] and Slender Fragrant Goldenrod [*Euthamia caroliniana* (L.) Greene ex Porter & Britton]), sunflowers (*Helianthus* L., including Woodland Sunflower [*Helianthus divaricatus* L.]), goldenrods (including Canada Goldenrod [*Solidago canadensis* L.], Giant Goldenrod, Grey-stemmed Goldenrod [*Solidago nemoralis* Aiton], and Rough-stemmed Goldenrod [*Solidago rugosa* Miller]), and asters (including Heart-leaved Aster, Calico Aster, Smooth Aster [*Symphyotrichum laeve* (L.) Á. Löve & D. Löve], and White Heath Aster [*Symphyotrichum ericoides* (L.) G.L. Nesom]). It has also been found on Indian mallow (*Abutilon* Miller), ragweed (*Ambrosia* L., including Great Ragweed [*Ambrosia trifida* L.]), goosefoot (*Chenopodium* L.), ash (*Fraxinus* L.), Sweet Pea (*Lathyrus odoratus* L.), pinweed (*Lechea* L.), Rough Water Horehound (*Lycopus asper* L.), Alfalfa, beebalm (*Monarda* L.), White Rattlesnakeroot (*Nabalus albus* (L.) Hooker), sumac (*Rhus* L.), raspberry (*Rubus* L.), willows, Sassafras (*Sassafras albidum* (Nuttall) Nees), sanicle (*Sanicula* L.), snowberry (*Symphoricarpos* Duhamel), germander (*Teucrium* L.), and Stinging Nettle (*Urtica dioica* L.).

Conservation status—The species is Unrankable (SU) in Quebec, Critically Imperilled (S1) in Ontario, Imperilled–Critically Imperilled (S1S2) in Manitoba, and Possibly Extirpated (SH) in Saskatchewan (Argus and Pryer 1990; NatureServe 2021). In the United States, it is Unrankable (SU) in Delaware and Iowa; Critically Imperilled (S1) in Kansas, Maryland, and Wisconsin; Imperilled (S2) in New Jersey and Virginia; Apparently Secure (S4) in New York; Possibly Extirpated (SH) in Ohio, Pennsylvania, Rhode Island, and West Virginia; Presumed Extirpated in the District of Columbia; and considered an inexact rank (S1?) in Massachusetts, Maryland, and North Carolina (NatureServe 2021). In the remaining states where it is present, conservation status has not been determined.

Herbarium voucher—Canada, Quebec, Chambly County, St. Lambert, 9 August 1935, *L.M. Terrill et al. 884* (MT 00070338).

Cuscuta polygonorum Engelmann
Smartweed Dodder, Cuscute des Renouées

Type—USA, Missouri: West of St. Louis, August 1839, *Lindheimer s.n.* (holotype: MO).

Description—**Inflorescences** glomerulate; pedicels 0.2–1 mm long. **Flowers** 4-merous, 2–2.7 mm; dome-like cells absent; **calyx** cupulate, ca. equalling the corolla tube, divided ½–⅔ to the base, lobes not carinate or basally overlapping, triangular-ovate, margins entire, apex obtuse to rounded; **corolla** white when fresh, becoming creamy to light brown when dry, cupulate to shallowly campanulate, 1.8–2.4 mm, lobes erect or spreading, 1.1–1.6 mm long, triangular, apex acute, usually inflexed; **infrastaminal scales** reaching the filament bases, bifid or with 2–3 irregular distal segments each bearing 1–2 fimbriae; **styles** 0.4–0.9 mm; stigmas capitate. **Capsules** depressed-globose, 1.6–3 × 2.5–5 mm, not thickened or raised around the large interstylar aperture, not translucent, withered corolla persistent around the capsule base. **Seeds** 1.1–1.4 × 0.9–1.3 mm. **2*n*** = ?

Distribution in Canada—Ontario and Quebec. In Quebec it has been found in three locations within the Montréal area (see below).

Ecology and host range—In Ontario and Quebec, it flowers between July and September. Mostly found in wet places including swamps, sloughs, wooded floodplains, moist thickets, dried ponds, pond edges, lake shores, low plains, marshes, wet meadows, gravel bars, riverbanks, rocky river shores, and other riparian habitats. Occasionally recorded in upland habitats, including forests and open lands and wet anthropogenic habitats, including canals. The most common hosts are knotweed, including Emerged Knotweed (*Persicaria amphibia var. emersa* (Michaux) JC Hickman), Red Knotweed (*Persicaria hydropiperoides* (Michaux) Small), Pale Knotweed (*Persicaria lapathifolia* (L.) Delarbre), and Dotted Smartweed. The genus *Persicaria* (L.) Miller was formerly included in the genus *Polygonum* L., which gave the specific epithet of the species. It is occasionally found on beggarticks (*Bidens* L., including Nodding Beggarticks [*Bidens cernua* L.], Purple-stemmed Beggarticks [*Bidens connata* Muhlenberg ex Willdenow], Devil's Beggarticks [*Bidens frondosa* L.], and Tall Beggarticks [*Bidens vulgata* Greene]), Spotted Water-hemlock (*Cicuta maculata* L.), Large St. John's Wort (*Hypericum majus* (A. Gray) Britton), touch-me-not, morning glory (*Ipomoea* L.), American Water-willow, Canada Wood Nettle (*Laportea canadensis* (L.) Weddell), water-horehound, Ditch Stonecrop (*Penthorum sedoides* L.), Beefsteak Plant (*Perilla frutescens* (L.) Britton), dock (*Rumex* L.), asters, and Rough Cocklebur (*Xanthium strumarium* L.). *Cuscuta polygonorum* is exclusively annual and its hosts are always herbaceous.

Conservation status—*Cuscuta polygonorum* is Unrankable (SU) in Quebec and considered Critically Imperilled (S1) in Ontario (NatureServe 2021). In the United States, it is Unrankable (SU) in Delaware and Iowa; Critically Imperilled (S1) in the District of Columbia, Maryland, New York, Virginia, West Virginia, and Wisconsin; Imperilled (S2) in Kansas, Michigan, New Jersey, and Pennsylvania; Vulnerable–Apparently Secure (S3S4) in Massachusetts; and Possibly Extirpated (SH) in North Dakota (NatureServe 2021). In the remaining states where it is present, conservation status has not been determined.

Herbarium vouchers—Canada, Quebec, MRC Beauharnois-Salaberry, Îles de la Paix, Île à Tambault (Station 2): berge, 4 September 1965, *M. Morency 1651* (MT 00070339). Vaudreuil-Soulanges, Île-Perrot, près de la Pointe-du-Moulin. Rivages graveleux et rocheux, 05 September 2005, *S.H. Hay, C. Morisset SH05-189* (MT), *SH05-190* (MT), *SH05-191* (MT), *SH05-192* (MT). MRC Deux-Montagnes (WGS84), 45.59833°N 73.83303°W, Baie des Grandes Largeurs, rivière des Milles-Îles, Boisbriand. Grimpant sur *Persicaria amphibia* et *Xanthium strumarium*. Haut rivage limoneux. Dominé par *Persicaria amphibia*, *Lythrum salicaria*, *Carex vesicaria*, *Echinochloa muricata*, *Eragrostis hypnoides*, *Acalypha rhomboidea*, *Bidens* spp., 27 October 2016, *É. Léveillé-Bourret et al.1040* (MT).

Discussion

Taxonomy

All *Cuscuta* species native to Quebec (*C. coryli*, *C. cephalanthi*, Field Dodder [*Cuscuta campestris* Yuncker], Swamp Dodder [*Cuscuta gronovii* Willdenow ex Roemer & Schultes], and *C. polygonorum*) belong to *Cuscuta* subgenus *Grammica* (Loureiro) Engelmann ex Yuncker, characterized by having two unequal styles, globose stigmas, and alveolate seed coats when dry (papillate when rehydrated). Translucent laticifers are often visible in the calyx, corolla, and ovary. They also have indehiscent capsules enclosing two to four seeds. The three *Cuscuta* species newly identified for Quebec have evolved in different major clades of subgenus *Grammica* (Stefanović *et al.* 2007; García *et al.* 2014). Two species introduced to Quebec from Europe (Costea and Tardif 2006), Flax Dodder (*Cuscuta epilinum* Weihe) and Clover Dodder (*Cuscuta epithymum* (L.) L., have not been collected in the province in the last 50 years. They both belong to *Cuscuta* subgenus *Cuscuta* and can be easily distinguished from native dodders by their stigmas, which are elongated and linear.

Cuscuta cephalanthi is closely related to Swamp Dodder (*Cuscuta gronovii* Willdenow ex Roemer & Schultes), both belonging to *Cuscuta* section *Oxycarpae* (Engelmann ex Yuncker) Costea & Stefanović (Costea *et al.* 2015a). *Cuscuta gronovii* is the most common native dodder in Canada and North America (Yuncker 1932; Costea *et al.* 2006a). These two species occur in the same types of riparian habitats, but *C. cephalanthi* can be recognized by its smaller, 4-merous flowers and persistent corolla capping the capsule (see identification key and Figure 1). The presence of *C. cephalanthi* in Quebec was to be expected because it is reported from neighbouring geographic areas in

Canada and the United States: Ontario (Crins and Ford 1988), New York, Vermont, New Hampshire, and Maine (NatureServe 2021).

Cuscuta coryli has strong evolutionary affinity with *C. indecora* (*Cuscuta* section *Indecorae* (Yuncker) Costea & Stefanović; Yuncker 1932; Costea *et al*. 2006b, 2015a). *Cuscuta indecora* var. *indecora* has been reported in Canada only from Saskatchewan (Costea *et al*. 2004), but may be expected in the southern areas of Ontario and Quebec, as it is present in the neighbouring states (Crins and Ford 1988; Costea *et al*. 2006b). *Cuscuta indecora* var. *indecora* differs from *C. coryli* in the 5-merous, larger flowers, with abundantly fringed infrastaminal scales (see identification key and Figure 2).

Cuscuta polygonorum is classified in *Cuscuta* section *Cleistogrammica* Engelmann (Costea *et al*. 2015a), which also includes Field Dodder (*Cuscuta campestris* Yunker), the most widespread weedy species of *Cuscuta* worldwide (Yuncker 1932; Parker and Riches 1993; Costea and Tardif 2006; Costea *et al*. 2006c). *Cuscuta polygonorum* is similar to *C. campestris* in fruit and identification errors are possible if only capsules are present. However, even at this stage, *C. polygonorum* can be recognized by the persistent calyx at the base of capsules, which has four non-overlapping lobes (Figure 3b,g). *Cuscuta campestris* has 5-merous flowers and calyx lobes that overlap at the base; if flowers are present, its corolla is larger, with well-developed infrastaminal scales that protrude from the corolla tube (Figure 3).

Biology, ecology, and conservation

Cuscuta cephalanthi and *C. coryli* are annuals, but, when parasitizing woody plants, they can behave as perennials, overwintering as a haustorial endophyte inside the host and regenerating vegetatively in the spring (Yuncker 1932; Costea and Tardif 2006; Meulebrouck *et al*. 2009). In contrast, *C. polygonorum* is exclusively annual, growing on herbaceous and often annual hosts. This biological information is important when considering population genetics and population dynamics, as *Cuscuta* species perennating inside the host tend to reproduce vegetatively and have a high degree of clonality (Meulebrouck *et al*. 2009), while annual ones are necessarily more diverse genetically. These life-history aspects are virtually unstudied in these species and in *Cuscuta* more broadly. Dispersal of the three species has not been studied. However, similar to other *Cuscuta*, seed dispersal is likely accomplished by water or via bird endozoochory (Costea *et al*. 2016, 2019; Ho and Costea 2018). The indehiscent capsules can float for more than two weeks (Ho and Costea 2018).

Based on the few herbarium collections available for these three species in Quebec, and in Canada more broadly, they are likely rare, or overlooked, or both, and may require protection if threats exist. Unfortunately, conservation of *Cuscuta* species is challenging because, historically, most research and management efforts have focussed on the control and eradication of weedy *Cuscuta*, while rare or overlooked species have been neglected (Costea and Stefanović 2009). We do not know why species, such as *C. gronovii*, *C. indecora*, and *C. campestris*, can become aggressive pests (Parker and Riches 1993; Costea and Tardif 2006), whereas some of their closest relatives, such as *C. cephalanthi* (a close relative of *C. gronovii*), *C. coryli* (a close relative of *C. indecora*), and *C. polygonorum* (a close relative of *C. campestris*), are rare. Several studies have suggested that the size of the host range plays a decisive role in determining the success or rarity of *Cuscuta* species (Costea and Stefanović 2009; García *et al*. 2018; Costea *et al*. 2020). However, the three species discussed here seem capable of parasitizing numerous hosts and it is unknown why they are not as widespread (or, at least, not as frequently collected) as their weedy relatives. *Cuscuta* seedlings must survive while searching the plant community for a compatible host (Behdarvandi *et al*. 2015). Once they locate a host, they must establish haustorial contact with it (Dawson *et al*. 1994). Little is known about the impact of biotic and abiotic factors during the search and attack of the hosts, but they likely modulate the population dynamics of *Cuscuta* species. For these reasons, the traditional focus on pest-control methods must be complemented with targetted biological and ecological studies in natural plant communities to understand the underlying factors explaining rarity versus invasiveness.

Cuscuta are generally less collected than other plants (Austin 1979; Stefanović *et al*. 2007), and we hope this article will stimulate the search for rare species in Quebec and elsewhere in Canada. Species conservation measures cannot be taken without a species conservation status, and the latter cannot be assessed without extensive fieldwork to determine the distribution, threats, size, and dynamics of populations in the wild.

Author Contributions

Conceptualization: É.L.-B. and M.C.; Data Curation: C.W.B.; Investigation: M.C. and C.W.B.; Methodology: M.C.; Resources: É.L.-B. and M.C.; Visualization: M.C.; Writing – First Draft: M.C. and C.W.B.; Writing – Review and Editing: É.L.-B., M.C., and C.W.B.

Acknowledgements

We thank the curators/directors of cited herbaria (see Appendix 1), who made available their specimens for study. We are grateful to Marlène Ferland and Juan Carlos Villarreal Aguilar (Herbier Louis-Marie — Université Laval) for resending to Wilfrid Laurier University the only available specimen of *Cuscuta cephalanthi* to verify its identity. Two anonymous reviewers kindly provided comments that improved the quality of the article. This research was supported by a Natural Sciences and Engineering Research Council Discovery grant to M.C. (327013).

Literature Cited

Argus, G.W., and K.M. Pryer. 1990. Rare Vascular Plants in Canada: Our Natural Heritage. Canadian Museum of Nature, Ottawa, Ontario, Canada.

Austin, D.F. 1979. Comments on *Cuscuta* — for collectors and curators. Bulletin of the Torrey Botanical Club 106: 227–228. https://doi.org/10.2307/2484559

Behdarvandi, B., F.C. Guinel, and M. Costea. 2015. Differential effects of ephemeral colonization by arbuscular mycorrhizal fungi in two *Cuscuta* species with different ecology. Mycorrhiza 25: 573–585. https://doi.org/10.1007/s00572-015-0632-9

Brouillet L., F. Coursol, S.J. Meades, M. Favreau, M. Anions, P. Bélisle, and P. Desmet. 2010+. VASCAN, the database of vascular plants of Canada. Accessed 15 November 2020. http://data.canadensys.net/vascan/.

Callaway, R.M., and S.C. Pennings. 1998. Impact of a parasitic plant on the zonation of two salt marsh perennials. Oecologia 114: 100–105. https://doi.org/10.1007/s004420050425

Costea, M., H. El Miari, R. Farag, C. Fleet, and S. Stefanović. 2020. *Cuscuta* sect. *Californicae* (Convolvulaceae) revisited: 'cryptic' speciation and host range differentiation. Systematic Botany 45: 638–651. https://doi.org/10.1600/036364420X15935294613428

Costea, M., H. El Miari, L. Laczkó, R. Fekete, A.V. Molnár, Á. Lovas-Kiss, and A.J. Green. 2019. The effect of gut passage by waterbirds on the seed coat and pericarp of diaspores lacking "external flesh": evidence for widespread adaptation to endozoochory in angiosperms. PLoS ONE 14: e0226551. https://doi.org/10.1371/journal.pone.0226551

Costea, M., M.A. García, K. Baute, and S. Stefanović. 2015b. Entangled evolutionary history of *Cuscuta pentagona* clade: a story involving hybridization and Darwin in the Galapagos. Taxon 64: 1225–1242. https://doi.org/10.12705/646.7

Costea, M., M.A. García, and S. Stefanović. 2015a. A phylogenetically based infrageneric classification of the parasitic plant genus *Cuscuta* (dodders, Convolvulaceae). Systematic Botany 40: 269–285. https://doi.org/10.1600/036364415x686567

Costea, M., G.L. Nesom, and S. Stefanović. 2006a. Taxonomy of *Cuscuta gronovii* and *Cuscuta umbrosa* (Convolvulaceae). SIDA, Contributions to Botany 22: 197–207.

Costea, M., G.L. Nesom, and S. Stefanović. 2006b. Taxonomy of the *Cuscuta indecora* (Convolvulaceae) complex in North America. SIDA, Contributions to Botany 22: 209–225.

Costea, M., G.L. Nesom, and S. Stefanović. 2006c. Taxonomy of the *Cuscuta pentagona* complex (Convolvulaceae) in North America. SIDA, Contributions to Botany 22: 151–175.

Costea, M., and S. Stefanović. 2009. *Cuscuta jepsonii* (Convolvulaceae): an invasive weed or an extinct endemic? American Journal of Botany 96: 1744–1750. https://doi.org/10.3732/ajb.0800425

Costea, M., S. Stefanović, M.A. García, S. De La Cruz, M.L. Casazza, and A.J. Green. 2016. Waterfowl endozoochory: an overlooked long-distance dispersal mode for *Cuscuta* (dodder). American Journal of Botany 103: 957–962. https://doi.org/10.3732/ajb.1500507

Costea, M., and F.J. Tardif. 2006. The biology of Canadian weeds. 133. *Cuscuta campestris* Yuncker, *C. gronovii* Willd. ex Schult., *C. umbrosa* Beyr. ex Hook., *C. epithymum* (L.) L. and *C. epilinum* Weihe. Canadian Journal of Plant Science 86: 293–316. https://doi.org/10.4141/p04-077

Costea, M., F.J. Tardif, and V.L. Harms. 2004. *Cuscuta indecora* (Convolvulaceae) new for Canada. SIDA, Contributions to Botany 21: 1229–1230.

Crawley, M.J. 1990. The population dynamics of plants. Philosophical Transactions of the Royal Society B: Biological Sciences 330: 125–140. https://doi.org/10.1098/rstb.1990.0187

Crins, W.J., and B.A. Ford. 1988. The parasitic dodders (Cuscuta: Cuscutaceae) in Ontario. Canadian Field Naturalist 102: 209–215. Accessed 28 May 2021. https://www.biodiversitylibrary.org/page/28243478.

Dawson, J.H., L.J. Musselman, P. Wolswinkel, and I. Dörr. 1994. Biology and control of *Cuscuta*. Reviews of Weed Science 6: 265–317.

García, M.A., M. Costea, M. Kuzmina, and S. Stefanović. 2014. Phylogeny, character evolution, and biogeography of *Cuscuta* (dodders; Convolvulaceae) inferred from coding plastid and nuclear sequences. American Journal of Botany 101: 670–690. https://doi.org/10.3732/ajb.1300449

García, M.A., S. Stefanović, C. Weiner, M. Olszewski, and M. Costea. 2018. Cladogenesis and reticulation in *Cuscuta* sect. *Denticulatae* (Convolvulaceae). Organisms Diversity & Evolution 18: 383–398. https://doi.org/10.1007/s13127-018-0383-5

Ho, A., and M. Costea. 2018. Diversity, evolution and taxonomic significance of fruit in *Cuscuta* (dodder, Convolvulaceae); the evolutionary advantages of indehiscence. Perspectives in Plant Ecology, Evolution and Systematics 32: 1–17. https://doi.org/10.1016/j.ppees.2018.02.001

Knepper, D.A., R.A. Creager, and L.J. Musselman. 1990. Identifying dodder seed as contaminants in seed shipments. Seed Science and Technology 18: 731–741.

Marie-Victorin, F. 1964. Flore Laurentienne. Second Edition. Les Presses de l'Université de Montréal, Montréal, Quebec, Canada.

Marie-Victorin, F. 1995. Flore Laurentienne. Third Edition. Les Presses de l'Université de Montréal, Montréal, Quebec, Canada.

Meulebrouck, K., E. Ameloot, R. Brys, L. Tanghe, K. Verheyen, and M. Hermy. 2009. Hidden in the host—unexpected vegetative hibernation of the holoparasite

Cuscuta epithymum (L.) L. and its implications for population persistence. Flora 204: 306–315. https://doi.org/10.1016/j.flora.2008.03.005

NatureServe. 2021. NatureServe Explorer. NatureServe, Arlington, Virginia, USA. Accessed 18 June 2021. https://explorer.natureserve.org/.

Olszewski, M., M. Dilliott, I. García-Ruiz, B. Bendarvandi, and M. Costea. 2020. *Cuscuta* seeds: diversity and evolution, value for systematics/identification and exploration of allometric relationships. PloS ONE 15: e0235738. https://doi.org/10.1371/journal.pone.0234627

Parker, C., and C.R. Riches. 1993. Parasitic Weeds of the World: Biology and Controls. University of Arizona Press, Tucson, Arizona, USA.

Press, M.C., and G.K. Phoenix. 2005. Impacts of parasitic plants on natural communities. New Phytologist 166: 737–751. https://doi.org/10.1111/j.1469-8137.2005.01358.x

Riviere, S., C. Clayson, K. Dockstader, M.A. Wright, and M. Costea. 2013. To attract or to repel? Diversity, evolution and role of the "most peculiar organ" in the *Cuscuta* flower (dodder, Convolvulaceae)—the infrastaminal scales. Plant Systematics and Evolution 299: 529–552. https://doi.org/10.1007/s00606-012-0741-2

Scoggan, H.J. 1978. The Flora of Canada. Part 4: Dicotyledoneae. National Museum of Natural Science, Ottawa, Ontario, Canada.

Stefanović, S., M. Kuzmina, and M. Costea. 2007. Delimitation of major lineages within *Cuscuta* subgenus *Grammica* (Convolvulaceae) using plastid and nuclear DNA sequences. American Journal of Botany 94: 568–589. https://doi.org/10.3732/ajb.94.4.568

Wright, M.A.R., M.D. Ianni, and M. Costea. 2012. Diversity and evolution of pollen-ovule production in *Cuscuta* (dodders, Convolvulaceae) in relation to floral morphology. Plant Systematics and Evolution 298: 369–389. https://doi.org/10.1007/s00606-011-0550-z

Wright, M.A.R., M. Welsh, and M. Costea. 2011. Diversity and evolution of the gynoecium in *Cuscuta* (dodders, Convolvulaceae) in relation to their reproductive biology: two styles are better than one. Plant Systematics and Evolution 296: 51–76. https://doi.org/10.1007/s00606-011-0476-5

Yuncker, T.G. 1932. The genus *Cuscuta*. Memoirs of the Torrey Botanical Club 18: 109–331.

Yuncker, T.G. 1965. North American Flora, Series II, Part 4, *Cuscuta*. New York Botanical Garden, Bronx, New York, USA.

Received 24 November 2020
Accepted 9 August 2021
Associate Editor: J.M. Saarela

APPENDIX 1. Herbaria from which *Cuscuta* specimens were examined.

Abbreviation	Herbarium	Location
ACAD	E.C. Smith Herbarium, Acadia University	Wolfville, Nova Scotia, Canada
ALTA	University of Alberta	Edmonton, Alberta, Canada
ARIZ	University of Arizona	Tucson, Arizona, USA
ASU	Arizona State University	Tempe, Arizona, USA
BM	The Natural History Museum	London, United Kingdom
BRIT	BRIT Philecology Herbarium, Botanical Research Institute of Texas	Fort Worth, Texas, USA
CAS	California Academy of Sciences	San Francisco, California, USA
CHSC	The Chico State Herbarium, California State University, Chico	Chico, California, USA
CONN	George Safford Torrey Herbarium, University of Connecticut	Storrs, Connecticut, USA
DAO	National Collection of Vascular Plants, Agriculture and Agri-Food Canada	Ottawa, Ontario, Canada
DUKE	Duke University	Durham, North Carolina, USA
F	Field Museum of Natural History	Chicago, Illinois, USA
G	Conservatoire et Jardin botaniques de la Ville de Genève	Geneva, Switzerland
GH	Harvard University	Cambridge, Massachusetts, USA
HAM	Royal Botanical Gardens	Burlington, Ontario, Canada
IND	Indiana University	Bloomington, Indiana, USA
JEPS	Jepson Herbarium, University of California	Berkeley, California, USA
K	Royal Botanic Gardens	Richmond, United Kingdom
LSU	Shirley C. Tucker Herbarium, Louisiana State University	Baton Rouge, Louisiana, USA
MICH	University of Michigan	Ann Arbor, Michigan, USA
MT	Herbier Marie-Victorin, Université de Montréal	Montréal, Quebec, Canada
MTMG	McGill University	Sainte-Anne-de-Bellevue, Quebec, Canada

Abbreviation	Herbarium	Location
MO	Missouri Botanical Garden	Saint Louis, Missouri, USA
NCSC	North Carolina State University	Raleigh, North Carolina, USA
NFLD	Ayre Herbarium, Memorial University of Newfoundland	St. John's, Newfoundland, Canada
NHIC	Natural Heritage Information Centre, Ontario Ministry of Natural Resources and Forestry	Peterborough, Ontario, Canada
NMC	New Mexico State University	Las Cruces, New Mexico, USA
NSPM	The Nova Scotia Museum of Natural History, Collections	Halifax, Nova Scotia, Canada
NY	William and Lynda Steere Herbarium, The New York Botanical Garden	Bronx, New York, USA
OAC	University of Guelph	Guelph, Ontario, Canada
OKLA	Oklahoma State University	Stillwater, Oklahoma, USA
OSC	Oregon State University	Corvallis, Oregon, USA
P	Muséum National d'Histoire Naturelle	Paris, Île-de-France, France
QFA	Herbier Louis-Marie, Université Laval	Québec, Quebec, Canada
QUE	Herbier du Québec, Complexe scientifique	Sainte-Foy, Quebec, Canada
RSA	California Botanic Garden	Claremont, California, USA
SD	San Diego Natural History Museum	San Diego, California, USA
SASK	W.P. Fraser Herbarium, University of Saskatchewan	Saskatoon, Saskatchewan, Canada
SFS	Herbier Rolland-Germain, Université de Sherbrooke	Sherbrooke, Quebec, Canada
TEX	Billie L. Turner Plant Resources Center, University of Texas at Austin	Austin, Texas, USA
TRT	Green Plant Herbarium, Royal Ontario Museum	Toronto, Ontario, Canada
TRTE	Erindale College, University of Toronto	Mississauga, Ontario, Canada
TUP	Trent University	Peterborough, Ontario, Canada
UBC	Beaty Biodiversity Museum, University of British Columbia	Vancouver, British Columbia, Canada
UC	University Herbarium, University of California	Berkeley, California, USA
UCR	University of California, Riverside	Riverside, California, USA
UNB	Connell Memorial Herbarium, University of New Brunswick	Fredericton, New Brunswick, Canada
UNM	University of New Mexico	Albuquerque, New Mexico, USA
US	United States National Herbarium, Smithsonian Institution	Washington, District of Columbia, USA
USAS	George F. Ledingham Herbarium, University of Regina	Regina, Saskatchewan, Canada
UWO	Dr. Laurie L. Consaul Herbarium, Western University	London, Ontario, Canada
UWPG	University of Winnipeg	Winnipeg, Manitoba, Canada
WAT	University of Waterloo	Waterloo, Ontario, Canada
WIN	University of Manitoba	Winnipeg, Manitoba, Canada
WIS	University of Wisconsin	Madison, Wisconsin, USA
WLU	Wilfrid Laurier University	Waterloo, Ontario, Canada

The Canadian Field-Naturalist

Relative abundance and range extensions of bird species in central Labrador

Marcel A. Gahbauer[1,*] **and Karen Rashleigh**[2]

[1]Migration Research Foundation, P.O. Box 10005, Ste.-Anne-de-Bellevue, Quebec H9X 0A6 Canada
[2]Stantec, 141 Kelsey Drive, St. John's, Newfoundland and Labrador A1B 0L2 Canada
[*]Corresponding author: marcel@migrationresearch.org

Gahbauer, M.A., and K. Rashleigh. 2021. Relative abundance and range extensions of bird species in central Labrador. Canadian Field-Naturalist 135(3): 262–277. https://doi.org/10.22621/cfn.v135i3.2419

Abstract

Bird communities in Labrador remain poorly described, including in the lower Churchill River valley, which lies within an offshoot of the boreal shield ecozone and features vegetation communities typically found more than 100 km to the south. Between 2006 and 2016, we conducted 1139 point counts in June and early July at 617 sites along 63 routes within and adjacent to the lower Churchill River valley. We documented 80 species during the surveys and a further nine species incidentally. The most numerous species were Swainson's Thrush (*Catharus ustulatus*), Ruby-crowned Kinglet (*Corthylio calendula*), and Dark-eyed Junco (*Junco hyemalis*). Relative bird abundance was highest in hardwood and mixedwood forests and lowest in areas dominated by Black Spruce (*Picea mariana*). Among the species we observed were 19 that we considered to be regionally rare, based on existing documentation. The most abundant of these were Least Flycatcher (*Empidonax minimus*), Cedar Waxwing (*Bombycilla cedrorum*), and Magnolia Warbler (*Setophaga magnolia*), each with more than 80 observations over multiple years, spanning 10 or more areas within the lower Churchill River valley. Almost all of the regionally rare species were strongly associated with either hardwood forests, large conifers, or dense riparian vegetation. These features are relatively widespread within the lower Churchill River valley, but scarce elsewhere in Labrador. It is unclear whether the results observed represent recent range expansions or our surveys were simply the first to document long-standing regional populations; regardless, we recommend that our records be considered in future revisions to range maps for these species.

Key words: Birds; boreal; distribution; habitat association; Labrador; range extension

Introduction

Accurate data on the distribution and abundance of birds are rare for much of northern Canada and biased toward the few areas that have more observers and somewhat greater accessibility. This applies to Labrador, where the only comprehensive publication on birds of the region remains *Birds of the Labrador Peninsula and Adjacent Areas* (Todd 1963), although it focussed largely on northeastern Ontario and northern Quebec. Only limited data pertain to the current boundaries of Labrador and are certain to be inadequate to describe current bird communities given the likelihood of changes in distribution and abundance over the course of several decades. A somewhat updated overview for the lower Churchill River was provided by Hunter and Associates (1981), with a summary of historical data supplemented by limited field work in 1980.

Over the past two decades, first breeding records for Labrador have been documented for Northern Harrier (*Circus hudsonius*, near Churchill Falls; Chubbs *et al.* 2000) and Black-headed Gull (*Chroicocephalus ridibundus*, on Lake Melville; Chaulk *et al.* 2004). Further, Whitaker's (2017) summary of research in the Torngat Mountains of Labrador documented confirmed breeding of Spotted Sandpiper (*Actitis macularius*) and seven songbird species far north of previously recognized range limits.

Other recent research on bird communities in Labrador has included small-scale studies associated with forest clearing (Simon *et al.* 2000, 2002; Schwab *et al.* 2001, 2006), exploration of microhabitat preferences of Boreal Chickadee (*Poecile hudsonicus*) and Cape May Warbler (*Setophaga tigrina*; Ethier and Wilson 2019), use of microphone arrays by Hennigar *et al.* (2019) to investigate effects of traffic noise on breeding forest birds near Happy Valley-Goose Bay (HVGB), and analysis of bird distribution in relation to vegetation and altitude in the Mealy Mountains east of HVGB (Lewis and Starzomski 2015). The increasing popularity of eBird (2019) is adding to the knowledge of bird distribution in central Labrador, as are other citizen science efforts such as the Breeding Bird Survey (USGS 2018) and Christmas Bird Count (NAS 2018). However, the overwhelming majority of citizen science data are limited to the vicinity of HVGB and, to a lesser extent, along the Trans-Labrador Highway (TLH).

Whereas most of Labrador is within the taiga shield ecozone, the lower Churchill River valley and a narrow band along Lake Melville are within the boreal shield ecozone (ESWG 1996). This area is disjunct from the remainder of the boreal shield ecozone, which is otherwise largely restricted to below the southern boundary between Quebec and Labrador (80–150 km south of the lower Churchill River valley; Figure 1). Summers are warmer and winters less severe than in the adjacent taiga shield ecozone, especially in sheltered parts of the valley (Way *et al*. 2017). As a result, the area is known to support species more generally associated with boreal forests farther south, notably a greater diversity of plants, including stands of deciduous and mixed forest. However, despite its relative ecological richness within Labrador, Todd (1963) documented this area through only a single expedition in July and August of 1939. Much of the valley is remote and although accessible by canoe, is rarely travelled in that manner.

Although mostly undisturbed at the time of our research, part of the lower Churchill River valley was modified with the implementation of a dam at Muskrat Falls in 2019, creating a 101 km^2 reservoir upstream of Muskrat Falls, including 41 km^2 of newly flooded lands. A potential second dam at Gull Island has been proposed but is not yet scheduled for development.

To understand pre-development conditions and establish a baseline against which the effects of future land use changes can be evaluated, a comprehensive suite of field surveys was undertaken in 2006 and 2007, with supplementary efforts at certain locations in 2014–2016, as part of the environmental assessment of the Lower Churchill Hydroelectric Generation Project. The extent of coverage by these surveys greatly surpassed any previous landbird monitoring efforts in the region. The primary objectives of our study were to describe bird communities in the lower Churchill River valley by land cover type as a basis for future comparison, and to describe the distribution and abundance of species that are at the northern limit of their range in or near central Labrador.

Methods

Study area

Our primary study area was within ~3 km on either side of the lower Churchill River in central Labrador, from the Metchin River (53.313°N, 63.366°W) in the west to Lake Melville (53.334°N, 60.190°W) in the east, a linear distance of 210 km (270 km along the river; Figure 1). The actual width of the river valley varies; there are parts that are nearly a forested canyon and others where the slope is so gradual that there is no clear distinction of where the valley edge lies.

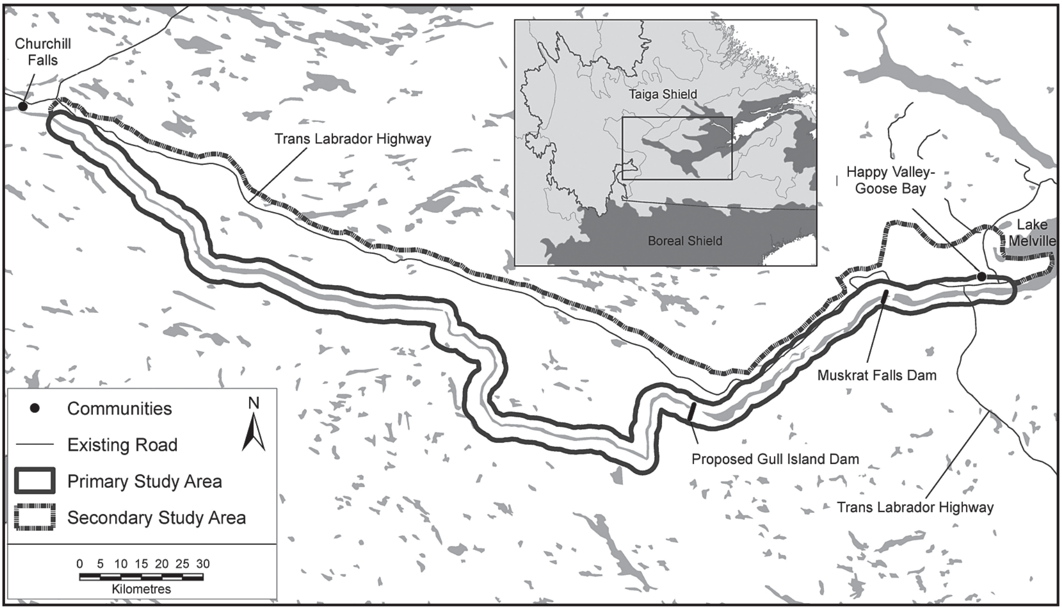


FIGURE 1. Location of the study area, with inset showing the relative distribution of the Boreal Shield and Taiga Shield Ecozones in Labrador.

Our focus was primarily within the river valley, but in areas where it was particularly narrow (e.g., upstream of Gull Island) or bordered by steep cliffs (e.g., parts of Lake Winokapau), some of our survey routes were on the adjacent plateau.

For comparative purposes we also conducted some surveys in two secondary study areas just north of the primary study area: 1) upland habitat near the TLH over a distance of nearly 150 km from east of Churchill Falls (53.492°N, 63.667°W) to north of Gull Island (53.068°N, 61.442°W), primarily along an existing power transmission line; and 2) ~25 km along the Goose River, from north of Muskrat Falls (53.393°N, 60.752°W) to Lake Melville (53.394°N, 60.386°W).

Land cover classification

The study area falls within the boreal shield ecozone, bounded on either side by the subarctic forest of the taiga shield ecozone (Figure 1). Black Spruce (*Picea mariana* (Miller), Britton, Sterns, and Poggenburgh) is the dominant tree species, with Balsam Fir (*Abies balsamea* (L.) Miller), Trembling Aspen (*Populus tremuloides* Michaux), and White Birch (*Betula papyrifera* Marshall) locally common on slopes and near the valley bottom. Small stands of White Spruce (*Picea glauca* (Moench) Voss) and Balsam Poplar (*Populus balsamifera* L.) are limited to a few flood plain locations along the lower Churchill River valley.

We identified seven distinct land cover categories within the study area (Table 1) and trained all field staff to classify sites consistently according to their definitions. Black Spruce (BS) is by far the most abundant land cover type in the study area, typically occurring as open stands with a carpet of Reindeer Lichen (*Cladonia rangiferina*) in uplands, and closed stands with Ostrich-plume Moss (*Ptilium crista-castrensis*) dominating the understorey on slopes and in lowlands. Mixed conifer forest (MC) is primarily found on floodplains, where large White Spruce or Balsam Fir trees are interspersed with some Black Spruce, and on Balsam Fir-dominated slopes, mostly in the area between Gull Island and Lake Winokapau. Mixedwood forest (MW) is mostly in floodplains and on southward facing slopes and is more frequent in the eastern half of the study area; deciduous trees are primarily Trembling Aspen. Hardwood forests (HA) are scarce in the study area, with larger stands mostly limited to along the Lower Churchill River east of Gull Island; Trembling Aspen is typically dominant, but in some stands White Birch is also common. Riparian (RI) areas were defined as the vegetation along river shorelines, typically comprising shrubs and forbs. Wetlands (WE) comprise marshes and wet meadows within the lower Churchill River floodplain (e.g., at Upper Brook), as well as upland Speckled Alder (*Alnus incana* subsp. *rugosa* (Du Roi) R.T. Clausen) swamps, fens, and bogs. The disturbed (DI) category primarily (>90%) comprises regenerating burns (e.g., at Metchin River and east of Edward's Brook), but also includes the area cleared for the work camp east of Gull Island.

Site selection

Surveys were conducted at 617 point count stations along 63 routes, 46 (73%) of which were in the primary study area, with the remainder split between the TLH uplands ($n = 8$; 13%) and Goose River (9; 14%; Figure 2a,b). We did not record the length or area of routes, nor the distance of individual point count stations from rivers or roads. The greatest concentration

Table 1. Categorization of land cover types in the lower Churchill River valley.

Land cover type	Description
Black Spruce (BS)	Open to closed forest with Black Spruce (*Picea mariana* (Miller) Britton, Sterns, and Poggenburgh), comprising >90% of trees; ground cover generally heavily dominated by Reindeer Lichen (*Cladonia rangiferina*) or feather mosses (*Ptilium* spp.)
Mixed conifer (MC)	Forest with coniferous species comprising >90% of trees, including at least 10% White Spruce (*Picea glauca* (Moench) Voss) or Balsam Fir (*Abies balsamea* (L.) Miller); ground cover generally mosses and forbs
Mixedwood (MW)	Forest with deciduous species (mostly Trembling Aspen, *Populus tremuloides* Michaux) comprising 10–49% of trees, mixed with Black Spruce, White Spruce, and/or Balsam Fir; ground cover varied
Hardwood (HW)	Forest with deciduous species (mostly Trembling Aspen) comprising >50% of trees; ground cover mostly forbs
Riparian (RI)	Shoreline vegetation, typically dominated by Speckled Alder (*Alnus incana* subsp. *rugosa* (Du Roi) R.T. Clausen), willows (*Salix* spp.), Sweet Gale (*Myrica gale* L.), grasses, and sedges
Wetland (WE)	Marshes, wet meadows, alder swamps, fens, and bogs; often surrounded by or even including some Black Spruce
Disturbed (DI)	Burns with <20 years of regeneration, and other disturbed lands

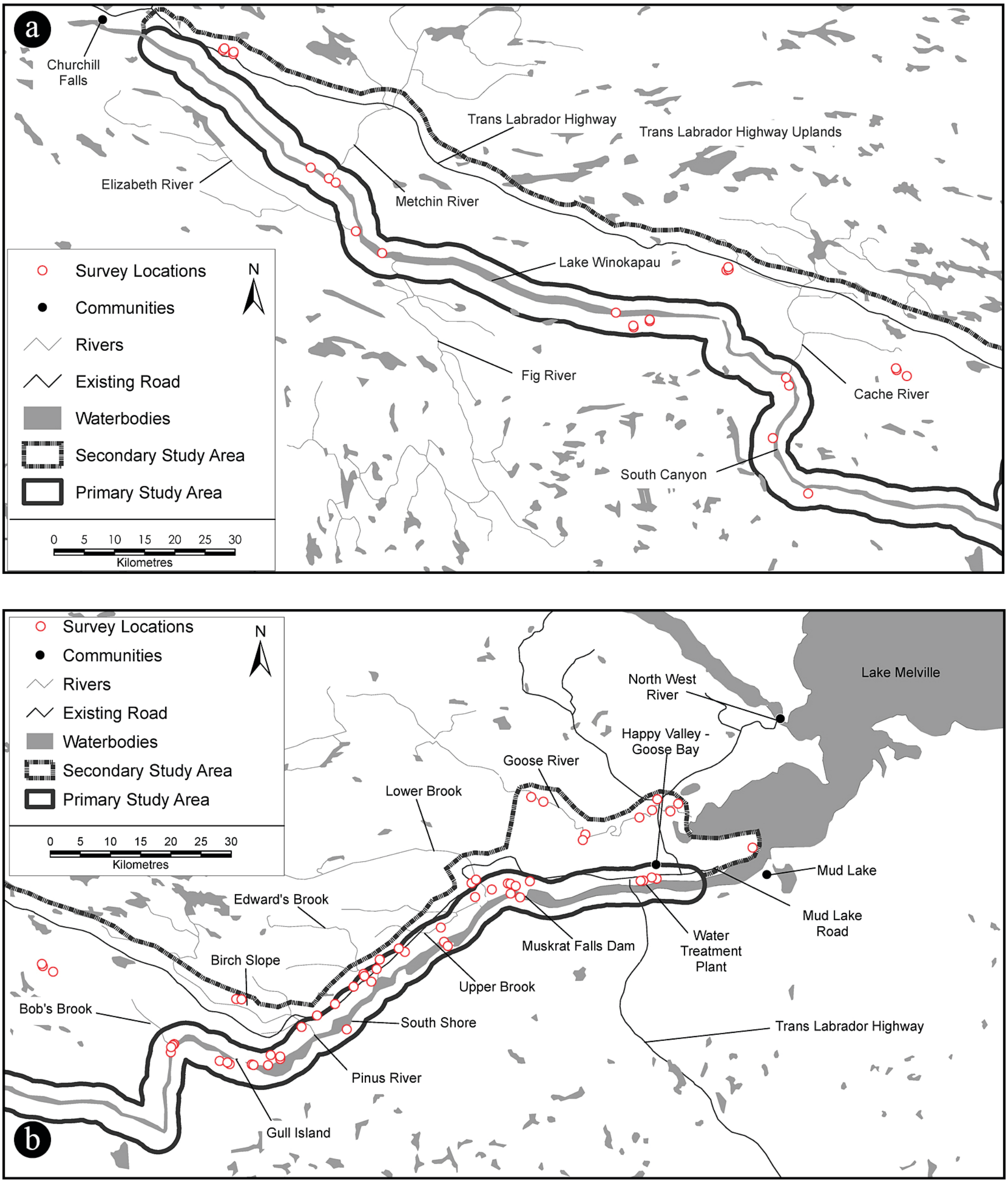


FIGURE 2. Point count survey locations in the a. western and b. eastern portions of the lower Churchill River valley.

of routes (24; 38%) was in the 50 km section between Muskrat Falls and Gull Island, within or immediately adjacent to the projected footprint of the future Muskrat Falls reservoir. Locations of all routes were constrained by requiring road access or suitable helicopter landing sites within 500 m, to maximize time available for surveys. Especially between Gull Island and Lake Winokapau, the combination of steep slopes and nearly continuous forest cover limited landing options considerably, and nearly all suitable access points were used. Elsewhere, less common land cover types (especially MC, MW, and HA) were generally targetted wherever accessible, to boost their limited sample size. Survey routes in the more widespread land cover types (most notable BS and WE) were selected arbitrarily from among accessible options to provide a geographically balanced sample. Overall, 48% of routes were accessed by road and 52% by helicopter.

Each route comprised 6–13 point count stations, typically spaced 250 m to 350 m apart, and at least 100 m from any road. For routes near the river, roughly half of the stations were placed below the future reservoir level, and half above. Route design was also influenced by topographic limitations (e.g., rivers and steep slopes) and a preference for a looped layout for efficiency. Individual station locations were pre-selected using aerial imagery and ecological land classification mapping such that, at minimum, the 50 m radius around the point was in a single land cover type, and preferably 100 m. In the field, observers visually assessed each location prior to conducting the first survey and adjusted the position by up to 50 m to achieve greater land cover homogeneity. Global positioning system coordinates were taken at each survey point and flagging tape was placed to facilitate use of the identical location in future years.

Survey effort was greatest in 2006 and 2007, with baseline surveys in those two years accounting for 70% of the 1139 point counts conducted (Table 2). All routes surveyed in 2006 were repeated in 2007, except for seven along the Goose River, and 16 additional routes were covered in 2007 to address geographic gaps in the original sampling strategy and to target land cover types that were undersampled in 2006. Five of the original routes were revisited again in both 2014 and 2015, and six others in 2016. Eight new routes (13% of the total) were added in 2014 and 2015: six in or adjacent to the future Muskrat Falls reservoir and two near the Goose River delta.

Data collection

We collected bird data primarily through point counts, following a standard single-observer, fixed-radius protocol as described by Bibby *et al.* (2000). Each count was undertaken by a single observer with multiple previous years of boreal bird survey experience; across all years, 13 observers collected data, but there were no more than five in any single year. *Post hoc* data review showed no significant differences within years among observers in terms of mean number of species or individuals detected per point. All birds seen or heard were noted, although any flying past were flagged as incidental sightings and not included in analyses. Each individual was treated as a distinct observation. Distance to each observation was classified as being <50 m, <100 m, or ≥100 m from the observer. Care was taken to track the movements of individuals during a point count, to avoid double counting; if in doubt, the lower number was recorded. Surveys were timed to coincide with the peak of the breeding bird season from mid-June to early July (Table 2). Sunrise across the dates and locations of the survey ranged from 0435 to 0455, but because helicopter flight was not possible before civil dawn, and to avoid bias for sites accessible by road, all counts began after 0500 and ended by 0935. All counts were five minutes in duration.

We conducted a literature review to identify species considered to be regionally rare in the study area. We defined species as rare if they are classified as S1 (Critically Imperilled) in Labrador by NatureServe (2019), absent from Labrador according to maps in the most recent NatureServe (2019) or Birds of North America (Billerman *et al*. 2020) species accounts, or considered to occur in Labrador, but not within the study area according to at least three out of four field guides (Floyd 2008; Peterson 2012; Sibley 2016; Dunn and Alderfer 2017). For historical context, we referenced Todd (1963). We also compared our results with data from the four Breeding Bird Survey routes within our study area (Happy Valley: 1978, 1994–2001, 2003–2007, 2009–2011, 2013–2017; Goose Bay: 2016; Bob's Brook: 2011–2014, 2017; Main Wilson River: 2016–2017; USGS 2018), and eBird records from the Study Area (eBird 2019).

Data analysis

Birds detected before or after point counts, flying over during counts, over 100 m from point count locations, or while walking between counts were all noted as incidental observations. These were not used for calculations of relative abundance or assessment of land cover type association but were included in reporting the distribution of regionally rare species. We calculated relative abundance within each land cover type as the number of individuals detected per 100 point counts. We summarized results by land

TABLE 2. Breeding bird point count survey effort in central Labrador by year; TLH = Trans Labrador Highway.

Year	Survey dates	# routes	# points	Core focus
2006	24 June–4 July	39	342	Primary study area and Goose River
2007	11–28 June	48	450	Primary study area and TLH uplands
2014	18–25 June	9	108	Future Muskrat Falls reservoir
2015	20–25 June	10	121	Future Muskrat Falls reservoir
2016	20–26 June	14	118	TLH uplands

cover type and year, but for discussion of rare species, pooled results across all years.

For each of the regionally rare species, we compared their distribution from our field data with the published maps of NatureServe (2019), Birds of North America (Billerman *et al.* 2020), and the latest Smithsonian (Floyd 2008), Peterson (2012), Sibley (2016), and National Geographic (Dunn and Alderfer 2017) field guides. In each case, we estimated (to the nearest 50 km) the distance from the nearest edge of the previously mapped distribution to the farthest observation within the study area.

Results

Over the five years of field effort, we detected 80 bird species at point counts in the study area, with a single-year high of 73 species in 2007 (Table 3; Table S1). We observed an additional nine species

Table 3. Survey effort and summary results by year and primary land cover type (BS = Black Spruce, MC = mixed conifer, MW = mixedwood, HA = hardwood, RI = riparian, WE = wetland, DI = disturbed).

	Primary land cover type							
	BS	MC	MW	HA	RI	WE	DI	Total
2006								
Number of point count routes	32	22	19	7	14	16	6	39
Number of point count stations	111	40	62	22	65	33	9	342
Number of species observed	30	26	36	28	43	31	6	66
Number of individuals observed	300	153	291	106	394	183	34	1461
Mean # individuals/point count	2.7	3.8	4.7	4.8	6.1	5.5	3.8	4.3
2007								
Number of point count routes	40	20	24	10	18	20	9	48
Number of point count stations	158	52	82	35	70	33	20	450
Number of species observed	46	39	44	38	53	46	19	73
Number of individuals observed	711	300	536	302	416	237	87	2589
Mean # individuals/point count	4.5	5.8	6.5	8.6	5.9	7.2	4.4	5.8
2014								
Number of point count routes	10	5	5	2	1	2	2	10
Number of point count stations	49	18	31	2	6	2	0	108
Number of species observed	26	20	28	6	13	9	—	38
Number of individuals observed	240	135	218	9	27	13	—	642
Mean # individuals/point count	4.9	7.5	7.0	4.5	4.5	6.5	—	5.9
2015								
Number of point count routes	12	5	7	2	1	4	4	12
Number of point count stations	66	6	27	4	5	9	4	121
Number of species observed	30	15	25	13	9	12	12	43
Number of individuals observed	241	39	164	31	11	24	21	531
Mean # individuals/point count	3.7	6.5	6.1	7.8	2.2	2.7	5.3	4.4
2016								
Number of point count routes	14	7	5	0	6	8	4	14
Number of point count stations	52	9	9	0	12	12	24	118
Number of species observed	28	10	17	—	21	15	18	39
Number of individuals observed	219	49	38	—	75	62	91	534
Mean # individuals/point count	4.2	5.4	4.2	—	6.3	5.2	3.8	4.5
Total								
Number of point count routes	52	28	34	11	21	26	11	63
Number of point counts	436	125	211	63	158	89	57	1139
Number of species observed	60	44	52	40	62	51	52	80
Number of individuals observed	1711	676	1247	448	923	519	233	5757
Mean # individuals/point count	3.9	5.4	5.9	7.1	5.8	5.8	4.1	5.1

only incidentally. The five most numerous species each had an overall mean relative abundance of ≥35 individuals/100 point counts; in descending order of abundance they were Swainson's Thrush (*Catharus ustulatus*), Ruby-crowned Kinglet (*Corthylio calendula*), Dark-eyed Junco (*Junco hyemalis*), Yellow-rumped Warbler (*Setophaga coronata*), and Tennessee Warbler (*Leiothlypis peregrina*; Table 4). These five species accounted for 44% of all observations; the 10 most abundant species comprised 67%. Three of the species we observed are listed under Canada's *Species at Risk Act* (Government of Canada 2019): Olive-sided Flycatcher (*Contopus cooperi*; four observations), Bank Swallow (*Riparia riparia*; 43), and Rusty Blackbird (*Euphagus carolinus*; 16).

Land cover associations

Across all years, the mean number of individuals observed per point count was much higher in hardwood forest than any other land cover type (7.1 versus 5.9 in mixedwood forest and an overall average of 5.1); it was lowest overall in Black Spruce (3.9; Table 3). Results varied somewhat among years, especially for land cover types with smaller sample sizes, but Black Spruce was below average in all years, whereas mixedwood, hardwood, riparian, and wetland were each above average in all but one year of sampling.

In the Black Spruce land cover type, the five most abundant species (in descending order) were Ruby-crowned Kinglet, Dark-eyed Junco, Yellow-rumped Warbler, Swainson's Thrush, and Canada Jay (*Perisoreus canadensis*), ranging from 26 to 64 individuals/100 point counts (Table 4).

In mixed conifer forest, the five most abundant species were Swainson's Thrush, Ruby-crowned Kinglet, Tennessee Warbler, Yellow-rumped Warbler, and Dark-eyed Junco, ranging from 39 to 82 individuals/100 point counts; Northern Waterthrush (*Parkesia noveboracensis*) and White-throated Sparrow (*Zonotrichia albicollis*) also exceeded 30 individuals/100 point counts (Table 4).

In mixedwood forest, the five most abundant species were Swainson's Thrush, Tennessee Warbler, Ruby-crowned Kinglet, Black-throated Green Warbler (*Setophaga virens*), and Yellow-rumped Warbler, ranging from 40 to 86 individuals/100 point counts; White-throated Sparrow and Fox Sparrow (*Passerella iliaca*) also exceeded 30 individuals/100 point counts (Table 4).

In hardwood forest, the five most abundant species were Swainson's Thrush, Tennessee Warbler, Black-throated Green Warbler, Least Flycatcher (*Empidonax minimus*), and White-throated Sparrow, ranging from 54 to 89 individuals/100 point counts; Ruby-crowned Kinglet, Yellow-bellied Flycatcher (*Empidonax flaviventris*), and Fox Sparrow also exceeded 30 individuals/100 point counts (Table 4).

In riparian areas, the five most abundant species were Yellow Warbler (*Setophaga petechia*), Swainson's Thrush, Northern Waterthrush, Fox Sparrow, and White-throated Sparrow, ranging from 30 to 88 individuals/100 point counts (Table 4).

In wetlands, the five most abundant species were Ruby-crowned Kinglet, Dark-eyed Junco, White-throated Sparrow, Swainson's Thrush, and Fox Sparrow, ranging from 36 to 55 individuals/100 point counts; Lincoln's Sparrow (*Melospiza lincolnii*) and Canada Jay also exceeded 30 individuals/100 point counts (Table 4).

In disturbed areas, the five most abundant species were Dark-eyed Junco, White-throated Sparrow, Black-backed Woodpecker (*Picoides arcticus*), Hermit Thrush (*Catharus guttatus*), and Bank Swallow, ranging from 25 to 105 individuals/100 point counts (Table 4).

The top five species overall were among the five most common species in at least three of the seven land cover types within the study area (Table 4). Another ten species were among the top five in at least one land cover type and a further four species (Spotted Sandpiper; Yellow-bellied Flycatcher; Boreal Chickadee; Lincoln's Sparrow) accounted for at least 5% of observations in one or more land cover types (Table 4).

Extralimital records

Of the 80 species detected during point counts, 14 (18%) are considered to be regionally rare based on their NatureServe (2019) status for Labrador or range maps that show them to be absent from Labrador (Table 5). The most abundant of these were Least Flycatcher (118 individual bird observations), Magnolia Warbler (117), and Cedar Waxwing (*Bombycilla cedrorum*; 82). We observed an additional five regionally rare species only incidentally: Sora (*Porzana carolina*), Black-capped Chickadee (*Poecile atricapillus*), Bohemian Waxwing (*Bombycilla garrulus*), Black-and-white Warbler (*Mniotilta varia*), and Common Yellowthroat (*Geothlypis trichas*; Table 5).

Two of the species observed are shown as entirely absent from Labrador in all six range maps we reviewed (no audio recordings or photographs are available for these records). We documented Brown Creeper (*Certhia americana*) in five sites ranging from Lake Winokapau east to Gull Island, all in conifer-dominated land cover types, but with more than half of the records occurring in the regionally uncommon mixed conifer forest. We observed Song Sparrow (*Melospiza melodia*) in nine sites from Metchin River to east of HVGB, primarily (80%) in riparian areas and wetlands near the shoreline of the lower Churchill River and major tributaries, most notably Elizabeth River and Upper Brook.

Table 4. Relative abundance (number per 100 point counts) of common birds in the lower Churchill River valley by land cover type (BS = Black Spruce, MC = mixed conifer, MW = mixedwood, HA = hardwood, RI = riparian, WE = wetland, DI = disturbed), sorted by overall mean relative abundance (rank abundance in each land cover type in parentheses; top five species in each land cover type in bold). Common birds includes 19 species that accounted for >5% of observations in at least one land cover type, plus seven other species (*) that accounted for at least 1% of observations overall.

	BS	MC	MW	HA	RI	WE	DI	Total
Swainson's Thrush	**39.2**	**81.6**	**86.3**	**88.9**	**51.9**	**36.0**	12.3	**55.5**
(*Catharus ustulatus*)	**(4)**	**(1)**	**(1)**	**(1)**	**(2)**	**(4)**	(9)	**(1)**
Ruby-crowned Kinglet	**64.4**	**68.8**	**49.8**	38.1	17.7	**55.1**	22.8	**51.4**
(*Corthylio calendula*)	**(1)**	**(2)**	**(3)**	(6)	(11)	**(1)**	(6)	**(2)**
Dark-eyed Junco	**60.8**	**39.2**	30.3	28.6	13.9	**50.6**	**105.3**	**45.9**
(*Junco hyemalis*)	**(2)**	**(5)**	(8)	(9)	(14)	**(2)**	**(1)**	**(3)**
Yellow-rumped Warbler	**47.5**	**40.8**	**39.8**	28.6	19.0	23.6	17.5	**37.0**
(*Setophaga coronata*)	**(3)**	**(4)**	**(5)**	(9)	(10)	(9)	(7)	**(4)**
Tennessee Warbler	22.7	**51.2**	**58.3**	**77.8**	24.7	24.7	5.3	**35.0**
(*Leiothlypis peregrina*)	(6)	**(3)**	**(2)**	**(2)**	(7)	(8)	(15)	**(5)**
White-throated Sparrow	15.8	32.8	37.0	**54.0**	**29.7**	**49.4**	**50.9**	30.0
(*Zonotrichia albicollis*)	(8)	(7)	(6)	**(5)**	**(5)**	**(3)**	**(2)**	(6)
Fox Sparrow	19.9	28.0	32.2	33.3	**30.4**	**36.0**	10.5	25.7
(*Passerella iliaca*)	(7)	(8)	(7)	(8)	**(4)**	**(4)**	(11)	(7)
Canada Jay	**25.7**	16.8	18.0	11.1	5.1	30.3	12.3	19.3
(*Perisoreus canadensis*)	**(5)**	(9)	(10)	(16)	(25)	(7)	(9)	(8)
Black-throated Green Warbler	7.8	11.2	**46.9**	**57.1**	17.1	4.5	—	18.8
(*Setophaga virens*)	(11)	(13)	**(4)**	**(3)**	(12)	(26)		(9)
Yellow Warbler	2.1	12.8	9.5	11.1	**88.0**	23.6	1.8	18.7
(*Setophaga petechia*)	(17)	(12)	(15)	(16)	**(1)**	(9)	(24)	(10)
Northern Waterthrush	5.3	36.0	21.8	19.0	**38.6**	23.6	1.8	18.3
(*Parkesia noveboracensis*)	(14)	(6)	(9)	(12)	**(3)**	(9)	(24)	(11)
American Robin*	7.6	14.4	18.0	15.9	10.1	11.2	15.8	11.8
(*Turdus migratorius*)	(12)	(11)	(10)	(15)	(18)	(14)	(8)	(12)
Boreal Chickadee	12.2	16.0	16.1	6.3	6.3	5.6	8.8	11.5
(*Poecile hudsonicus*)	(9)	(10)	(12)	(21)	(23)	(22)	(12)	(13)
Alder Flycatcher*	1.4	8.0	8.5	19.0	23.4	22.5	3.5	9.2
(*Empidonax alnorum*)	(24)	(14)	(17)	(12)	(8)	(12)	(17)	(14)
Yellow-bellied Flycatcher	2.3	8.0	14.7	36.5	5.1	3.4	—	7.5
(*Empidonax flaviventris*)	(17)	(14)	(14)	(7)	(25)	(29)		(15)
Hermit Thrush	10.3	4.0	2.8	1.6	0.6	11.2	**26.3**	7.3
(*Catharus guttatus*)	(10)	(22)	(26)	(32)	(50)	(14)	**(4)**	(16)
Magnolia Warbler*	2.3	6.4	8.5	4.8	21.5	5.6	1.8	6.9
(*Setophaga magnolia*)	(17)	(19)	(17)	(23)	(9)	(22)	(24)	(17)
Least Flycatcher	0.9	4.8	6.6	**55.6**	9.5	3.4	—	6.8
(*Empidonax minimus*)	(34)	(21)	(19)	**(4)**	(20)	(29)		(18)
Lincoln's Sparrow	1.6	3.2	1.4	4.8	16.5	31.5	5.3	6.5
(*Melospiza lincolnii*)	(23)	(23)	(36)	(23)	(13)	(6)	(15)	(19)
Red-breasted Nuthatch*	2.3	7.2	15.2	4.8	3.8	2.2	1.8	5.5
(*Sitta canadensis*)	(17)	(17)	(13)	(23)	(28)	(35)	(24)	(20)
Orange-crowned Warbler*	5.0	2.4	9.5	19.0	1.9	2.2	1.8	5.5
(*Leiothlypis celata*)	(15)	(25)	(15)	(12)	(37)	(35)	(24)	(20)
White-winged Crossbill*	6.4	3.2	6.2	3.2	3.8	5.6	1.8	5.2
(*Loxia leucoptera*)	(13)	(23)	(21)	(29)	(28)	(22)	(24)	(22)
Pine Siskin*	3.9	7.2	6.6	9.5	7.6	—	—	5.1
(*Pinus spinus*)	(16)	(17)	(19)	(20)	(22)			(22)
Spotted Sandpiper	0.5	2.4	0.9	—	29.1	1.1	—	4.7
(*Actitis macularius*)	(39)	(25)	(40)		(6)	(44)		(24)
Bank Swallow	1.1	1.6	0.5	—	12.0	2.2	**24.6**	3.8
(*Riparia riparia*)	(24)	(29)	(41)		(15)	(35)	**(5)**	(26)
Black-backed Woodpecker	0.7	—	1.4	—	1.3	—	**31.6**	2.3
(*Picoides arcticus*)	(36)		(36)		(42)		**(3)**	(31)

TABLE 5. Summary of observations of regionally rare birds in the lower Churchill River valley, 2006–2007 and 2014–2016 Land cover type: BS = Black Spruce, MC = mixed conifer, MW = mixedwood, HA = hardwood, RI = riparian, WE = wetland, DI = disturbed,

Species	Historical range in Labrador (sources*)	Sites observed (no. observations)	Land cover types observed (no. observations)	Years observed	Expansion of known breeding range (sources*†)
Sora (*Porzana carolina*) 1 incidental observation	Absent from Labrador (1,2,7); present around HVGB (4); limited to SW corner of Labrador (3,5,6)	Upper Brook (1)	WE (1)	2007	<50 km W from HVGB (4); >200 km E from SW Labrador (3,5,6); >600 km NE from Baie Comeau (1,2)
Downy Woodpecker (*Dryobates pubescens*) 2 point count observations 1 incidental observation	Absent from Labrador (2,5,6,7); limited to SW corner of Labrador (1) or southern edge of Labrador (3,4)	Birch Slope (1); Edward's Brook (1); Lower Brook (1)	MW (1) HA (2)	2007, 2014	>100 km N from S edge of Labrador (3,4); >150 km N from edge of range in E Quebec (1,2,5,6,7)
Yellow-bellied Sapsucker (*Sphyrapicus varius*) 4 point count observations 2 incidental observations	Absent from Labrador (4); present in SW Labrador (1,2,3,5,6); present around Gull Island (7)	Birch Slope (3); Edward's Brook (2); Lower Brook (1)	MW (2) HA (4)	2007, 2014, 2015	n/a (7); >150 km E from SW Labrador (1,2,3,5,6); >250 km NE from SW border of Labrador (4)
Least Flycatcher (*Empidonax minimus*) 77 point count observations 41 incidental observations	Absent from Labrador (1,2); present around HVGB (3,4,5,6,7)	Fig River (1); Lake Winokapau (1); Gull Island (5); Birch Slope (31); South Shore (5); Edward's Brook (15); Upper Brook (28); Lower Brook (9); Muskrat Falls (6); Water Treatment Plant (16); Goose River (1)	BS (6) MC (5) MW (20) HA (45) RI (36) WE (6)	2006, 2007, 2014, 2015, 2016	>150 km W from Happy Valley–Goose Bay (3,4,5,6,7); >400 km NE from Sept-Iles (1,2)
Red-eyed Vireo (*Vireo olivaceus*) 21 point count observations 15 incidental observations	Absent from Labrador (1,2,7); present around HVGB (3,4,5,6) and in SW Labrador (3)	Gull Island (4); Birch Slope (10); South Shore (2); Edward's Brook (3); Upper Brook (5); Lower Brook (7); Muskrat Falls (3); Water Treatment Plant (2)	BS (1) MC (1) MW (9) HA (22) RI (3)	2006, 2007, 2015	n/a (3,4,5,6); >350 km NW from N Newfoundland (1); >400 km NE from Anticosti Island (2)
Philadelphia Vireo (*Vireo philadelphicus*) 8 point count observations 1 incidental observation	Absent from Labrador (1,2,3,7); present around HVGB (4,6); rare in lower Churchill River valley (5)	Gull Island (2); Birch Slope (3); Edward's Brook (2); Upper Brook (1); Lower Brook (1)	BS (1) MW (2) HA (6)	2006, 2007, 2014	n/a (4,5,6); >250 km N from edge of range in E Quebec (1); >350 km NE from E of Sept-Iles (2,3)
Black-capped Chickadee (*Poecile atricapillus*) 1 incidental observation	Absent from Labrador (1,2,7); present around HVGB (3,4,5,6) and in SW Labrador (3,5,6)	Birch Slope (1)	HA (1)	2006	<50 km W from HVGB (3,4,5,6); >350 km NW from N Newfoundland (1,2)
Brown Creeper (*Certhia americana*) 5 point count observations 7 incidental observations	Absent from Labrador (1,2,3,4,5,6); historical record from HVGB (7)	Lake Winokapau (1); Cache River (3); South Canyon (1); TLH (2); Gull Island (5)	BS (3) MC (7) MW (2)	2006, 2007, 2016	n/a (7); >200 km N from edge of range in E Quebec (1,3,4,5); >350 km NE from E of Sept-Iles (2,6)

TABLE 5. *Continued.*

Species	Historical range in Labrador (sources*)	Sites observed (no. observations)	Land cover types observed (no. observations)	Years observed	Expansion of known breeding range (sources*†)
Winter Wren (*Troglodytes hiemalis*) 19 point count observations 25 incidental observations	Absent from Labrador (1,2,7); widespread in southern Labrador (3,4,5,6)	Metchin River (6); Elizabeth River (2); Lake Winokapau (1); South Canyon (4); Bob's Brook (2); Gull Island (19); Edward's Brook (1); Upper Brook (1); Lower Brook (1); Muskrat Falls (1); Goose River (2); Mud Lake Road (4)	BS (9) MC (14) MW (19) HA (1) DI (1)	2006, 2007, 2015, 2016	n/a (3,4,5,6); >150 km N from edge of range in E Quebec (1,2)
Golden-crowned Kinglet (*Regulus satrapa*) 7 point count observations 25 incidental observations	Absent from Labrador (1,2); present around HVGB (5,6,7); limited to SW Labrador (3,4)	Fig River (4); Lake Winokapau (4); Cache River (5); Gull Island (4); Pinus River (8); Lower Brook (2); Muskrat Falls (3); Water Treatment Plant (2)	BS (3) MC (18) MW (9) HA (2)	2006, 2007, 2014	>150 km W from Happy Valley–Goose Bay (5,6,7); >150 km E from SW Labrador (4); >200 km E from SW Labrador (3); >350 km NE from E of Sept-Iles (2); >400 km NE from Anticosti Island (1)
Bohemian Waxwing (*Bombycilla garrulus*) 8 incidental observations	Absent from Labrador (1,2,7); limited to SW Labrador (3,4); widespread in Labrador (5,6)	Birch Slope (8)	HA (8)	2007	n/a (5,6); >100 km E from E of Churchill Falls (3,4); >1000 km E from E coast James Bay (2); >2000 km E from Churchill, Manitoba (1)
Cedar Waxwing (*Bombycilla cedrorum*) 33 point count observations 49 incidental observations	Absent from Labrador (1,2,7); southern Labrador, extending to HVGB (3,4,5,6)	Metchin River (8); Elizabeth River (8); Cache River (1); Gull Island (4); Birch Slope (7); Edward's Brook (2); South Shore (2); Upper Brook (13); Lower Brook (3); Muskrat Falls (2); Water Treatment Plant (5); Goose River (2); Mud Lake Road (25)	BS (1) MW (11) HA (15) RI (38) WE (14) DI (3)	2006, 2007	n/a (5,6); >50 km N from limit of range in southern Labrador (3,4); >400 km N from E of Sept-Iles (1,2)
Purple Finch (*Haemorhous purpureus*) 4 point count observations 3 incidental observations	Absent from Labrador (1,7); limited to Central Labrador, including the lower Churchill River valley (2,3,4,5,6)	Elizabeth River (1); Pinus River (2); Lower Brook (1); Muskrat Falls (2); Water Treatment Plant (1)	BS (4) MC (2) MW (1)	2006, 2007, 2015	n/a (2,3,4,5,6); >300 km N from Quebec north shore (1)
Song Sparrow (*Melospiza melodia*) 10 point count observations 15 incidental observations	Absent from Labrador (1,2,3,4,5,6,7)	Metchin River (1); Elizabeth River (6); TLH (1); Gull Island (4); South Shore (2); Lower Brook (2); Upper Brook (4); Water Treatment (4); Mud Lake Road (1)	BS (3) MW (1) HA (1) RI (11) WE (9)	2006, 2007, 2014	>300 km N from edge of range in E Quebec (1,2,3,4,5,6)

TABLE 5. *Continued.*

Species	Historical range in Labrador (sources*)	Sites observed (no. observations)	Land cover types observed (no. observations)	Years observed	Expansion of known breeding range (sources*†)
Black-and-white Warbler (*Mniotilta varia*) 1 incidental observation	Absent from Labrador (1,2,7); present around HVGB (3,4,5,6)	Edward's Brook (1)	HA (1)	2007	<50 km W from HVGB (3,4,5,6); >350 km NW from N Newfoundland (1,2)
Nashville Warbler (*Leiothlypis ruficapilla*) 13 point count observations 2 incidental observations	Absent from Labrador (1,2,3,4); rare in Central Labrador (5); rare in SW and Central Labrador (6); historical records around HVGB (7)	Fig River (2); Bob's Brook (1); Pinus River (4); Birch Slope (1); Edward's Brook (1); Muskrat Falls (1); Water Treatment Plant (5)	BS (6) MW (8) HA (1)	2006, 2007	n/a (5,6); >150 km W from Happy Valley – Goose Bay (7); >300 km N from Quebec north shore (1,2); >400 km NE from Sept Iles (3); >400 km NE from Anticosti Island (4)
Common Yellowthroat (*Geothlypis trichas*) 2 incidental observations	Absent from Labrador (7); limited to southern edge of Labrador (1,2,3,4); rare in central Labrador (5); rare in SW Labrador (6)	Gull Island (1); Upper Brook (1)	WE (1) RI (1)	2006, 2016	n/a (5); >100 km E from SW Labrador (6); >100 km N from S edge of Labrador (1,2,3,4)
Cape May Warbler (*Setophaga tigrina*) 17 point count observations 9 incidental observations	Absent from Labrador (1,2,3,7); limited to SW Labrador (4); rare in SW Labrador and around HVGB (5,6)	Fig River (3); Gull Island (5); Edward's Brook (3); Upper Brook (2); Muskrat Falls (6); Water Treatment Plant (4); Mud Lake Road (3)	BS (6) MC (11) MW (9)	2006, 2007, 2014, 2015	>100 km E of SW Labrador (5,6); >250 km E from SW Labrador (4); >300 km NE from SW Quebec / Labrador border (3); >350 km NE from E of Sept Iles (1,2)
Magnolia Warbler (*Setophaga magnolia*) 78 point count observations 39 incidental observations	Absent from Labrador (1,2); present near HVGB (7); widespread in southern Labrador (3,4,5,6)	West T-line (1); Metchin River (4); Fig River (2); Lake Winokapau (2); Cache River (6); South Canyon (1); Bob's Brook (11); Gull Island (15); Birch Slope (3); Edward's Brook (5); Upper Brook (6); Lower Brook (2); Muskrat Falls (14); Water Treatment Plant (16); Goose River (23); Mud Lake Road (6)	BS (6) MC (19) MW (26) HA (5) RI (45) WE (6) DI (10)	2006, 2007, 2014, 2015, 2016	n/a (3,4,5,6); >350 km N from Quebec north shore (1,2)

*1. NatureServe (2019); 2. Rodewald (2019); 3. Dunn and Alderfer (2017); 4. Peterson (2012); 5. Sibley (2016); 6. Floyd (2008); 7. Todd (1963).

†No distance provided for species considered absent by Todd (1963) as distribution of most species not mapped.

Another two species are recognized by some references as occurring within Labrador, although only outside the study area. We found Downy Woodpecker (*Dryobates pubescens*) and Yellow-bellied Sapsucker (*Sphyrapicus varius*) at the same three sites (Birch Slope, Edward's Brook, and Lower Brook), within a span of <40 km along the north side of the lower Churchill River that supports a particularly high density of hardwood and mixedwood forest.

A further seven species have been previously documented as occurring within part of the study area but were found outside of mapped range during our surveys. Most notably, Least Flycatcher is recognized as having an outlier population around HVGB. We recorded it as far west as Fig River and Lake Winokapau, over 150 km to the west; however, 98% of observations were between Goose Island and HVGB. It was highly associated with mixedwood, hardwood, and riparian areas. Golden-crowned Kinglet (*Regulus satrapa*) has been mapped as occurring in southwest Labrador and around HVGB, but we found it to be widespread from Fig River to the HVGB Water Treatment Plant, primarily in association with large White Spruce in mixed conifer and mixedwood forest types. Cedar Waxwing is mapped as being absent from Labrador or limited to the southern edge of Labrador up to near HVGB, but we observed it at 13 sites from Metchin River to Lake Melville, heavily associated with riparian areas and wetlands, and secondarily with hardwood and mixedwood forest. Cape May Warbler is considered to have, at most, a limited distribution in Labrador, but we found it in seven sites from Fig River east to Lake Melville; it was restricted to conifer-dominated land cover types, but notably more common in mixed conifer and mixedwood forest than in areas dominated by Black Spruce. Additionally, for three species mapped as occurring around HVGB, we had single incidental observations upstream: Sora at Upper Brook, Black-capped Chickadee at Birch Slope, and Black-and-white Warbler at Edward's Brook.

We also confirmed the presence of three species that are shown by at least one reference to occur rarely within the study area. Sibley (2016) recognizes Philadelphia Vireo (*Vireo philadelphicus*) as rare in the lower Churchill River valley, consistent with our nine detections of the species at five sites between Gull Island and Lower Brook, almost all associated with hardwood and mixedwood forest. Floyd (2008) and Sibley (2016) have mapped Nashville Warbler (*Leiothlypis ruficapilla*) as rare in central Labrador, which aligns with our 15 observations at seven sites between Fig River and the Water Treatment Plant, all but one of which were in Black Spruce or mixedwood forest. Sibley (2016) also identified Common Yellowthroat as rare in central Labrador; we had only two incidental observations in riparian and wetland sites at Gull Island and Upper Brook, ~35 km apart.

Finally, we confirmed the presence of another five species that are shown to occur throughout the study area in some maps, but not others. Of these, Magnolia Warbler was the most abundant and widespread, with 117 individual bird observations at 16 sites spanning the entire study area, and across all land cover types, although most frequently in riparian and mixedwood forest. Winter Wren (*Troglodytes hiemalis*) was also numerous and widely distributed, with 44 observations at 12 sites along almost the full length of the lower Churchill River, especially in areas with mixedwood and mixed conifer forest. Purple Finch (*Haemorhous purpureus*) also occurred over a large area, at five sites from Elizabeth River to the Water Treatment Plant, but was scarce, with only seven observations in total, all associated with coniferous or mixedwood forest. Red-eyed Vireo (*Vireo olivaceus*) had a more restricted distribution, but was locally common, with 36 observations at eight sites between Gull Island and the Water Treatment Plant, overwhelmingly in hardwood and mixedwood forest. There was only one sighting of Bohemian Waxwing, a flock of eight individuals in hardwood forest on Birch Slope in 2007.

Discussion

Our lower Churchill River valley bird surveys represent the most extensive documentation to date of any landbird communities in Labrador. Between 2006 and 2016, we observed 80 species during point counts, predominantly (56; 70%) passerines and woodpeckers. This is an unusually high level of avian diversity for Labrador, but the overall bird community is fairly typical for boreal Canada (Kirk *et al.* 1996) and reflects the presence of several species that require the habitat diversity limited to the lower Churchill River valley.

Including incidental observations, the total of 89 species we observed is similar to the cumulative sum of 83 species documented on the HVGB Breeding Bird Survey route over 22 years of effort between 1978 and 2016 (USGS 2018). However, 16 species were observed on that route only once, and another two species (American Bittern [*Botaurus lentiginosus*] and European Starling [*Sturnus vulgaris*]) appear to be strictly limited to the area immediately around HVGB, as we did not observe them on any of our surveys in the lower Churchill River valley. Conversely, 11 of the species we observed have never been documented on the HVGB Breeding Bird Survey route: Green-winged Teal (*Anas crecca*), Semipalmated Plover (*Charadrius semipalmatus*), Least Sandpiper

(*Calidris minutilla*), Solitary Sandpiper (*Tringa solitaria*), Bald Eagle (*Haliaeetus leucocephalus*), Yellow-bellied Sapsucker, Brown Creeper, Golden-crowned Kinglet, Song Sparrow, Nashville Warbler, and Common Yellowthroat. Only two additional species have been observed on other Breeding Bird Survey routes in the region but not on our surveys: Surf Scoter (*Melanitta perspicillata*) at Bob's Brook in 2014, and Arctic Tern (*Sterna paradisaea*) at Main Wilson River in 2017 (USGS 2018).

The only previous study focussing extensively on the lower Churchill River valley was a historical review supplemented by limited field effort in 1980 (Hunter and Associates 1981). It reported 60 passerine and woodpecker species, compared to 56 in our study, but also included several species that were transient migrants not expected to be in the lower Churchill River valley during the breeding season (e.g., Horned Lark [*Eremophila alpestris*], American Pipit [*Anthus rubescens*]). Of the potential breeding species listed by Hunter and Associates (1981), the only ones we did not observe were Evening Grosbeak (*Coccothraustes vespertinus*), Chestnut-sided Warbler (*Setophaga pensylvanica*), and Blackburnian Warbler (*Setophaga fusca*). These three species are shown in recent range maps (e.g., Peterson 2012; Dunn and Alderfer 2017) as having range limits >400 km to the southwest, comparable to the distribution mapped in some field guides for species that we did observe in large numbers (e.g., Magnolia Warbler). Conversely, we found nine species for which Hunter and Associates (1981) reported no previous records: Downy Woodpecker, Least Flycatcher, Black-capped Chickadee, Brown Creeper, Winter Wren, Bohemian Waxwing, Philadelphia Vireo, Nashville Warbler, and Cape May Warbler. However, four of these species (Brown Creeper, Winter Wren, Philadelphia Vireo, and Cape May Warbler) were also documented by Hennigar *et al.* (2019) in the area north of HVGB in 2016 and 2017.

Abundance of some species has changed over time. For example, one to five Rusty Blackbirds were observed daily during surveys of the lower Churchill River valley in 1980 (Hunter and Associates 1981) whereas we had only 16 total observations over our 41 days of effort between 2006 and 2016, perhaps reflecting the significant long-term population decline of this species (COSEWIC 2017). Other bird populations may have been elevated during our study because of a Spruce Budworm (*Choristoneura fumiferana*) outbreak around HVGB that began in 2007 and peaked in 2013 but persisted broadly until 2016 (Lavigne 2019). In particular, Cape May Warbler and Tennessee Warbler are considered Spruce Budworm specialists, but Golden-crowned Kinglet has also been shown to respond particularly strongly to such events, and numerous others to a lesser extent (Holmes *et al.* 2009; Venier *et al.* 2009).

We found abundance and diversity to be consistently greatest in hardwood, mixedwood, and mixed conifer forests. These land cover types provide greater structural diversity than others, as they not only have a richer and more varied layer of ground vegetation and shrubs, but also are the only areas where large trees thrive, especially White Spruce. Within Labrador, these land cover types are largely limited to the boreal shield ecozone. Even within it, they occur primarily in the lower Churchill River valley floodplain and adjacent slopes. We also found above average bird abundance and diversity in many riparian areas, although many of these were narrow strips of vegetation adjacent to hardwood, mixedwood, or mixed conifer forests, and those associated land cover types may have contributed to the birds observed. Conversely, bird abundance and diversity tended to be lowest in Black Spruce forests and disturbed areas, which have the least structural complexity. This is consistent with the findings of Lewis and Starzomski (2015) at higher elevations in the Mealy Mountains east of HVGB, where vegetation was somewhat different, but vegetation structure was also strongly associated with the composition of the avian community.

Overall, we found Ruby-crowned Kinglet, Swainson's Thrush, and Dark-eyed Junco to be the most abundant breeding birds in the lower Churchill River valley; these were also among the top five species detected by Hennigar *et al.* (2019) north of HVGB. Each of these three species was among the two most abundant in three land cover types and occurred at least uncommonly in all others. Nonetheless, we found that the avian community differed notably among all seven land cover types. For the most part, observed land cover associations were typical (e.g., Billerman *et al.* 2020), and species with narrower ecological niches (e.g., Red-eyed Vireo in deciduous forest [Cimprich *et al.* 2020]; and Black-backed Woodpecker in recent burns [Tremblay *et al.* 2020]) were more restricted in their distribution than generalists (e.g., American Robin [*Turdus migratorius*], Vanderhoff *et al.* 2020). Only a few species deviated notably from typical habitat associations. Tennessee Warbler was most abundant in hardwood and mixedwood forest, as expected (Rimmer and McFarland 2020), but almost equally numerous in mixed conifer forest, which is unusual but perhaps explained by the limited extent of typically preferred habitat and the availability of a diverse understorey in mixed conifer stands. Conversely, Black-throated Green Warbler is generally associated with coniferous stands in most of its range (Morse and Poole 2020) but in our study area was found on average five times more frequently in mixedwood and hardwood forests, possibly reflecting its preference for large-diameter trees (Robichaud and Villard 1999). Similarly, Yellow-bellied Flycatcher is typically considered to be a bird of moist spruce and fir forests (Gross and Lowther 2020), but in the lower Churchill River valley was far more abundant in hardwood forests.

Most of the birds observed during our study are typical of south-central Labrador. But there were 19 species that are generally considered rare or poorly documented in Labrador. Most of these are strongly associated with hardwood forests (Downy Woodpecker, Yellow-bellied Sapsucker, Least Flycatcher, Black-capped Chickadee, Red-eyed Vireo, Black-and-white Warbler), large mature conifers (Brown Creeper, Winter Wren, Golden-crowned Kinglet, Purple Finch, Cape May Warbler), or shrubby riparian zones (Cedar Waxwing, Song Sparrow, Common Yellowthroat). Their presence in the lower Churchill River valley is not surprising given that these vegetation types are reasonably common within the boreal shield ecozone. Many of these may be long-established peripheral populations, rather than evidence of range extensions, but given the limited historical data from the region it is impossible to know.

We only confirmed breeding for two of the regionally rare species (Downy Woodpecker and Yellow-bellied Sapsucker), as most of our effort was during short early morning point counts in June, which were not particularly conducive to observing nesting behaviour and too early for there to be fledged young of most species. However, we are confident that the remaining species are at least probable breeders, based on the total number observed in the study area and records in similar locations over multiple years. In particular, Magnolia Warbler (78 individual records) and Least Flycatcher (77) ranked among the 20 most abundant species overall at our point counts and were also observed incidentally on many other occasions. All 19 of the regionally rare species have previous eBird records for the study area (ranging from one in 2009 for Common Yellowthroat to >100 for Least Flycatcher spanning 1987–2018, and >1000 for Bohemian Waxwing during winter months since 2008), but entirely limited to HVGB and immediate surroundings (eBird 2019).

For some of these species (e.g., Hairy Woodpecker, Red-eyed Vireo, Cape May Warbler), recent editions of field guides have started to show small dots representing a disjunct population around HVGB, north of the limit of their continuous range. Floyd (2008) and Sibley (2014) have introduced a "rare" indicator to their maps and indicated that Nashville Warbler and Common Yellowthroat occur at low densities within the lower Churchill River valley and surrounding areas, consistent with our observations. However, our findings indicate that many of the species previously recognized as occurring in HVGB also are present to varying extents along much of the lower Churchill River valley. We acknowledge that it is uncertain whether our observations represent true range extensions, or simply the first documentation of long-established populations. Regardless, we encourage authors of future revisions to consider extending their mapping accordingly. This is particularly important for NatureServe (2019) and the Birds of the World series (Billerman *et al.* 2020). These are the leading references for bird species in North America, yet are the least reflective of current bird distributions, with Purple Finch being the only one of the regionally rare species to be shown as occurring in the lower Churchill River valley in either resource.

Although we documented the presence of many regionally rare species in the lower Churchill River valley, our survey effort was nonetheless not comprehensive. Our efforts focussed largely on forest birds, and while we found some waterbirds and raptors incidentally, the timing of our surveys was not optimal for detecting most of these species. Additionally, our field effort was constrained by access and was particularly limited in the western two-thirds of the study area, which is largely away from any roads, and where even helicopter landing options are scarce in some areas. We preferentially targetted uncommon land cover types that tend to support a broader diversity of birds (most notably hardwood and mixedwood forest and wetlands) but were not able to access all such locations in the study area. Undoubtedly, at least some individuals present within the 100 m point count radius were undetected during the 5 min sampling period. It is thus quite likely that our results underestimated the distribution and abundance of regionally rare species. However, it is also probable that the regional abundance of some of these species has declined since flooding of the Muskrat Falls Reservoir, given that many of them are closely associated with uncommon land cover types that were disproportionately extensive within that area. This was most notable of three species (Sora, Semipalmated Plover, and Least Sandpiper) that we observed only at Upper Brook. Conversely, there may be some rebound over time as novel riparian and other vegetation communities develop along the new shoreline. We therefore encourage further exploration and documentation of birds in the lower Churchill River valley, to assess the implications of this change to the landscape, and to monitor for potential further additions to the community.

Author Contributions

Writing – Original Draft: M.A.G. and K.R.; Writing – Review & Editing: M.A.G. and K.R.; Conceptualization: M.A.G.; Investigation: M.A.G. and K.R.; Methodology: M.A.G.; Formal Analysis: M.A.G. and K.R.

Acknowledgements

We thank Nalcor for supporting the extensive field survey program and the publication of this manuscript. Perry Trimper was instrumental in study design, logistical coordination, and providing historical knowledge of the region. The expertise of Universal Helicopters and Canadian Helicopters pilots was critical to accessing remote parts of the study area. Aside from the authors, other lead observers during the study were Stacey Camus, Leanne Elson, Matt Ginn, Stephen Gullage, Rich LaPaix, Bruce MacTavish, Tina Newbury, Tony Parr, Rodger Titman, Todd Watts, and Jon Willians. We would also like to thank the local field assistants who contributed to the bird surveys: Matthew Andrew, Penute Andrew, Jodie Ashini, Mary Ann Aylward, Randy Best, Don Blake, Chris Gregoire, Gary Gregoire, Jerome Jack, Peter McKay, James Michel, Apenam Pone, and Clarence Snow. Figures were prepared by Tony Parr. Thanks to Diane Ingraham and Greg Johnson at Stantec Consulting Ltd., David Wilson, and an anonymous reviewer for valuable feedback on earlier versions of this manuscript.

Literature Cited

Bibby, C.J., N.D. Burgess, D.A. Hill, and S. Mustoe. 2000. Bird Census Techniques, Second Edition. Academic Press, London, United Kingdom.

Billerman, S.M., B.K. Keeney, P.G. Rodewald, and T.S. Schulenberg. 2020. Birds of the World. Cornell Lab of Ornithology, Ithaca, New York, USA. Accessed 22 October 2021. https://birdsoftheworld.org/bow/home.

Chaulk, K.G., G.J. Robertson, and W.A. Montevecchi. 2004. Breeding range update for three seabird species in Labrador. Northeastern Naturalist 11: 479–485. https://doi.org/10.1656/1092-6194(2004)011[0479:brufts]2.0.co;2

Chubbs, T.E., B.M. MacTavish, K. Oram, and P.G. Trimper. 2000. First confirmed breeding records and other incidental sightings of Northern Harriers in Labrador. Journal of Raptor Research 34: 56–57.

Cimprich, D.A., F.R. Moore, and M.P. Guilfoyle. 2020. Red-eyed Vireo (*Vireo olivaceus*), version 1.0. *In* Birds of the World. *Edited by* P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.reevir1.01

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2017. COSEWIC assessment and status report on the Rusty Blackbird *Euphagus carolinus* in Canada. COSEWIC, Ottawa, Ontario, Canada.

Dunn, J.L., and J. Alderfer. 2017. National Geographic Field Guide to the Birds of North America. Seventh Edition. National Geographic Society, Washington, DC, USA.

eBird. 2019. eBird: an online database of bird distribution and abundance. Cornell Lab of Ornithology, Ithaca, New York, USA. Accessed 14 March 2019. https://ebird.org.

ESWG (Ecological Stratification Working Group). 1996. A National Ecological Framework for Canada. Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research, and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa, Ontario, Canada.

Ethier, J.P., and D.R. Wilson. 2019. Using microhabitat arrays to investigate microhabitat selection by declining breeding birds. Ibis 162: 873–884. https://doi.org/10.1111/ibi.12785

Floyd, T. 2008. Smithsonian Field Guide to the birds of North America. HarperCollins, New York, New York, USA.

Government of Canada. 2019. Species at Risk Act S.C. 2002, c. 29. Accessed 30 April 2020. https://laws-lois.justice.gc.ca/PDF/S-15.3.pdf.

Gross, D.A., and P.E. Lowther. 2020. Yellow-bellied Flycatcher (*Empidonax flaviventris*), version 1.0. *In* Birds of the World. *Edited by* A.F. Poole. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.yebfly.01

Hennigar, B., J.P. Ethier, and D.R. Wilson. 2019. Experimental traffic noise attracts birds during the breeding season. Behavioral Ecology 30: 1591–1601. https://doi.org/10.1093/beheco/arz123

Holmes, S.B., C.J. Sanders, D. Fillman, and D.A. Welsh. 2009. Changes in a forest bird community during an outbreak cycle of the spruce budworm in northwestern Ontario. Bird Populations 9: 13–28.

Hunter and Associates. 1981. Lower Churchill biophysical update. Report prepared for Lower Churchill Development Corporation, St. John's, Newfoundland and Labrador, Canada.

Kirk, D.A., A.W. Diamond, R.A. Hobson, and A.R. Smith. 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. Canadian Journal of Zoology 74: 1749–1770. https://doi.org/10.1139/z96-193

Lavigne, D. 2019. Forest pest update for Newfoundland and Labrador. Unpublished report prepared for SERG International Workshop - February 2019. Newfoundland and Labrador Department of Fisheries and Land Resources, St. John's, Newfoundland and Labrador, Canada.

Lewis, K.P., and B.M. Starzomski. 2015. Bird communities and vegetation associations across a treeline ecotone in the Mealy Mountains, Labrador, which is an understudied part of the boreal forest. Canadian Journal of Zoology 93: 477–486. https://doi.org/10.1139/cjz-2014-0309

Morse, D.H., and A.F. Poole. 2020. Black-throated Green Warbler (*Setophaga virens*), version 1.0. *In* Birds of the World. *Edited by* P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.btnwar.01

NAS (National Audubon Society). 2018. The Christmas Bird Count Historical Results (online). Accessed 15 March 2019. http://www.christmasbirdcount.org.

NatureServe. 2019. NatureServe Explorer: an online encyclopedia of life (web application), Version 7.1. Nature-

Serve, Arlington, Virginia, USA. Accessed 18 March 2019. http://explorer.natureserve.org.

Peterson, R.T. 2012. Field Guide to Birds of Eastern and Central North America. Sixth Edition. Houghton Mifflin Harcourt, Boston, Massachusetts, USA.

Rimmer, C.C., and K.P. McFarland. 2020. Tennessee Warbler (*Leiothlypis peregrina*), version 1.0. *In* Birds of the World. *Edited by* A.F. Poole. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.tenwar.01

Robichaud, I., and M.-A. Villard. 1999. Do Black-throated Green Warblers prefer conifers? Meso- and microhabitat use in a mixedwood forest. Condor 101: 262–271. https://doi.org/10.2307/1369989

Schwab, F.E., N.P.P. Simon, and C.G. Carroll. 2001. Breeding songbird abundance related to secondary succession in the subarctic forests of western Labrador. Ecoscience 8: 1–7. https://doi.org/10.1080/11956860.2001.11682624

Schwab, F.E., N.P.P. Simon, S.W. Stryde, and G.J. Forbes. 2006. Effects of postfire snag removal on breeding birds of western Labrador. Journal of Wildlife Management 70: 1464–1469. https://doi.org/10.2193/0022-541x(2006)70[1464:eopsro]2.0.co;2

Sibley, D.A. 2016. Field Guide to Birds of Eastern North America. Second Edition. Alfred A. Knopf, New York, New York, USA.

Simon, N.P.P., F.E. Schwab, and A.W. Diamond. 2000. Patterns of breeding bird abundance in relation to logging in western Labrador. Canadian Journal of Forest Research 30: 257–263. https://doi.org/10.1139/x99-203

Simon, N.P.P., F.E. Schwab, and R.D. Otto. 2002. Songbird abundance in clear-cut and burned stands: a comparison of natural disturbance and forest management. Canadian Journal of Forest Research 32: 1343–1350. https://doi.org/10.1139/x02-057

Todd, W.E.C. 1963. Birds of the Labrador Peninsula and Adjacent Area. University of Toronto Press, Toronto, Ontario, Canada.

Tremblay, J.A., R.D. Dixon, A. Saab, P. Pyle, and M.A. Patten. 2020. Black-backed Woodpecker (*Picoides arcticus*), version 1.0. *In* Birds of the World. *Edited by* P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, New York, USA. http://doi.org/10.2173/bow.bkbwoo.01

USGS (United States Geological Survey). 2018. North American Breeding Bird Survey – Species totals report for route by year. Accessed 12 February 2019. https://www.pwrc.usgs.gov/BBS/PublicDataInterface/index.cfm?fuseaction=PublicDataInterface.viewRouteSummaryReport.

Vanderhoff, N., P. Pyle, M.A. Patten, R. Sallabanks, and F.C. James. 2020. American Robin (*Turdus migratorius*), version 1.0. *In* Birds of the World. *Edited by* P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.amerob.01

Venier, L.A., J.L. Pearce, D.R. Fillman, D.K. McNicol, and D.A. Welsh. 2009. Effects of spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks on boreal mixed-wood bird communities. Avian Conservation and Ecology 4(1): 3.

Way, R.G., A.G. Lewkowicz, and P.P. Bonnaventure. 2017. Development of moderate-resolution gridded monthly air temperature and degree-day maps for the Labrador-Ungava region of northern Canada. 2017. International Journal of Climatology 37: 493–508. https://doi.org/10.1002/joc.4721

Whitaker, D. 2017. Expanded range limits of boreal birds in the Torngat Mountains of northern Labrador. Canadian Field-Naturalist 131: 55–62. https://doi.org/10.22621/cfn.v131i1.1957

Received 16 December 2019
Accepted 9 August 2021
Associate Editor: J.R. Foote

SUPPLEMENTARY MATERIAL:

TABLE S1. List of 80 bird species observed on point counts, and nine species observed incidentally during the field program in the lower Churchill River valley, Labrador, in summer of 2006, 2007, 2014, 2015, and 2016.

The Canadian Field-Naturalist

Comparative reproductive parameters of sympatric Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) in parkland Manitoba

Gordon S. Hammell[1,*], **Howard V. Singer**[2], and **Llwellyn M. Armstrong**[2]

[1]P.O. Box 37, Erickson, Manitoba R0J 0P0 Canada
[2]Ducks Unlimited Canada, Institute for Wetland and Waterfowl Research, P.O. Box 1160, Stonewall, Manitoba R0C 2Z0 Canada
[*]Corresponding author: gmhammell@gmail.com

Hammell, G.S., H.V. Singer, and L.M. Armstrong. 2021. Comparative reproductive parameters of sympatric Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) in parkland Manitoba. Canadian Field-Naturalist 135(3): 278–292. https://doi.org/10.22621/cfn.v135i3.2507

Abstract

Waterfowl managers are concerned that Lesser Scaup (*Aythya affinis*) breeding populations remain below conservation goals. Contrasting population growth trajectories for sympatric, phylogenetically similar Lesser Scaup and Ring-necked Duck (*Aythya collaris*) at Erickson, Manitoba, Canada, prompted investigations that might help explain these trends and provide insight for population management of both species. We collected data (2008–2018) on productivity (broods/pair), water levels, hatching dates, age class-specific brood sizes, duckling daily survival rate, and brood female response to disturbance and compared results between species over time. Ring-necked Duck productivity was greater (0.42 versus 0.28, $P < 0.01$), hatching dates were earlier (19 July versus 27 July, $P < 0.001$), and females attempted to hide their broods more often than did Lesser Scaup (16% versus 3%, $P < 0.001$), but Ring-necked Duck age class-specific brood sizes were smaller than for Lesser Scaup (Ia broods: 6.1 versus 6.8, $P = 0.02$; IIa broods: 5.6 versus 6.2, $P = 0.02$). Duckling daily survival rates were similar. Productivity of both species was positively related to annual change in pond water level and both demonstrated similar rates of response to change. There was no support for an association between productivity and one- or two-year lagged pond water levels. Consistent with previous findings, our results suggest that greater Ring-necked Duck productivity is a likely proximate cause for the differing population growth trajectories between the species. We suggest that better Ring-necked Duck nest placement may be a contributing factor to the greater nest success observed.

Key words: Lesser Scaup; Ring-necked Duck; productivity; hatching dates; brood size; duckling survival

Introduction

Knowledge of how reproductive rates change spatio-temporally under differing environmental conditions is important for the effective management of waterfowl populations, and may aid our understanding of species-specific population growth rates. Sympatric phylogenetically and morphologically similar species whose breeding, nesting, and brood habitats are similar might be expected to have similar reproductive rates (Martin 1995; Sæther and Bakke 2000). However, under the influence of a stochastic environment, anthropogenic influences, density dependence, or other factors (e.g., intrinsic nesting behaviour; Koons and Rotella 2003a), a species' demographic traits (e.g., clutch size, nest success, and duckling, juvenile, and adult female survival and thus population growth rate) may differ from another closely related species (Koons *et al*. 2006, 2014; Sæther *et al.* 2016).

Ring-necked Duck (*Aythya collaris*) and Lesser Scaup (*Aythya affinis*) are phylogenetically and morphologically similar diving ducks (Livezey 1996) whose breeding ranges overlap in central, western, and northwestern North America (Anteau *et al*. 2014; Roy *et al*. 2020) but whose long-term continental populations are trending inversely. The annual Breeding Waterfowl Population Survey suggests the Ring-necked Duck continental population is stable or increasing (1998–2019) but that the combined continental population of Lesser and Greater Scaup (*Aythya marila*: counted together on surveys) has declined from highs of five to seven million birds in the 1970s to three to five million in the past decade, ~20% below the North American Waterfowl

---

A contribution towards the cost of this publication has been provided by the Thomas Manning Memorial Fund of the Ottawa Field-Naturalists' Club.

Management Plan population goal (US F&WS 2019). Lesser Scaup constitute about 90% of the combined scaup population and most of the decline has been attributed to this species because of widespread decline in the Canadian western boreal forest, where most Lesser Scaup breed (Afton and Anderson 2001). Whereas change in reproductive and/or survival rates could explain distinct population trends of Ring-necked Duck and Lesser Scaup, only nest success has been suggested as a proximate cause, and at only one site (Koons and Rotella 2003a). Nest success is considered an important driver of waterfowl population change (Baldassarre and Bolen 2006) but adult female survival, and duckling and juvenile survival are also important (McAuley and Longcore 1988; Brook and Clark 2005; Koons *et al.* 2017; Roy *et al.* 2019). However, field studies comparing juvenile and adult female survival rates for sympatric Ring-necked Duck and Lesser Scaup have not been done.

Near a long-term waterfowl study area in southwestern Manitoba, the Lesser Scaup breeding population has declined from the early 1980s to about 2000 when numbers appear to have stabilized. In contrast, Ring-necked Duck breeding density has increased dramatically from the 1970s (Koons and Rotella 2003a; Hammell 2014, 2016; Figure 1). Such distinctive long-term population trends for these phylogenetically and morphologically similar species affords testing of hypotheses regarding species difference in reproductive metrics. We collected data of reproductive metrics and associated covariates from 2008 to 2018 to determine if there were species-related

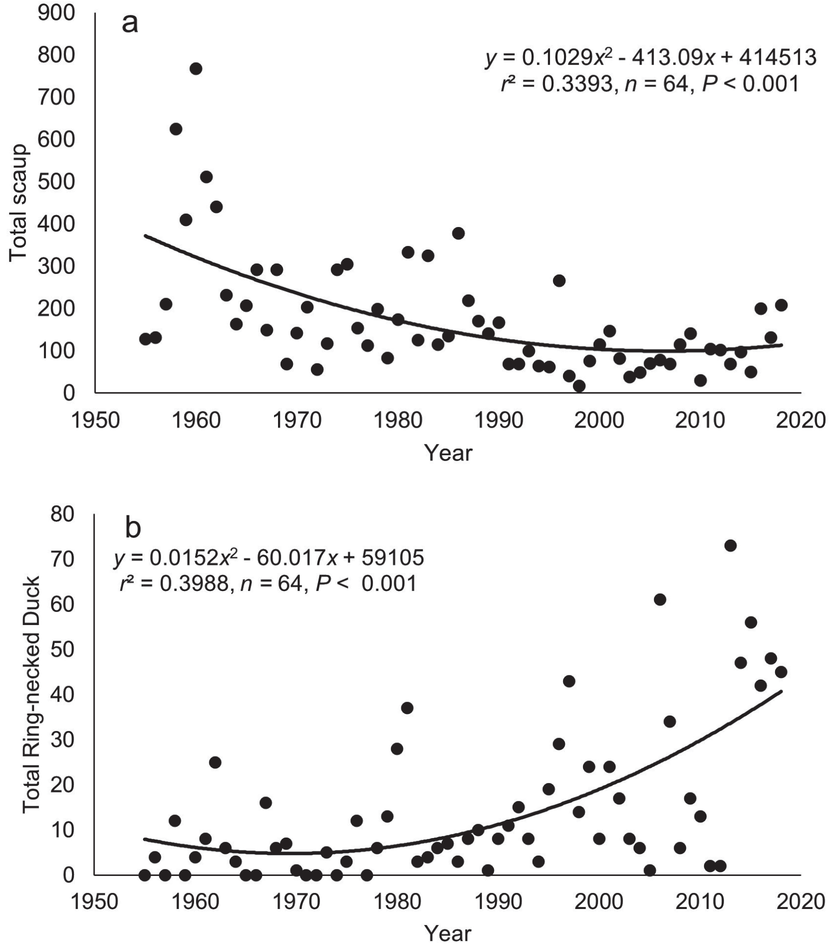


FIGURE 1. Total number of a. Lesser Scaup (*Aythya affinis*) and Greater Scaup (*Aythya marila)* and b. Ring-necked Duck (*Aythya collaris*) from Canadian Wildlife Service/United States Fish and Wildlife Service annual waterfowl counts in the three segments nearest the study area near Erickson, Manitoba, 1955–2018 (stratum 40: transect 4, segment 4; transect 6, segments 3 and 4). The solid and dash lines represent polynomial trend lines. Data from Migratory Bird Data Centre [n.d.].

differences in this region that may help to explain their disparate population trends.

Study Area

The study area is situated in the parkland pothole region of southwestern Manitoba near Erickson, Manitoba (50.47035°N, 99.89584°W). The intensively studied areas constitute a block (6.8 km^2) and a roadside transect (21.7 km long and 400 m on either side of the road) established 4.0–12.5 km to the southeast in 2009 and collectively constitute an area of 22.6 km^2 (hereafter the primary study area, see Hammell 2016 for map). The 2009–2018 transect was established to increase pair and brood sample sizes as preliminary data collection in 2008 indicated that the Lesser Scaup breeding population on the block (19–23 pairs, 1970–1972) had decreased significantly (two pairs, 2008; Hammell 2014). In 2008–2018, the block contained about 141 wetlands: 53 class I and 50 class II, 10 class III, seven class IV, and 21 class V; size range ≤0.1–11.5 ha (Stewart and Kantrud 1971). Relative to other agricultural areas of Manitoba, the study site has changed little in wetland area or upland use from the early 1970s (Hammell 2014). During a record wet year in 2011, several permanent ponds (class V) joined to form several larger wetlands (largest 21.7 ha). The 2009–2018 transect consisted of all class II–V wetlands with observable water (32 class II [temporary], 56 class III [seasonal], 41 class IV, and 32 class V) and required walking and driving to survey adequately. We chose a 400 m (rather than 200 m) width because evidence suggests that wider transects better represent pond density, size and distribution and, thus, more reliably represent breeding densities of Lesser Scaup and Ring-necked Duck (Austin *et al.* 2000). To increase sample sizes, additional hatch date and brood size data were collected from other ponds near the primary study area. The uplands in the Erickson area are a mixture of lands sown to cereal and oilseed crops, hay, pasture, and native woodland. The area and changes over time are described in more detail by Rogers (1964), Sunde and Barica (1975), Afton (1984), Koons and Rotella (2003a), and Hammell (2014).

Methods

Breeding pair surveys

To record breeding populations of Lesser Scaup and Ring-necked Duck on the block, one or two observers walked a fixed route at approximately weekly intervals between 0600 and 1400 from mid-May to mid-June 2008–2018 (three to six annual surveys). All class II–V wetlands were visited and scanned from one or more elevated locations. We checked class I, tillage, and class II wetlands with closed emergent vegetative stands while en route to other ponds but did not visit these consistently as both species are rarely observed on them (Hammell 1973). Observed pairs and single males and females counted on small, isolated ponds, away from "primary waiting areas" (Dzubin 1955: 183), were considered as indicated pairs. We used data from surveys conducted after migration but during the pre-egg-laying and early-laying periods to avoid the bias of non-paired males being counted as representing pairs; migration ended when pair numbers stabilized on the block. We approximated timing of first egg laying by backdating from estimated date of earliest brood appearance (see *Brood surveys* below) assuming egg laying plus incubation for Lesser Scaup (Koons 2001) and Ring-necked Duck (Mendall 1958; Roy *et al.* 2019) were 36 and 35 days, respectively.

For breeding pair counts on the 2009–2018 roadside transect, we used criteria similar to those for the block area. We conducted counts between 0530 and 1800 as Lesser Scaup were highly visible throughout the day and previous research has shown no differences in numbers of indicated pairs for counts conducted from 0530 to 1330 (Diem and Lu 1960). We assumed that Ring-necked Duck were also highly visible throughout this period (G.S.H. pers. obs.). From 2009 to 2018, we conducted three annual roadside surveys during late migration to early nesting (21–25 May, 31 May–4 June, 6–12 June). We walked to distant or hidden wetlands and viewed them from several locations to ensure complete coverage. For 2009 and 2010, time constraints allowed only a partial survey of this transect (40% of class II and III wetlands, 60% of class IV and V wetlands), taking about eight hours to complete. For 2011–2018, we visited all ponds (classes II–V) within 400 m of the road, over two days (three days in 2018), taking 17 h to complete. Some ponds were bisected by the roadside transect; thus, we recorded pairs on the entire pond and included this total in the total transect pair count.

As the 2009 and 2010 transect pair data were incomplete, results were adjusted for biases described above to estimate the number of pairs on the entire transect for those years. Using 2011–2018 data, we developed a correction factor (CF) for each survey count using numbers of pairs observed on all ponds and numbers observed only on ponds that were in addition to those surveyed in 2009 and 2010:

$$CF = \frac{PR_{missed}}{PR_{total}}$$

where, in 2011–2018, PR_{missed} is the number of pairs counted on wetlands that were not visited in 2009 or 2010, and PR_{total} is the total number of pairs counted on all wetlands. This factor is the proportion of the count on missed ponds and was determined within each year for those counts considered post-migration and these values were averaged. The average ($CF_{average}$) of the yearly count averages for 2011–2018 was applied to average counts for 2009 and 2010, e.g.,

$$\text{Estimated total pairs all ponds (2009)} = \frac{\text{average pairs recorded (2009)}}{[1.00 - CF_{average}]}$$

This analysis indicated that the mean number of Lesser Scaup and Ring-necked Duck pairs recorded in 2009 and 2010 on the partly surveyed transect represented about 70% of the total number of pairs of each species on the entire transect. This adjustment was applied to the 2009 and 2010 raw data. Exclusion of the 2009–2010 missed pond data in the following years would have biased productivity estimates (broods/pair) high because our pond sample would not be representative of local habitat conditions (i.e., over-representation of brood ponds). Estimated pairs and broods on the block area were added to those on the roadside transect and this total represented the pair and brood estimate on the primary study area.

Brood surveys

Broods of Lesser Scaup near Erickson are relatively easily found, as they usually swim to open areas in the centre of a pond when disturbed (Hammell 1973; Anteau *et al.* 2014). Ring-necked Duck females react similarly by swimming to the centre or opposite edge of the pond from the observer, infrequently swimming into the outer edge of the emergent vegetation but often remaining visible (G.S.H. pers. obs.). We interpreted a female taking a brood partially or completely into emergent vegetation or out of sight into another area of a pond as an attempt to hide a brood. For both species, we described a brood as a group of up to 12 ducklings attended by a female or two to 12 isolated ducklings with no female and whose age did not correspond with that of other nearby broods. To compare per capita productivity (broods/pair), larger groups (13–24 ducklings) were considered two broods. Brood data recorded on ponds on the primary study area were used to determine productivity and data collected on nearby ponds using similar methods increased sample sizes for hatch date, brood size, and survivability analysis. We recorded presence or absence of an adult female, if females attempted to hide their brood, and brood age and size. We used brood age, size, and location to avoid duplication in counts. To satisfy the general assumptions necessary for accurate estimation of duckling survival (Walker 2004; Walker and Lindberg 2005), we considered losses of ducklings between counts to represent mortality (known fates) and not emigration to other broods or ponds because (i) ponds were monitored for broods with additional ducklings and for orphaned ducklings, (ii) females with broods of age classes <IIa (Gallop and Marshall 1954) rarely accepted ducklings of an age discernably different from their own and, (iii) ducklings do not leave a pond unless led by a female. Mortality was not considered to be affected by investigator activity because broods were approached cautiously at a distance and females did not flush from their brood. For both species, within-brood duckling mortalities were deemed largely independent of one another because ~90% of losses were ≤ two ducklings (McAuley and Longcore 1988). Occasionally, brood size increased between counts due to exchange of similarly aged ducklings, brood amalgamation, or adoption of orphaned ducklings. If the increase could not be explained using clues from previous brood counts, presence of additional brood females, and known size and age of other broods on the same pond or on nearby ponds, then, the brood observations were censored prior to the increased count. This study lacked marked individuals, but as noted by others (Gauthier 1987; McAuley and Longcore 1988) using similar methods to ours to determine duckling survival of unmarked diving duck broods, ease of brood observation and repeated pond visitation provided confidence in our critical assumptions that we were observing the same broods repeatedly. We are unaware of any biases in our daily survival rate (DSR) methods, but if they did occur, they would apply equally to both species over the time series.

Occasionally, Lesser Scaup and Ring-necked Duck broods contained ducklings of other waterfowl species, usually Redhead (*Aythya americana*) and these ducklings were removed from the recorded brood size. We estimated brood ages based on juvenile plumage characteristics (Gallop and Marshall 1954). For each brood, a hatching date was estimated from several brood observation dates, by backdating using duckling approximate age in days. Brood surveys began during the last week of June and, because Lesser Scaup and Ring-necked Duck females usually move their broods from smaller to larger (usually class V) ponds as they mature (Hammell 1973; Corcoran *et al.* 2007; G.S.H. pers. obs.), surveys were conducted on class IV and V ponds until broods reached age class IIa (Lesser Scaup: 21–28 days old; Ring-necked Duck: 17–24). However, ducklings can become stranded in small transition wetlands (e.g., class III) if their brood female is depredated during movements to larger brood ponds and therefore class III ponds with remaining water were occasionally surveyed for broods as well. Greatest duckling losses and most brood movement occur before ducklings reach age class IIa (Mendall 1958; Afton 1983; McAuley and Longcore 1988; Dawson and Clark 1996; Brook 2002; Corcoran *et al.* 2007). Also, because most brood-rearing Lesser Scaup females spend increasing amounts of time away from their broods after they reach age class IIa, ducklings often form groups on lakes making it difficult to distinguish individual broods (Hines 1977; Afton 1984). Similarly, some Ring-necked Duck females abandon broods (Maxson and Pace 1992), or are depredated after age class IIa and broods can lose their integrity. Thus, age class IIa broods are relatively stable in size and location, and represent a good index of juveniles fledged (Afton 1984; Koons and Rotella 2003b). Although brood monitoring declined after broods reached age class IIa, we were able to record opportunistically, a limited amount of survival data on broods greater than age class IIa and these data were also compared.

Brood search effort averaged about seven visits/pond annually during 2008–2018: mean 7.6, range 5.5–9, no. ponds 35–54). Because broods move freely over the entire area of a lake (G.S.H. pers. obs.), placing a brood "in" or "out" of the transect was difficult when the transect line bisected a lake. Thus, we counted all broods on bisected lakes and assumed that these broods resulted from the total pair count for that lake. Occasionally, broods disappeared between counts and may have moved to a nearby pond or suffered total brood loss; the extent of such possible losses was unknown. Brood surveys on the transect were incomplete in 2009 and 2010 (three potential brood ponds unobserved out of 47), thus, a correction factor was applied to these data similar to that for pairs. This analysis resulted in one Lesser Scaup and one Ring-necked Duck brood being added to 2009 and 2010 total estimates.

To compare Lesser Scaup and Ring-necked Duck productivity response to changing wetland water level during 2009–2018, we collected relative water-level change measured from a fixed point on permanent stakes hammered into the pond substrate of 15 class IV and V wetlands on or near the block area and averaged the results. At Erickson, both species nest overwater (nest surrounded by water when found): Lesser Scaup, ~60%; Ring-necked Duck, ~100% (Hammell 1973; Koons and Rotella 2003a), and changing water levels may affect nest success (Navarre 2020) and productivity. We developed a wetland scoring system (Table 1; Table S1) that incorporated three Lesser Scaup reproductively significant periods of the breeding season as a guide: overall local spring wetland condition (dry to flooded based on G.S.H. pers. obs.), pre-nesting wetland condition (water-level drop or rise [cm] from early May to early June), and nesting wetland condition (water-level drop or rise [cm] from egg laying to first brood in mid July). Generally, the wetter the annual period, defined by higher and/or more stable water levels, the higher the score for that period. A yearly score was determined for each of the three periods and the sum of these scores represented the score for that year. We chose these periods because Lesser Scaup breeding propensity at Erickson is positively related to spring wetland condition (conditions on arrival at the breeding grounds affect the pair's decision to remain and conditions up to the nesting period determine the decision of the female to initiate egg laying [Afton 1984]), and because at Erickson, ~60% of Lesser Scaup nest overwater and overwater nests are more successful than dryland nests (Hammell 1973; Koons and Rotella 2003b), then productivity may be influenced by water-level stability during the egg-laying and incubation period (Navarre 2020). At Erickson, Ring-necked Duck initiate egg laying ~15 days before Lesser Scaup (Koons and Rotella 2003a) and little is known about factors affecting breeding propensity but like Lesser Scaup, we expected Ring-necked Duck productivity to change with wetland water levels as noted by Mendall (1958).

Data analysis

We used linear regression (McDonald 2014; Excel Data Analysis Add-in module [Microsoft, Redmond, Washington, USA]) to track breeding pair population and productivity trends over time on the primary study area. To examine trends in brood/pair ratios relative to wetland water levels, total annual counted broods was modelled using a Poisson distribution in

TABLE 1. Assigned score and scoring parameters describing spring wetland condition, and water-level change during the Lesser Scaup (*Aythya affinis*) pre-nesting and nesting season, 2009–2018, Erickson, Manitoba.

Score	Spring wetland condition	Pre-nesting and nesting period water-level change (cm)
5	Flooded beyond basin	> +10
4	Wet grass zone flooded	+5 to +10
3	Sedge* zone flooded	> 0 to + 4.9
2	Sedge zone dry	< 0 to −4.9
1	Bulrush/cattail† zone dry	−5 to −10
0	Mudflats showing	> −10

*Sedge = *Carex* spp.
†Bulrush/cattail = *Scirpus* spp./ *Typha* spp.

a regression with natural log-transformed total annual counted pairs treated as an offset variable. Analyses were conducted using SAS software, version 9.4 (SAS Institute Inc., Cary, North Carolina, USA). We fit a total of five candidate model forms including (i) the effect of species (Ring-necked Duck and Lesser Scaup), (ii) the effect of year-specific mean wetland score from the current year, (iii) an additive model containing both effects, (iv) a multiplicative model including an interaction between species and wetland score, and (v) an intercept-only baseline model. An alternate model set was fit substituting wetland score from the previous year or two years prior because nest success of some *Anas* spp. in the prairie pothole region was negatively related to pond density and primary productivity during previous years (Walker *et al*. 2013). Also, in boreal habitat, a strong negative two-year lag correlation was found between rodent abundance (alternative prey) and Lesser Scaup productivity (Brook *et al*. 2005). In parkland habitat, such as our study area, similar time-lagged variation in productivity might occur with Lesser Scaup and Ring-necked Duck. For models including lagged effects of wetland score, we created a consistent data subset excluding the years 2009 and 2010. We used AIC (Burnham and Anderson 2002) to rank the five candidate models using all years and then a separate ranking of 11 models (using the three alternatives for wetland score) fit to the reduced dataset. We considered models within 4 AIC units of the top-ranking models as competing and well supported, except when the competing models had similar fit as quantified by maximized log-likelihood and little penalty for adding additional uninformative parameters to the model (Arnold 2010).

As we were interested in reproductive parameter differences between species over the entire study period rather than individual years, we pooled brood size (Ia: Lesser Scaup 1–6 day old, Ring-necked Duck 1–5; IIa: Lesser Scaup 21–28 day old, Ring-necked Duck 17–24) and hatching date data across years. We recorded class Ia and IIa brood size to look for differences between species in duckling survival and juvenile production. We estimated time of first brood hatch, length of hatch period, mean hatch date, and chronology from brood age because time of hatch is related to productivity (Guyn and Clark 1999; Dawson and Clark 2000; Esler *et al*. 2001; Blums *et al*. 2002). Estimated measures of productivity, day of first brood hatch, and length of hatching period were tested for species' differences using Wilcoxon signed-rank test for paired data (McDonald 2014). Mean hatching dates and brood size were tested with Wilcoxon rank-sum test (Excel Data Analysis Add-in module [Microsoft]). We assigned hatching dates to weekly hatching periods and compared results using a Kolmogorov-Smirnov test (Holliday 2012) because each species has a unique annual hatching distribution, the shape of which might provide insight into breeding propensity and frequency of re-nesting (e.g., a severely truncated unimodal distribution might suggest little re-nesting effort while an extended unimodal or bimodal one might suggest significant re-nesting effort or age specific distribution). We tested data with non-parametric Wilcoxon tests because the distribution of variables was unknown, sample sizes were small, or both. Because unpublished analysis of data distributions (hatch date, brood size) indicated that they were similarly shaped and reasonably symmetric, we interpreted results as being tests of differences in mean values.

Mean estimates and CI for duckling DSR for the exposure period between first sighting and age class IIa (and >IIa) were calculated using procedures outlined by Mayfield (1975) and Johnson (1979), and 95% CI for DSRs were examined for overlap to test for significant differences. Amalgamated Lesser Scaup broods (zero or more females with >12 ducklings) were seen most years and were not excluded from the data set, as these broods and single broods have similar duckling survival (Afton 1993). Amalgamated Ring-necked Duck broods were uncommon but were similarly included. However, we removed data for some or all of these broods on multi-brood ponds if we were unable to accurately determine brood identity, age, and duckling number because of brood mixing and duckling exchange.

We determined the proportion of females that attempted to hide their brood upon disturbance because such behaviour might have survival advantages, especially when evading avian predators (Mendall 1958). We determined the proportion of broods that disappeared (moved or suffered total loss) after having been first observed. We pooled all years by species because of small sample sizes and tested these metrics for differences with a Fisher's exact test (McDonald 2014). When a brood female or duckling disappeared, we assumed this occurred at the mid-point of the observation interval (Mayfield 1975) because Mayfield's method yields results that are very close to the maximum likelihood estimators under the more appropriate model with an unknown date of loss (Johnson 1979). All statistical tests unless otherwise stated were considered significant at the $P \leq 0.05$ level.

Results

Productivity

Total counts of pairs and IIa broods for Lesser Scaup and Ring-necked Duck for all years on the 22.6 km² primary study area were variable. For both species, estimated annual breeding pair numbers (Lesser Scaup: 29–47; Ring-necked Duck: 34–71) and productivity (broods/pair) 2009–2018 showed no trends ($P > 0.05$; Table 2, Figure 2a,b). Mean productivity estimates for Ring-necked Duck were larger than for Lesser Scaup (Wilcoxon signed-rank test: $W = 2$, $P < 0.01$) and Ring-necked Duck annual productivity was greater than Lesser Scaup in eight of 10 years (Table 2). For the models fit to data from all years (Table 3), the best approximations included additive effects of wetland score and species. A model with an interaction between species and wetland score was not competitive because it included one additional, uninformative parameter ($\beta_{(\text{species}\times\text{wetland score})} = -0.05$, SE 0.05). Ring-necked Duck had a higher brood/pair ratio than did Lesser Scaup (Ring-necked Duck, $\beta_{(\text{species})} = 0.41$, SE 0.12) and brood/pair ratios were positively correlated with wetland score ($\beta_{(\text{wetland score})} = 0.11$, SE 0.03; Figure 3). For models fit to the reduced dataset (Table 4), there was no support for an association between brood/pair indices and one- or two-year lagged wetland scores (minimum ΔAIC > 10).

Mean hatch date and hatching chronology

Mean hatch date in 2008–2018 for Lesser Scaup was 27 July (SE 0.61 day, $n = 285$) and was significantly later than for Ring-necked Duck, 19 July (SE 0.64 day, $n = 461$; Wilcoxon rank-sum test: $t_{744} = -8.37$, $P < 0.001$). Lesser Scaup mean date of first recorded brood, 9 July (SE 1.9 day, $n = 11$ years), was 11 days later than for Ring-necked Duck, 28 June (SE 1.8 day, $n = 11$ years; Wilcoxon signed-rank test: $W = 0$, $P < 0.001$). The distribution of broods hatching at weekly intervals for both species were unimodal and did not differ significantly (Kolmogorov-Smirnov test statistic: 0.2727, $P = 0.81$; Figure 4). Ring-necked Duck hatching period of 73 days (17 June to 29 August, $n = 11$ years) was 20 days longer than for Lesser Scaup (28 June to 20 August, $n = 11$ years). Mean annual length of hatching period for Ring-necked Duck (47.7 days, range 36–61, $n = 11$ years) was greater than for Lesser Scaup (35.5 days, range 21–44, $n = 11$ years; Wilcoxon signed-rank test: $W = 0$, $P = < 0.001$).

Brood size, brood loss, duckling survival, propensity to hide brood

Mean size of Lesser Scaup Ia broods (6.8, SE 0.2, $n = 148$, range 1–12) was greater than that of Ring-necked Duck (6.1, SE 0.2, $n = 187$, range 1–10; Wilcoxon rank-sum test: $t_{333} = -2.35$, $P = 0.02$). Mean size of Lesser Scaup IIa broods (6.2, SE 0.2, $n = 176$, range 1–11) was greater than that for Ring-necked Duck (5.6, SE 0.2, $n = 267$, range 1–11; Wilcoxon rank-sum test: $t_{441} = 2.34$, $P = 0.02$). There were small differences in age-specific duckling DSR estimates for Lesser Scaup and Ring-necked Duck but, relative to the SEs (Table 5), there were no differences between the two species. The proportion of Ringed-neck Duck females that attempted to hide their brood at least once on disturbance (0.16, SE 0.02, $n = 348$) was significantly higher than for Lesser Scaup (0.03, SE 0.01, $n = 247$; Fisher's exact test: $P < 0.001$). The proportion of Ring-necked Duck broods (0.20, SE 0.02, $n = 310$), that disappeared (moved or suffered total loss) after having been first observed was not significantly different from Lesser Scaup (0.17, SE 0.03, $n = 220$; Fisher's exact test: $P = 0.43$).

Discussion

Productivity

Comparative studies of sympatric Lesser Scaup and Ring-necked Duck reproductive success are few

TABLE 2. Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) productivity (IIa broods/pair) 2009–2018, on the 22.6 km² primary study area near Erickson, Manitoba.

Year	Lesser Scaup			Ring-necked Duck		
	Broods	Pairs	Broods/pair	Broods	Pairs	Broods/pair
2009	9	46	0.20	15	43	0.35
2010	14	38	0.37	18	34	0.53
2011	17	44	0.39	26	51	0.51
2012	2	34	0.06	10	36	0.28
2013	14	44	0.32	23	42	0.55
2014	19	40	0.48	33	69	0.48
2015	9	29	0.31	35	71	0.49
2016	13	43	0.30	19	64	0.30
2017	12	49	0.24	16	58	0.28
2018	5	42	0.12	16	41	0.39
Total or mean*	114	409	0.28	211	509	0.42

*Weighted means, adjusted for annual variation in numbers.

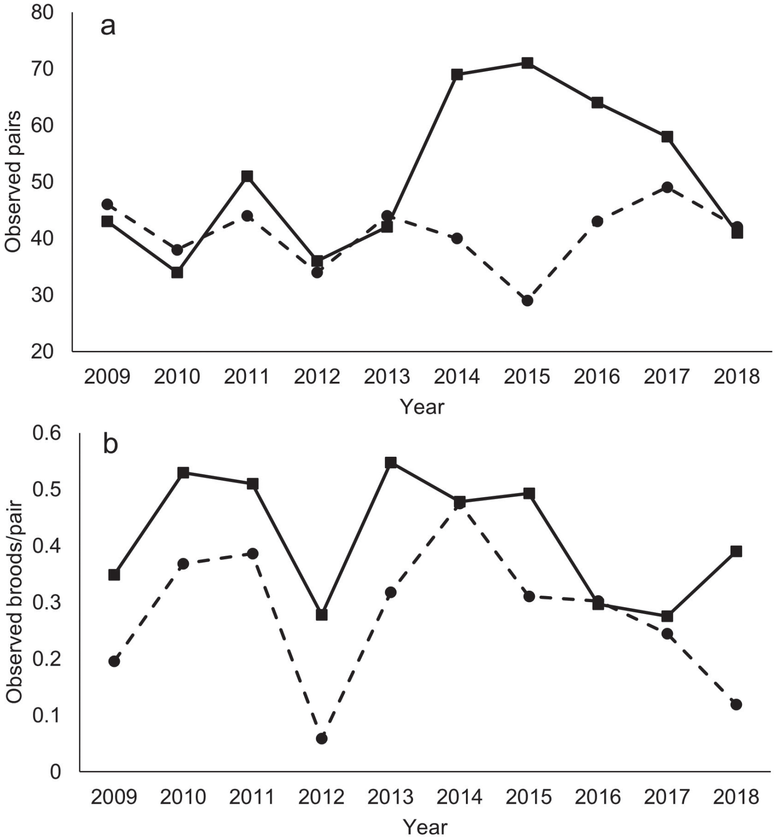


FIGURE 2. Lesser Scaup (*Aythya affinis*, circles, dash line) and Ring-necked Duck (*Aythya collaris*, squares, solid line) a. observed breeding population (pairs) and b. productivity (broods/pair) on the primary study area, 2009–2018, Erickson, Manitoba.

TABLE 3. Model form and model selection results for the full dataset ranked by decreasing ΔAIC of productivity (broods/pair) and wetland score for Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) on a 22.6 km² primary study area near Erickson, Manitoba, 2009–2018. All models include an intercept term. Wetland score describes relative pond water level breeding conditions (see text for description of scoring system).

Model form	k	−2 × log likelihood	ΔAIC
Species + Wetland Score*	3	107.74	0.00
Species × Wetland Score	4	108.68	2.93
Wetland Score	2	121.34	11.60
Species	2	125.53	15.78
Intercept Only	1	137.59	25.84

*AIC = 113.74.

but all report Ring-necked Duck reproductive performance greater than that for Lesser Scaup. Townsend (1966) at the Saskatchewan River Delta, Canada, reported percent nest success for Lesser Scaup and Ring-necked Duck to be 62% and 83% (1963) and 47% and 60% (1964), respectively. At parkland Erickson, during 1999–2000, Koons and Rotella (2003a) found that Ring-necked Duck nest success (equivalent to broods/pair at hatching) was three times that of Lesser Scaup. Results from a long-term study (1985–2018) of waterfowl production on a Yellowknife, Northwest Territories, study area (a boreal site) show mean Ring-necked Duck productivity, ~0.26 broods/pair, greater than that of Lesser Scaup, ~0.17 (ECCC 2018). Similarly, our overall estimate of Ring-necked Duck productivity is greater than that of Lesser Scaup (0.42 versus 0.28

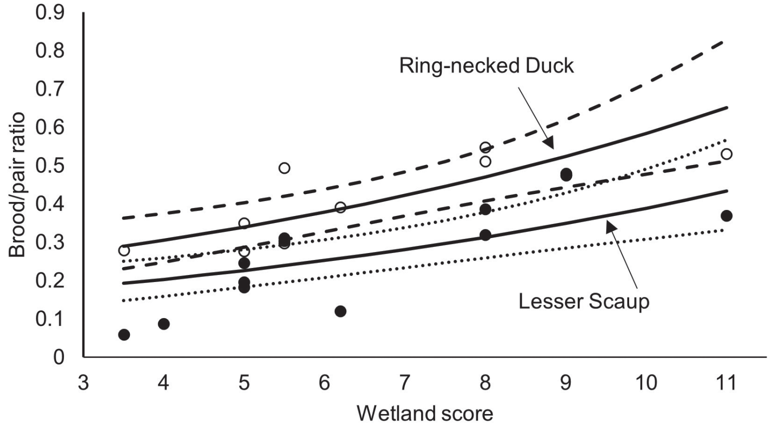


FIGURE 3. Relationship between observed (symbols) and predicted values (lines) from the best approximating models for productivity (IIa broods/pair) versus wetland score for Lesser Scaup (*Aythya affinis*, closed circles, solid and dotted lines) and Ring-necked Ducks (*Aythya collaris*, open circles, solid and dashed lines) on a 22.6 km² study area near Erickson, Manitoba, 2009–2018. Wetland score describes relative pond water level breeding conditions. Increasing score denotes improving pond condition (see text for description of scoring system).

TABLE 4. Model form and model selection results for the reduced data set including wetland score lag years ranked by decreasing ΔAIC of productivity (IIa broods/pair) and wetland score for Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) on a 22.6 km² study area near Erickson, Manitoba, 2009–2018. Wetland score describes relative pond water level breeding conditions (see text for description of scoring system). Lag1 and Lag2 refer to one and two years previous to current year. All models include an intercept term.

Model Form	k	−2 × log Likelihood	ΔAIC
Species + Wetland Score*	3	88.27	0.00
Species × Wetland Score	4	86.49	0.22
Wetland Score	2	97.47	7.20
Species + Lag2 (Wetland Score)	3	98.58	10.32
Species × Lag2 (Wetland Score)	4	97.04	10.77
Species + Lag1 (Wetland Score)	3	100.89	12.62
Species	2	103.95	13.68
Species × Lag1 (Wetland Score)	4	100.79	14.52
Lag2 (Wetland Score)	2	107.79	17.52
Lag1 (Wetland Score)	2	109.54	19.27
Intercept Only	1	113.26	20.99

*AIC = 94.27.

broods/pair, respectively). We are unaware of any studies suggesting equivocal or Lesser Scaup greater productivity, and Ring-necked Duck superior reproductive performance may hold across a continental scale.

In southern Manitoba parklands, several factors may be responsible for greater Ring-necked Duck nest (and IIa broods/pair) success. At Erickson, all Ring-necked Duck nest overwater whereas only about 60% of Lesser Scaup do (Hammell 1973; Koons and Rotella 2003b) and overwater nests of Lesser Scaup and Mallard (*Anas platyrhynchos*) here are more successful than dryland nests (Hammell 1973; Arnold *et al.* 1993). Also, Koons and Rotella (2003a) found that Ring-necked Duck overwater nests were twice as successful as those of Lesser Scaup and Ring-necked Duck nests were located farther from the pond edge than Lesser Scaup overwater nests (Koons 2001; Koons and Rotella 2003a). Hammell (1973) for Lesser Scaup and Ferguson (1977) for Horned Grebe (*Podiceps auritus*), found mean distance of successful overwater nests to pond edge was greater than that of unsuccessful nests. Townsend (1966) showed that overwater nests situated closest to open water (i.e., the wettest sites: floating sedge mats [*Carex* spp.]) were more successful than nests situated closer to drier sedge or sedge willow (*Salix* spp.) zones (but see

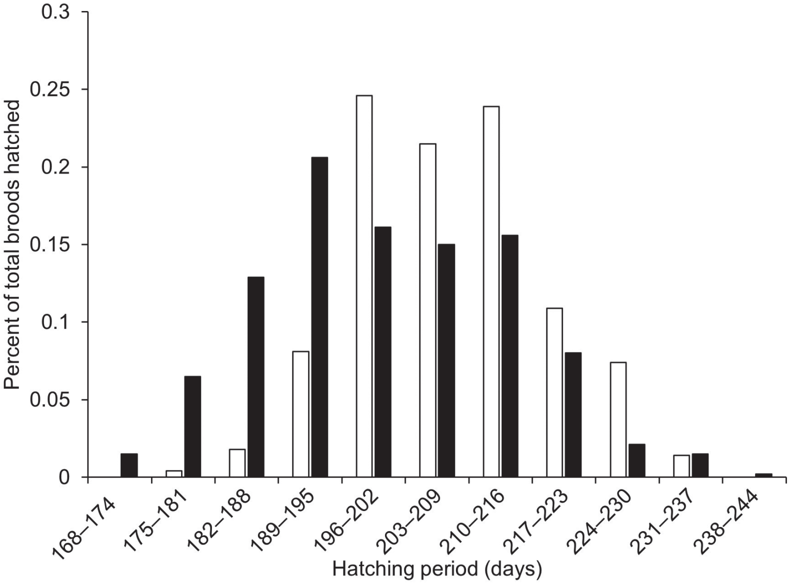


FIGURE 4. Histograms of the hatching distribution for Lesser Scaup (*Aythya affinis*, *n* = 284, open bars) and Ring-Necked Duck (*Aythya collaris*, *n* = 461, black bars) broods near Erickson, Manitoba, 2008–2018. Days are counted from 1 January.

TABLE 5. Number of broods, exposure, losses, and daily survival rate for Lesser Scaup (*Aythya affinis*) and Ring-necked Duck (*Aythya collaris*) from first sighting to age class IIa (<IIb), following age class IIa (>IIa), and the total period from first sighting to age class IIb–III, 2008–2018, near Erickson, Manitoba.

Species	No. broods*	No. intervals	Mean interval length (days)	Total exposure (duckling days)	Total duckling losses	Daily survival rate	SE
Lesser Scaup <IIb	198	518	6.8 (0.5–24)	21242	142	0.99332	0.000559
Ring-necked Duck <IIb	239	454	7.2 (1–31)	18812	124	0.99341	0.000590
Lesser Scaup >IIa	98	155	5.9 (1–15)	4842	13	0.99732	0.000743
Ring-necked Duck >IIa	117	173	7.0 (1–24)	6835	13	0.99810	0.000527
Lesser Scaup total	296	673	6.4 (0.5–24)	26084	155	0.99406	0.000476
Ring-necked Duck total	356	627	7.1 (1–31)	25647	137	0.99466	0.000455

*Includes broods on and off the 22.6 km² primary study area.

Maxson and Riggs 1996). For shorebirds, Frederick and Collopy (1989) found that as little as 5–10 cm of water can greatly deter mammalian predators. Nuechterlein *et al*. (2003), working with Red-necked Grebe (*Podiceps grisegena*), found that experimental artificial nests located farther from shore were more successful than those located directly adjacent to shore, concluding that nests that were located farther from the mainland or over deeper water presumably were safer from terrestrial predators such as Raccoon (*Procyon lotor*). All of the above suggest that overwater nest placement and greater distance from shore are important positive factors for nest success. Overwater nests located near the pond edge may experience high predation rates because Raccoon, Striped Skunk (*Mephitis mephitis*), and American Mink (*Vison vison*) often travel and forage along wetland shores (Mendall 1958; Urban 1970; Fritzell 1978; Lariviere and Messier 2000; Phillips *et al*. 2003; Barding and Nelson 2008). Therefore, additional nest protection afforded Ring-necked Duck by nest placement farther from pond edges may partly explain productivity differences.

Lesser Scaup and Ring-necked Duck suffer severe productivity loss when water levels recede due to multi-year drought (Rogers 1964) or anthropomorphic causes (e.g., marsh drawdown; Mendall 1958: 109) but productivity declines were large even during 2009–2018, a non-drought period in parkland habitat. Mean total yearly precipitation 1981–2010 for Wasagaming, Manitoba ~21 km north of the Erickson site, was 488 mm, compared to 555 mm recorded 2009–2018 (ECCC 2021). For both species, productivity was positively related to pond water level and both species demonstrated similar rate of response to change, suggesting that dry years affected both species to an equal degree and that resiliency to drought may not be a significant explanatory factor for productivity differences. Afton (1984) at Erickson also found Lesser Scaup productivity generally increased with improving water conditions but that some non-breeding occurred among first- and second-year females, and that the rate increased during dry years (low pond levels). Warren *et al.* (2014), at Red Rock Lakes in Montana, USA, found that Lesser Scaup breeding propensity was positively influenced by body and habitat (water level) conditions but not by age. Thus, failure by Lesser Scaup individuals and/or population cohorts to breed during our study might be an additional explanatory factor for lower productivity. Whether age-related and/or individual heterogeneity-related non-breeding applies to parkland Ring-necked Duck is unknown but first-year Ring-necked Duck females failed to breed in northern Minnesota, USA, in 1980, a dry year (Hohman 1984). Further investigation of parkland Ring-necked Duck demographics would be helpful. Interestingly, climate change predictions for the prairie-parkland region suggest hotter and drier summers (Sorenson *et al*. 1998; Sauchyn and Kulshreshtha 2008), conditions that, according to our results, would negatively affect Lesser Scaup and Ring-necked Duck productivity more frequently in future.

Walker *et al.* (2013) suggested that the negative relationship between nest success and pond density (“wetness”) in the previous one to two years results from change in predator abundance during wet-dry cycles. Wet, productive years may result in positive numeric reproductive response of waterfowl and alternative prey and increased predator abundance and higher rates of nest depredation in subsequent years. Conversely, dry years might result in decreased prey and predator abundance and lower rates of duck nest depredation. Our results did not support a time-lagged association of wetland score with productivity of Lesser Scaup and Ring-necked Duck. One plausible explanation is that in parkland habitat, nest success in both species is very sensitive to pond water level and local habitat conditions (i.e., wet versus dry) may be the proximate determinant of success, despite the abundance of predators. Time-lagged effects might be difficult to detect given the importance of wetland condition for these species. However, our data set may be of insufficient duration and/or sophistication (e.g., number of covariates considered) to detect differences.

Mean hatch date and hatching chronology

Earlier mean hatch date and mean date of first recorded brood for Ring-necked Duck is not surprising as research at Erickson reported their mean nest initiation date about 15 days earlier than for Lesser Scaup (Koons and Rotella 2003a). Nest initiation date is often negatively associated with recruitment for breeding waterfowl (Dawson and Clark 2000; Anderson *et al*. 2001; Esler *et al*. 2001; Blums *et al.* 2002; Brook 2002) so earlier hatching dates for Ring-necked Duck might give an advantage in recruitment probabilities. Ring-necked ducklings and their brood females would have more time than later hatching Lesser Scaup ducklings and their brood females to build nutrient reserves in preparation for migration and wintering. Also, overwater nest locations of earlier initiating Ring-necked Duck may be more secure from mammalian predators because water levels in wetland basins generally are highest in spring and decrease over time (Table S1). Whether such advantages are available to boreal Ring-necked Duck breeders is unclear because mean hatch dates for Ring-necked Duck were similar or later than Lesser Scaup in the past (Toft *et al*. 1984) but earlier more recently (DeVink *et al.* 2008).

Hatching distributions at Erickson were unimodal and similar but hatching period was much longer for Ring-necked Duck. They start hatching earlier, due to earlier nest initiations (Koons and Rotella 2003a) but the two species end nesting on about the same dates. At Yellowknife, Toft *et al*. (1984) found a unimodal distribution for Lesser Scaup but a pronounced bimodal one for Ring-necked Duck; hatching periods were of similar length. Presumably, a shorter open water season at higher latitudes necessitates both species initiating egg laying soon after arrival. Ring-necked Duck are strong re-nesters: 50–80% of females re-nest after loss of a first nest (Mendall 1958; Hunt and Anderson 1966 as cited in Roy *et al.* 2020), whereas Lesser Scaup are much less so: 16.4–39% (Keith 1961; Afton 1984). The length of the breeding season influences the ability to re-nest (Baldassarre and Bolen 2006) and the relatively lengthy open-water season in southern Manitoba (April–October) would provide opportunity if wetland conditions were favourable. We suspect that both Lesser Scaup and Ring-necked Duck were re-nesting most years, and perhaps Ring-necked Duck more so than Lesser Scaup, given their comparatively high propensity to re-nest in other areas, because wetland basins were full in spring for most years during this study and the right-skewed hatching distribution for both species (Figure 4) is consistent with expectations of re-nesting. However, only an age-related reproductive study for Ring-necked Duck, similar to Afton’s (1984) for Lesser Scaup at

Erickson, would determine the importance of re-nesting effort to the observed higher Ring-necked Duck productivity in southwestern Manitoba.

Brood size and duckling survival

Class Ia and IIa mean brood sizes for Lesser Scaup were greater than those for Ring-necked Duck by 0.7 and 0.6 ducklings, respectively. A larger class Ia mean brood size (and IIa size, assuming similar duckling DSR) for Lesser Scaup might be expected as mean clutch size for this species is greater than that for Ring-necked Duck: ~10 and ~9 eggs, respectively (Anteau *et al*. 2014; Roy *et al.* 2020). However, this Lesser Scaup IIa brood size productivity advantage does not appear to be sufficient to counter losses through lower nest success and other factors that are contributing to the contrasting population trajectories. Interestingly, in forested habitat in north-central Minnesota, ~500 km southeast of Erickson, where modelling of vital rates in Ring-necked Duck suggests a negative population growth (Roy *et al.* 2019), both Ring-necked Duck IIa brood size (4.3, SE 0.6) and brood survival (cumulative 30 day survival = 0.263, SE 0.035) appeared lower than equivalent metrics for Erickson parkland (Roy 2018).

Greater willingness by the female to hide her brood on perceiving a threat might express itself in increased duckling DSR and we observed a greater proportion of Ring-necked Duck than Lesser Scaup females attempting to hide their broods but there was no evidence of any difference in duckling DSR between species. The proportion of broods suffering total brood loss could be different for these species, especially during the first week post hatch when females brood the ducklings near shore or on floating vegetative mats and when greatest duckling loss occurs (Mendall 1958; Sarvis 1972 as cited in Roy *et al.* 2020; Afton 1983; McAuley and Longcore 1988; Koons 2001; Corcoran *et al*. 2007). Such total loss would not change our duckling DSR estimates from first sighting to age class IIa but would affect estimates for the entire hatch to age class IIa period. However, broods of both species presumably would be exposed to a similar suite of predators, especially during the first 10 days when losses are higher, because both females move their broods early in the brood period to large lakes, brood them in similar fashion generally away from dry shorelines on floating mats of vegetation or logs, and spend the majority of time in open water (Hammell 1973; Afton 1993; Maxson and Pace 1992; G.S.H. pers. obs.). Also, we observed no significant difference between species in the proportion of broods that disappeared (moved or suffered total loss) after having been first observed. Accordingly, we have assumed no difference in total brood loss and concluded both species have similar duckling survival at Erickson. If differences exist, our methods and/or data set may not be sufficient to detect them. Marked bird studies would provide more clarity.

Conclusion

Previous research on contrasting population growth trajectories for sympatric Lesser Scaup and Ring-necked Duck at Erickson, Manitoba had found that Ring-necked Duck nest success was greater than that of Lesser Scaup (Koons and Rotella 2003a). While no differences in nest habitat characteristics studied would explain this difference, nest success difference might be a reason for different population trends. Our long-term productivity and hatching results agree with the findings of Koons and Rotella (2003a). Greater Ring-necked Duck productivity, likely due in part to a combination of better nest placement (resulting in higher nesting success) and a probable greater re-nesting effort, is a potential proximate cause for contrasting population trends for these two species at Erickson. However, earlier Ring-necked Duck hatching dates may provide an additional reason for positive Ring-necked Duck population growth, giving survivorship and recruitment advantage to juveniles and brood females over those of Lesser Scaup by allowing Ring-necked Duck more time to add nutrient reserves in preparing for the rigours of fall migration. Consequently, indices of survivorship and recruitment and the relationship between hatch date and recruitment for parkland (or boreal) Ring-necked Duck are needed (but see Roy *et al*. 2019).

Our results highlight an important driver of the disparate population trends of these two species at Erickson, notably, the reproductive success advantage of Ring-necked Duck over Lesser Scaup. However, other factors associated with reproductive success may be involved. Some include population age structure (Trauger 1971; Afton 1984), experience and individual quality (Warren *et al*. 2014), and non-breeding season effects such as juvenile and adult survival and carry-over effects from wintering areas (Sedinger and Alisauskas 2014; Arnold *et al.* 2016; Warren 2018; Roy *et al.* 2019), but analysis of these factors is beyond the scope of our study. Development of region-specific integrated or other population models for these sympatric Lesser Scaup and Ring-necked Duck parkland populations might further identify drivers of population growth rate and help draft appropriate conservation strategies (Navarre 2020; Zhao *et al*. 2020).

Author Contributions

Writing – Original Draft: G.S.H.; Writing – Review & Editing: G.S.H., H.V.S., and L.M.A.; Conceptualization: G.S.H.; Investigation: G.S.H.; Methodology: G.S.H.; Formal Analysis: G.S.H., H.V.S., and L.M.A.; Funding Provision: G.S.H.

Acknowledgements

Thanks to I. Glass (Ducks Unlimited Canada) for providing library support. We thank the landowners and others around Erickson for their hospitality and permission to access their lands. We also thank G. Curry and H. Pengelly for help in the field. We appreciate the helpful comments of R.G. Clark (Environment and Climate Change Canada), R.W. Brook (Ontario Ministry of Natural Resources and Forestry), an anonymous reviewer, and Canadian Field-Naturalist editors that improved earlier drafts of this manuscript.

Literature Cited

Afton, A.D. 1983. Male and female strategies for reproduction in Lesser Scaup. Ph.D. thesis, University of North Dakota, Grand Forks, North Dakota, USA.

Afton, A.D. 1984. Influence of age and time on reproductive performance of female lesser scaup. Auk 101: 255–265. https://doi.org/10.1093/auk/101.2.255

Afton, A.D. 1993. Post-hatch brood amalgamation in lesser scaup: female behavior and return rates, and duckling survival. Prairie Naturalist 25: 227–235.

Afton, A.D., and M.G. Anderson. 2001. Declining scaup populations: a retrospective analysis of long-term population and harvest survey data. Journal of Wildlife Management 65: 781–796. https://doi.org/10.2307/3803028

Anderson, M.G., M.S. Lindberg, and R.B. Emory. 2001. Probability of survival and breeding for juvenile female canvasbacks. Journal of Wildlife Management 65: 403–415. https://doi.org/10.2307/3803090

Anteau, M., J.-M. DeVink, D.N. Koons, J.E. Austin, C.M. Custer, and A.D. Afton. 2014. Lesser Scaup (*Aythya affinis*), version 2.0. *In* Birds of North America. *Edited by* P.G. Rodewald. Cornell Lab of Ornithology, Ithaca, New York, USA. https//doi.org/10.2173/bna.338

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74: 1175–1178. https://doi.org/10.2193/2009-367

Arnold, T.W., A.D. Afton, M.J. Anteau, D.N. Koons, and C.A. Nicolai. 2016. Temporal variation in survival and recovery of lesser scaup. Journal of Wildlife Management 80: 850–681. https://doi.org/10.1002/jwmg.21074

Arnold, T.W., M.D. Sorenson, and J.J. Rotella. 1993. Relative success of overwater and upland mallard nests in southwestern Manitoba. Journal of Wildlife Management 57: 578–581. https://doi.org/10.2307/3809285

Austin, J.E., H.T. Sklebar, G.R. Guntenspergen, and T.K. Buhl. 2000. Effects of roadside transect width on waterfowl and wetland estimates. Wetlands 20: 660–670. https://doi.org/10.1672/0277-5212(2000)020[0660:eortwo]2.0.co;2

Baldassarre, G.A., and E.G. Bolen. 2006. Nesting, brood rearing and molting. *In* Waterfowl Ecology and Management. Second Edition. Kreiger Publishing Company, Malabar, Florida, USA.

Barding, E.E., and T.A. Nelson. 2008. Raccoons use habitat edges in northern Illinois. American Midland Naturalist 159: 394–402. https://doi.org/10.1674/0003-0031(2008)159[394:ruhein]2.0.co;2

Blums, P., R.G. Clark, and A. Mednis. 2002. Patterns of reproductive effort and success in birds: path analyses of long-term data from European ducks. Journal of Animal Ecology 71: 280–295. https://doi.org/10.1046/j.1365-2656.2002.00598.x

Brook, R.W. 2002. Breeding ecology and local population dynamics of lesser scaup (*Aythya affinis*) in boreal forest of western Canada. M.Sc. thesis, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

Brook, R.W., and R.G. Clark. 2005. Breeding season survival of female Lesser Scaup in the northern boreal forest. Arctic 58: 16–20. https//doi.org/10.14430/arctic384

Brook, R.W., D.C. Duncan, J.E. Hines, S. Carrière, and R.G. Clark. 2005. Effects of small mammal cycles on productivity of boreal ducks. Wildlife Biology 11: 3–11. https://doi.org/10.2981/0909-6396(2005)11[3:eosmco]2.0.co;2

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Second Edition. Springer, New York, New York, USA.

Corcoran, R.M., J.R. Lovvorn, M.R. Bertram, and M.T. Vivion. 2007. Lesser scaup nest success and duckling survival on the Yukon Flats, Alaska. Journal of Wildlife Management 71: 127–134. https://doi.org/10.2193/2005-534

Dawson, R.D., and R.G. Clark. 1996. Effects of variation in egg size and hatching date on survival of Lesser Scaup *Aythya affinis* ducklings. Ibis 138: 693–699. http://doi.org/10.1111/j.1474-919x.1996.tb04771.x

Dawson, R.D., and R.G. Clark. 2000. Effects of hatching date and egg size on growth, recruitment, and adult size of Lesser Scaup. Condor 102: 930–935. https://doi.org/10.1650/0010-5422(2000)102[0930:eohdae]2.0.co;2

DeVink, J.-M., R.G. Clark, S.M. Slattery, and D.L. Trauger. 2008. Are late-spring boreal Lesser Scaup (*Aythya affinis*) in poor body condition? Auk 125: 291–298. https://doi.org/10.1525/auk.2008.06171

Diem, K.L., and K.H. Lu. 1960. Factors influencing waterfowl censuses in the parklands, Alberta, Canada. Journal of Wildlife Management 24: 113–133. https://doi.org/10.2307/3796737

Dzubin, A. 1955. Some evidence of home range in waterfowl. Transactions of the North American Wildlife Conference 20: 278–298.

ECCC (Environment and Climate Change Canada). 2018. Abundance and productivity of waterfowl and other aquatic birds breeding in the boreal forest, summer, 2018. Unpublished newsletter. Canadian Wildlife Service, Yellowknife, Northwest Territories, Canada.

ECCC (Environment and Climate Change Canada). 2021. Historical climate data. Accessed 20 November 2021. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html.

Esler, D., J.B. Grand, and A.D. Afton. 2001. Intraspecific variation in nutrient reserve use during clutch formation by Lesser Scaup. Condor 103: 810–820. https://doi.org/10.1650/0010-5422(2001)103[0810:ivinru]2.0.co;2

Ferguson, R.S. 1977. Adaptations of the Horned Grebe for breeding in prairie pothole marshes. M.Sc. thesis, University of Manitoba, Winnipeg, Manitoba, Canada.

Frederick, P.C., and M.W. Collopy. 1989. The role of predation in determining reproductive success of colonially nesting wading birds in the Florida everglades. Condor 91: 860–867. https://doi.org/10.2307/1368070

Fritzell, E.K. 1978. Habitat use by prairie raccoons during the waterfowl breeding season. Journal of Wildlife Management 42: 118–127. https://doi.org/10.2307/3800698

Gallop, J.B., and W.H. Marshall. 1954. A guide for aging duck broods in the field. Technical session report. Mississippi Flyway Council, Louisiana Department of Wildlife and Fisheries, Baton Rouge, Louisiana, USA.

Gauthier, G. 1987. Brood territories in buffleheads: determinants and correlates of territory size. Canadian Journal of Zoology 65: 1402–1410. https://doi.org/10.1139/z87-221

Guyn, K.L., and R.G. Clark. 1999. Factors affecting survival of Northern Pintail ducklings in Alberta. Condor 101: 369–371. https://doi.org/10.2307/1370000

Hammell, G.S. 1973. The ecology of the lesser scaup (*Aythya affinis* Eyton) in southwestern Manitoba. M.Sc. thesis, University of Guelph, Guelph, Ontario, Canada.

Hammell, G.S. 2014. Erickson study area: duck breeding populations and habitat, then (1970–72) and now (2008–13). Bluejay 72: 123–139. Accessed 20 November 2021. https://bluejayjournal.ca/index.php/bluejay/article/view/212/209.

Hammell, G.S. 2016. Reproductive rates in Lesser Scaup (*Aythya affinis*) in southwestern Manitoba: another look at the data. Canadian Field-Naturalist 130: 110–121. https://doi.org/10.22621/cfn.v130i2.1834

Hines, J.E. 1977. Nesting and brood ecology of Lesser Scaup at Waterhen Marsh, Saskatchewan. Canadian Field-Naturalist 91: 248–255. Accessed 20 November 2021. https://www.biodiversitylibrary.org/page/28061461.

Hohman, W.L. 1984. Aspects of the breeding biology of Ring-necked Ducks (*Aythya collaris*). Ph.D. thesis, University of Minnesota, St. Paul, Minnesota, USA.

Holliday, I.E. 2012. Kolmogorov-Smirnov test (version 1.0.3) in Free Statistics Software (version 1.1.23-r7). Office for Research Development and Education. Accessed 20 November 2021. http://www.wessa.net/rwasp_Reddy-Moores%20K-S%20Test.wasp/.

Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96: 651–661. https://doi.org/10.1093/auk/96.4.651

Keith, L.B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. Wildlife Monographs 6: 3–88.

Koons, D.N. 2001. Lesser Scaup breeding ecology in the Canadian parklands. M.Sc. thesis, Montana State University, Bozeman, Montana, USA.

Koons, D.N., T.W. Arnold, and M. Schaub. 2017. Understanding the demographic drivers of realized population growth rates. Ecological Applications 27: 2102–2115. https://doi.org/10.1002/eap.1594

Koons, D.N., G. Gunnarsson, J.M. Schmutz, and J.J. Rotella. 2014. Drivers of waterfowl population dynamics: from teal to swans. Wildfowl Special Issue 4: 169–191. Accessed 26 February 2019. https://wildfowl.wwt.org.uk/index.php/wildfowl/article/view/2606.

Koons, D.N., and J.J. Rotella. 2003a. Comparative nesting success of sympatric Lesser Scaup and Ring-necked Ducks. Journal of Field Ornithology 74: 222–229. https://doi.org/10.1648/0273-8570-74.3.222

Koons, D.N., and J.J. Rotella. 2003b. Have Lesser Scaup, *Aythya affinis*, reproductive rates declined in parkland Manitoba? Canadian Field-Naturalist 117: 582–588. https://doi.org/10.22621/cfn.v117i4.827

Koons, D.N., J.J. Rotella, D.W. Willey, M. Taper, R.G. Clark, S. Slattery, R.W. Brook, R.M. Corcoran, and J.R. Lovvorn. 2006. Lesser Scaup population dynamics: what can be learned from available data? Avian Conservation and Ecology 1: 6. https://doi.org/10.5751/ace-00105-010306

Lariviere, S., and F. Messier. 2000. Habitat selection and use of edges by striped skunks in the Canadian prairies. Canadian Journal of Zoology 78: 366–372. https://doi.org/10.1139/z99-230

Livezey, B.C. 1996. A phylogenetic analysis of modern pochards (Anatidae: Aythyini). Auk 113: 74–93. https://doi.org/10.2307/4088937

Martin, T.E. 1995. Avian life history evolution in relation to nest site, nest predation and food. Ecological Monographs 65: 101–127. https://doi.org/10.2307/2937160

Maxson, S.J., and R.M. Pace, III. 1992. Diurnal time-activity budgets and habitat use of Ring-necked Duck ducklings in northeastern Minnesota. Wilson Bulletin 104: 472–484.

Maxson, S.J., and M.R. Riggs. 1996. Habitat use and nest success of overwater nesting ducks in westcentral Minnesota. Journal of Wildlife Management 60: 108–119. https://doi.org/10.2307/3802045

Mayfield, H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456–466.

McAuley, D.G., and J.R. Longcore. 1988. Survival of juvenile ring-necked ducks on wetlands of different pH. Journal of Wildlife Management 52: 169–176. https://doi.org/10.2307/3801219

McDonald, J.H. 2014. Fisher's exact test of independence, Wilcoxon signed-rank test, and Linear regression. Pages 77–85, 157–164, and 238–246. *In* Handbook of Biological Statistics. Third Edition. Sparky House Publishing, Baltimore, Maryland, USA. Accessed 20 November 2021. http://www.biostathandbook.com.

Mendall, H.L. 1958. Ring-necked Duck in the Northeast. University of Maine Studies, No. 73. University of Maine Press, Orono, Maine, USA.

Migratory Bird Data Centre. n.d. Division of migratory bird management, waterfowl breeding population and habitat survey, United States Fish and Wildlife Service. Accessed 20 November 2021. https://migbirdapps.fws.gov/mbdc/databases/mas/mas_options.asp.

Navarre, K. 2020. Temporal demography of lesser scaup: a species in decline. M.Sc. thesis, Colorado State University, Fort Collins, Colorado, USA.

Nuechterlein, G.L., D. Buitron, J.L. Sachs, and C.R. Hughes. 2003. Red-necked Grebes become semicolonial when prime nesting substrate is available. Condor 105: 80–94. https://doi.org/10.1093/condor/105.1.80

Phillips, M.L., W.R. Clark, M.A. Sovada, D.J. Horn,

R.K. Koford, and R.J. Greenwood. 2003. Predator selection of prairie landscape features and its relation to duck nest success. Journal of Wildlife Management 67: 104–114. https://doi.org/10.2307/3803066

Rogers, J.P. 1964. Effect of drought on reproduction of the lesser scaup. Journal of Wildlife Management 28: 213–222. https://doi.org/10.2307/3798080

Roy, C.L. 2018. Nest and brood survival of Ring-necked Ducks in relation to anthropogenic development and wetland attributes. Avian Conservation and Ecology 13(1): 20. https://doi.org/10.5751/ace-01212-130120

Roy, C.L., J.B. Berdeen, and M. Clark. 2019. A demographic model for ring-necked ducks breeding in Minnesota. Journal of Wildlife Management 83: 1720–1734. https://doi.org/10.1002/jwmg.21756

Roy, C.L., C.M. Herwig, W.L. Hohman, and R.T. Eberhardt. 2020. Ring-necked Duck (*Aythya collaris*), version 1.0. *In* Birds of the World. *Edited by* A.F. Poole. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.rinduc.01

Sæther, B.-E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81: 642–653. https://doi.org/10.2307/177366

Sæther, B.-E., V. Grøtan, S. Engen, T. Coulson, P.R. Grant, M.E. Visser, J.E. Brommer, B.R. Grant, L. Gustafsson, B.J. Hatchwell, K. Jerstad, P. Karell, H. Pietiäinen, A. Roulin, O.W. Røstad, and H. Weimerskirch. 2016. Demographic routes to variability and regulation in bird populations. Nature Communications 7: 12001. https://doi.org/10.1038/ncomms12001

Sauchyn, D., and S. Kulshreshtha. 2008. Prairies. Pages 275–328 *in* From Impacts to Adaptation: Canada in a Changing Climate 2007. *Edited by* D.S. Lemmen, F.J. Warren, J. Lacroix, and E. Bush. Government of Canada, Ottawa, Ontario, Canada. Accessed 20 November 2021. https://tinyurl.com/y2o7kueg.

Sedinger, J.S., and R.T. Alisauskas. 2014. Cross-seasonal effects and the dynamics of waterfowl populations. Wildfowl Special Issue 4: 277–304.

Sorenson, L.G., R. Goldberg, T.L. Root, and M.G. Anderson. 1998. Potential effects of global warming on waterfowl populations breeding in the northern Great Plains. Climatic Change 40: 343–369. http://doi.org/10.1023/A:1005441608819

Stewart, R.E., and H.A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. Resource publication 92. United States Fish and Wildlife Service, Washington, DC, USA. Accessed 20 November 2021. https://pubs.usgs.gov/rp/092/report.pdf.

Sunde, L.A., and J. Barica. 1975. Geography and lake morphometry of the aquatic study area in the Erickson–Elphinstone district of southwestern Manitoba. Technical report 510. Fisheries and Marine Service, Environment Canada, Winnipeg, Manitoba, Canada.

Toft, C.A., D.L. Trauger, and H.W. Murdy. 1984. Seasonal decline in brood sizes of sympatric waterfowl (*Anas* and *Aythya*, Anatidae) and a proposed evolutionary explanation. Journal of Animal Ecology 53: 75–92. https://doi.org/10.2307/4343

Townsend, G.H. 1966. A study of waterfowl nesting on the Saskatchewan River Delta. Canadian Field-Naturalist. 80: 74–88. Accessed 20 November 2021. https://www.biodiversitylibrary.org/page/28034092.

Trauger, D.L. 1971. Population ecology of Lesser Scaup (*Aythya affinis*) in subarctic taiga. Ph.D. thesis, Iowa State University, Ames, Iowa, USA.

Urban, D. 1970. Raccoon populations, movement patterns, and predation on a managed waterfowl marsh. Journal of Wildlife Management 34: 372–382. https://doi.org/10.2307/3799024

US F&WS (United States Fish and Wildlife Service). 2019. Waterfowl population status, 2019. U.S. Department of the Interior, Washington, DC, USA. Accessed 20 November 2021. https://www.fws.gov/migratorybirds/pdf/surveys-and-data/Population-status/Waterfowl/WaterfowlPopulationStatusReport19.pdf.

Walker, J. 2004. Nest and duckling survival of scaup at Minto Flats, Alaska. M.Sc. thesis, University of Alaska, Fairbanks, Alaska, USA. Accessed 20 November 2021. https://tinyurl.com/yyrka8ke.

Walker, J.A., and M.S. Lindberg. 2005. Survival of scaup ducklings in the boreal forest of Alaska. Journal of Wildlife Management 69: 592–600. https://doi.org/10.2193/0022-541x(2005)069[0592:sosdit]2.0.co;2

Walker, J., J.J. Rotella, S.E. Stephens, M.S. Lindberg, J.K. Ringelman, C. Hunter, and A. Smith. 2013. Time-lagged variation in pond density and primary productivity affects duck nest survival in the Prairie Pothole Region. Ecological Applications 23: 1061–1074. https://doi.org/10.1890/12-1755.1

Warren, J.M. 2018. Breeding season ecology and demography of Lesser Scaup (*Aythya affinis*) at Red Rock Lakes National Wildlife Refuge. Ph.D. thesis, Utah State University, Logan, Utah, USA.

Warren, J.M., K.A. Cutting, J.Y. Takekawa, S.E. De La Cruz, T.D. Williams, and D.N. Koons. 2014. Previous success and current body condition determine breeding propensity in Lesser Scaup: evidence for the individual heterogeneity hypothesis. Auk 131: 287–297. https://doi.org/10.1642/auk-13-236.1

Zhao, Q., T.W. Arnold, J.H. Devries, D.W. Howerter, R.G. Clark, and M.D. Weegman. 2020. Using integrated population models to prioritize region-specific conservation strategies under global change. Biological Conservation 252:108832. https://doi.org/10.1016/j.biocon.2020.108832

Received 24 April 2020
Accepted 9 July 2021
Associate Editor: J.R. Foote

SUPPLEMENTARY MATERIAL:

TABLE S1. Assigned scores for local spring wetland condition and selected Lesser Scaup (*Aythya affinis*) reproductive periods, 2009–2018, Erickson, Manitoba.

The Canadian Field-Naturalist

Distribution, status, and habitat characteristics of Columbia Quillwort (*Isoetes minima*, Isoetaceae) in Canada

Carrina Y. Maslovat[1,*], **Ryan Batten**[2], **Daniel F. Brunton**[3], and **Paul C. Sokoloff**[3]

[1]P.O. Box 311, Salt Spring Island, British Columbia V8K 2V9 Canada
[2]25 — 325 Kingston Street, Victoria, British Columbia V8V 1V5 Canada
[3]Beaty Centre for Species Discovery and Botany Section, Canadian Museum of Nature, Ottawa, Ontario K1P 6P4 Canada
*Corresponding author: Carrina.maslovat@icloud.com

Maslovat, C.Y., R. Batten, D.F. Brunton, and P.C. Sokoloff. 2021. Distribution, status, and habitat characteristics of Columbia Quillwort (*Isoetes minima*, Isoetaceae) in Canada. Canadian Field-Naturalist 135(3): 293–304. https://doi.org/10.22621/cfn.v135i3.2621

Abstract

In Canada, the globally rare lycophyte, Columbia Quillwort (*Isoetes minima*), is currently known from four subpopulations, all within a 25-km radius of Castlegar in the Selkirk and Monashee Mountain ranges of southern British Columbia. These constitute just over a quarter of all known subpopulations in Canada and the United States. The species is found in Canada in sloping pocket meadows that are naturally fragmented within a larger forested matrix. The plants grow in spring seepage areas in thin soils that discourage the establishment of larger, more vigorous vascular plant competitors. Long combined within *Isoetes howellii* (*sensu lato*), *I. minima* has only recently been confirmed to be a distinct species, and, in 2019, it was assessed as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). We build on information in the COSEWIC status report by describing the species' morphology and ecology in greater detail and provide a comparison of critical identification features of closely related species as well as a dichotomous key for *Isoetes* species in British Columbia.

Key words: *Isoetes minima*; British Columbia; Endangered; Species at Risk; Canada

Introduction

Quillworts (*Isoetes*, Isoetaceae, Isoetales) are an ancient and widespread lineage of perennial lycophytes with a fossil record that dates from the Late Devonian era (375 million years ago [mya]; Pigg 2001; Larsén and Rydin 2016). Contemporary lineages arose during the Jurassic Period (200–145 mya) and diversified in the mid-Paleogene (Tertiary Period; 45–60 mya; Pigg 2001; Wood *et al.* 2020).

Currently, there are ~200 named taxa (species, subspecies, hybrids) of *Isoetes* worldwide (Troia *et al.* 2016), with perhaps 100 more expected to be recognizable based on morphology (Brunton and Troia 2018). Molecular studies suggest that, in addition, there may be 50 or more morphologically cryptic taxa in North America alone (Schafran 2019). In the last 30 years, two species have been described in Canada (Britton and Goltz 1991; Brunton *et al.* 2019), and an undescribed taxon is suspected to exist along the Pacific coast of British Columbia (BC; D.F.B. unpubl. data).

In Canada, there are 13 described *Isoetes* species, six of which are found in BC (Cody and Britton 1989; Taylor *et al*. 1993, 2003; Brunton *et al.* 2019, 2020). Half of the BC species are aquatic or grow on emergent shores of rivers and ponds, while the other half are terrestrial species found in ephemeral pools and seeps (Klinkenberg 2020).

Isoetes minima A.A. Eaton (*I. howellii* var. *minima* (A.A. Eaton) N. Pfeiffer) is a sexual diploid ($2n = 2x = 22$; Taylor *et al.* 2003) within a complex group of western North American quillworts (Figure 1). In Canada, this group includes Bolander's Quillwort (*Isoetes bolanderi* G. Engelmann), Howell's Quillwort (*Isoetes howellii* G. Engelmann, including *Isoetes melanopoda* var. *californica* A.A. Eaton and *Isoetes underwoodii* L. Henderson), and Nuttall's Quillwort (*Isoetes nuttallii* A. Braun).

Isoetes minima was first collected on 16 May 1889 by W.N. Suksdorf near Waverly, north of Spokane in eastern Washington, United States (*W.N. Suksdorf 2365,* 16 May 1889, WS 119319). It was described by Eaton (1898) on the basis of being the only trilobed species with a partial (up to 75%) velum coverage of the sporangium. Eaton (1898: 30) used these features along with spore ornamentation characteristics, the most distinctive of which he described as

---

A contribution towards the cost of this publication has been provided by the Thomas Manning Memorial Fund of the Ottawa Field-Naturalists' Club.

FIGURE 1. Mature Columbia Quillwort (*Isoetes minima*) plant; coin (Canadian dime) is 18 mm wide (14 May 2017, Fairview Meadows, British Columbia). Photo: R. Batten.

"by the equator [equatorial ridge], which resembles a ship's wheel with the spinules for handspikes", to distinguish *I. minima* from the morphologically similar Pacific coastal species, *I. nuttallii* and Orcutt's Quillwort (*Isoetes orcuttii* A.A. Eaton), which grow in similar spring ephemeral situations.

Subsequently, however, these distinctions have been misinterpreted (Pfeiffer 1922) or not considered significant by *Isoetes* researchers, and *I. minima* has been synonymized within *I. howellii* (*sensu lato*) (Taylor 1970; Cody and Britton 1989; Taylor *et al.* 1993). On his 1889 collecting trip, Suksdorf collected a number of *I. howellii* plants that looked superficially similar to *I. minima*. Based on the study of this limited material, Pfeiffer (1922) reduced *I. minima* to a variety of *I. howellii*. This treatment was followed by Taylor *et al.* (1993) in the *Flora of North America North of Mexico*. Only recently did DNA analysis of a Canadian subpopulation provide support for the original morphological evidence of the distinct species status of *I. minima* (Taylor *et al.* 2003).

The confined geographic distribution of *I. minima* and its limited dispersal ability combine to make it one of the rarest *Isoetes* species in Canada (COSEWIC 2019a) and North America. This Columbia Region endemic species is restricted in distribution to the Columbia River catchment and has been designated, globally, as Critically Imperilled (G1), with fewer than 15 known subpopulations (Natureserve 2020). It is at the northern limit of its range in Canada; in the United States, it is known from at least three sites in Washington, two in Idaho, and six in Oregon (W. Fertig pers. comm. 10 August 2020; L. Kinter pers. comm. 6 August 2020; S. Vrilakas pers. comm. 12 August 2020; Figure 2). It is assessed as Endangered in Canada (COSEWIC 2019a) and is provincially red-listed and ranked S1S2 (Critically Imperilled–Imperilled; BC Conservation Data Centre 2020).

In light of the limited number of publications detailing its natural history, status, habitat preferences, and distribution in Canada, our study builds on information provided in the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) status report (COSEWIC 2019a) and is the most comprehensive documentation of the morphology, ecology, and key identification characters of this globally rare species. The species' morphology is described in detail with precise spore size measurements and diagnostic scanning electron microscope (SEM) images that show critically important spore morphology. The site ecology is described in detail including the identification of key associates. Critical features for the identification of this challenging species are presented in comparison with previously unreported diagnostic distinguishing features between *I. minima* and its closest generic allies. A dichotomous key for *Isoetes* species in BC is included.

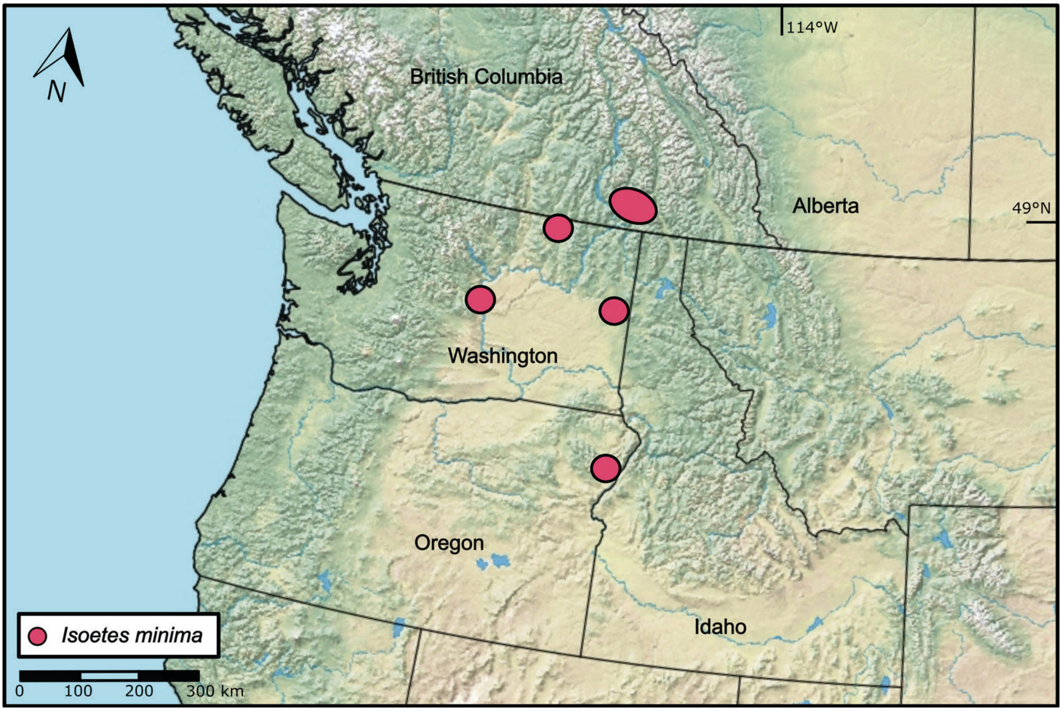


FIGURE 2. Global distribution of Columbia Quillwort (*Isoetes minima*). Basemap from SimpleMappr (Shorthouse 2010).

Methods

These investigations are based on field and herbarium studies of *I. minima* populations in Canada and the United States undertaken by us and others since 2008. In 2017, all three known sites within the Canadian range were surveyed by C.Y.M. and R.B. in the course of preparing the COSEWIC status report (COSEWIC 2019a). Herbarium records in the Canadian Museum of Nature (CAN), Agriculture and Agri-Food Canada (DAO), Daniel Brunton Private Herbarium (DFB), University of Guelph (OAC), University of British Columbia (UBC), Royal British Columbia Museum (V; acronyms of Thiers 2020), and the Consortium of Pacific Northwest Herbaria (https://www.pnwherbaria.org/data.php) were examined to identify known locations. The BC Conservation Data Centre database, the Canadian Wildlife Service (Pacific Region), Parks Canada (Conservation Programs Branch), the Ministry of Environment and Climate Change Strategy (Species Conservation Unit), and local stewardship officers (Research Ecologist, Ministry of Forests, Lands and Natural Resources) were canvassed for their knowledge of additional sites.

The three subpopulations known before 2017 were resurveyed by C.Y.M. and R.B. from 10 to 15 May 2017. *Isoetes minima* is easy to see early in the spring when surrounding vegetation is low in stature. Site details from previous records were consulted in advance to determine coordinates and site descriptors that guided plant searches. Spatial data were collected to help guide the definition of "subpopulation" for each site described in the status report. NatureServe (2004) defines subpopulation for all taxa as a group of occurrences that are separated by <1 km; or, if separated by 1–3 km, with no break in suitable habitat between them exceeding 1 km; or, if separated by 3–10 km, connected by linear water flow and having no break in suitable habitat between them >3 km. Universal transverse mercator (UTM) coordinates were recorded using a hand-held global positioning system unit (GPSMAP 62sc; Garmin Ltd., Olathe, Kansas, USA) at the centre of each cluster. (A "cluster" is a group of plants within a given subpopulation.) Other data collected included a count of the total number of plants by temporarily marking each plant with a wooden skewer (Figure 3). Habitat descriptions included associated species and repeat visits were made to each site later in the season to provide a more comprehensive associated species list as later species developed. Details of the condition of the population including threats and management concerns were described as well as the overall landscape context of the site. BC Conservation Data Centre element occurrence forms were completed for each location.

FIGURE 3. Columbia Quillwort (*Isoetes minima*) habitat (11 May 2017, Lloyd's Meadow, British Columbia); black sticks indicate position of mature plants and white sticks indicate location of sporelings. Photo: C. Maslovat.

In 2017, new subpopulations were searched for (C.Y.M., R.B., and D.F.B.) in areas beyond the known sites thought to have suitable habitat. Surveys undertaken in other suitable habitat in BC southwest of Rossland, west of Castlegar, east of Christina Lake, west of Creston (R.B. and C.Y.M.), and southeast of Montrose (D.F.B.) did not reveal additional subpopulations. All known suitable habitat in the area between patches of plants within confirmed sites were surveyed, with no new subpopulations found.

Megaspore and microspores of BC *I. minima* plants were examined through dissecting light microscopes and with SEM imagery. The extensive library of SEM spore images of *I. howellii* and related taxa prepared by D.M. Britton before 2007 (using methods described in Brunton and Britton 2006) was reviewed. Additional SEM images were generated by P.C.S. and D.F.B. For these new images, air-dried spores were attached to SEM stubs by means of adhesive carbon discs. These were sputter coated with a gold/palladium alloy and examined with a 2017 model SEM (FEI Apreo ThermoFisher Scientific, Hillsboro, Oregon, USA) at 15 kV and 25 pA, with a working distance of 10 mm and a spot size of 6.

Megaspore sizes reported for individual specimens represent the average width (across the equatorial region) of at least 20 (often 40) spores, as measured (D.F.B.) through a light dissecting microscope (Wild M3B, Leica, Heerbrugg, St-Gallen, Switzerland) at 40× magnification, with the aid of an in-mount graticule (ocular micrometer) for measurements. Comparable microspore measurements are based on the average of 20 (frequently 40) longitudinal measurements taken from SEM images of clusters of spores.

Results

History, distribution, and status in Canada

Isoetes minima is a relatively recent addition to the Canadian flora. The first record is from Beavervale Meadow, discovered by Oldriska and Adolf Ceska (*A. & O. Ceska #30,000*, 5 July 1996, V), and a second site (Lloyd's Meadow) was discovered later that month by Hans Roemer (*H. Roemer 96-164*, 12 July 1996, V). In 2002, a third site (Fairview Meadow) was found during a Botany BC field trip; data for that locality were submitted to the BC Conservation Data Centre by Sharon Hartwell (BC Conservation Data Centre 2017). The fourth subpopulation was found during the 2017 survey ~1 km east of Lloyd's Meadow (V). All subpopulations occur within 25 km of Castlegar, BC (Figure 4).

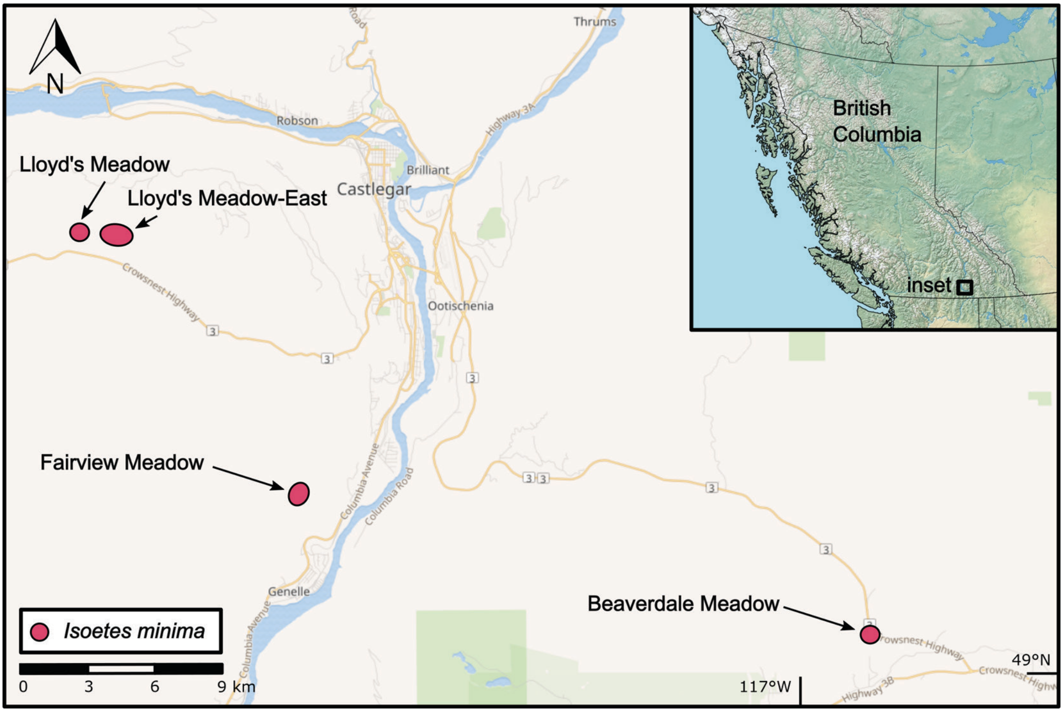


FIGURE 4. Columbia Quillwort (*Isoetes minima*) distribution in Canada (adapted from COSEWIC 2019a). Basemap from SimpleMappr (Shorthouse 2010).

The total population of *I. minima* in Canada in 2017 (COSEWIC 2019a) was 1019 mature individuals capable of reproduction (Table 1). Sporelings (immature plants) were observed at all of the sites.

Globally, *I. minima* is known from fewer than 15 subpopulations. In the United States, the sites are widely dispersed in Washington, Idaho, and Oregon, with distances between sites in Washington being as much as 200 km (Figure 2). The Canadian occurrences are approximately 100 km from the closest known United States sites.

Habitat characteristics

In Canada, the habitat of *I. minima* is confined to discrete forest openings within the Interior Cedar–Hemlock biogeoclimatic zone (BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development 2018). The range is within the Selkirk Foothills Ecosection, a transition zone divided by the BC–Washington border which lies between the Selkirk Mountains to the east and the Okanagan Highlands to the west (Demarchi 2011). The substrate is composed of granitic batholiths and sedimentary rocks, and the landforms have been altered by glaciers which rounded the mountains and left glacial debris on the valley floor, particularly south of Castlegar (Demarchi 2011).

This habitat is rare: it consists of small (170–300 ha), sloping pocket meadows (glades) within a larger forested matrix. It is further restricted by a narrow geographic area and by a limited range of elevation: 700–1160 m in Canada and 1370–2299 m in the United States (COSEWIC 2019a). Within the meadows, characteristic features of places where plants were found include a south-to-east facing aspect free from snow early in the spring; sustained spring (to early summer) seepage over thin soils; and gentle to moderate slopes (up to 20%). Spring seepages are naturally uncommon in the landscape, occurring where ephemeral underground moisture is carried on top of shallow bedrock and generally exhausted by mid-June. The thin (usually 3–7 cm, but infrequently 10–15 cm) soil discourages the establishment of larger, more vigorous vascular plants that would compete for light, moisture, and nutrients (COSEWIC 2019a).

Isoetes minima is found on acidic or circumneutral substrates throughout its range. Most sites are in full sun (Figure 3), but the species has been observed in smaller pocket meadows where there is partial shade from adjacent tree cover (COSEWIC 2019a). In Canadian subpopulations, *I. minima* is usually found on the upslope edge of exposed bedrock (COSEWIC 2019a).

TABLE 1. Subpopulation size and key associates of Canadian subpopulations of Columbia Quillwort (*Isoetes minima*; COSEWIC 2019a; this study).

Subpopulation	Mature plants (spore-bearing)	Immature plants	Total plants	Associated species
Beavervale Meadow 49.20°N, 117.45°W	57	12	69	False Mermaidweed (*Floerkea proserpinacoides* Willdenow); Dwarf Hesperochiron (*Hesperochiron pumilus* Grisebach); Darkthroat Shootingstar (*Primula pauciflora* (Green) A.R. Mast & Reveal); Buttercup-leaved Susksdorfia (*Suksdorfia ranunculifolia* (Hooker) Engelmann); Oregon Woodsia (*Woodsia oregana* D.C. Eaton); Nuttall's Larkspur (*Delphinium nuttallianum* Pritzel); Yellow Stonecrop (*Sedum stenopetalum* Pursh); Small-flower Blue-eyed Mary (*Collinsia parviflora* Douglas ex Lindley); One-flowered Broomrape (*Aphyllon uniflorum* (L.) Torrey & A. Gray); Spotted Knapweed (*Centaurea stoebe* L.)
East Lloyd's Meadow 49.30°N, 117.76°W	181	11	192	*F. proserpinacoides*; *H. pumilus*; Three-leaved Lewisia (*Lewisia triphylla* (Watson) Robinson); *S. ranunculifolia* (species list incomplete)
Fairview Meadow 49.24°N, 117.69°W	254	46	300	Large-flowered Clarkia (*Clarkia pulchella* Pursh); *F. proserpinacoides*; *H. pumilus*; *P. pauciflora*; *S. ranunculifolia*; *W. oregana*; *D. nuttallianum*; *S. stenopetalum*; *C. parviflora*; *A. uniflorum*; Narrow-leaved Montia (*Montia linearis* (Douglas ex Hooker) Greene); *C. stoebe*
Lloyd's Meadow 49.30°N, 117.78°W	527	57	584	*C. pulchella*; *F. proserpinacoides*; *H. pumilus*; *P. pauciflora*; *S. ranunculifolia*; *W. oregana*; *D. nuttallianum*; *S. stenopetalum*; *C. parviflora*; *A. uniflorum*; *M. linearis*; *C. stoebe*
Total individuals	1019	126	1145	

Immediately adjacent to *I. minima* plants, vegetation is either absent or dominated by thick moss mats (primarily *Philonotis fontana* (Hedwig) Bridel, *Niphotrichum elongatum* (Frisvoll) Bednarek-Ochyra & Ochyra, and *Bryum weigelii* (Biehler) J.R. Spence) and forbs, with a few shrubs infrequently present at the edges of the seeps. Characteristic associated forb species are included in Table 1. In Canada, *I. minima* is also associated with the federally rare plant, Dwarf Hesperochiron (*Hesperochiron pumilus* Grisebach), as well as other species limited to the same habitat, such as Pink-fairies (*Clarkia pulchella* Pursh) and False Mermaid-weed (*Floerkea proserpinacoides* Willdenow; Table 1). Indeed, the only Canadian occurrences of Dwarf Hesperochiron and Hairy Paintbrush (*Castilleja tenuis* (A. Heller) Chuang & Hickard), which have both been assessed by COSEWIC as Endangered, occur in one or more of the meadows where *I. minima* grows (COSEWIC 2019b and 2019c, respectively). The regionally rare False Mermaid-weed is present at all sites.

Identification and physical distinctions of Isoetes minima

Isoetes minima is among the smallest quillwort species in North America (Taylor *et al.* 2003) and the world (Brunton and Troia 2018). Although similar in appearance to dwarfed plants of *I. howellii*, with which it overlaps in range, Larsén and Rydin (2016) provide molecular evidence that it is more closely related to the predominantly coastal *I. orcuttii* and *I. nuttallii*. Regardless, *I. minima* is a relatively distinctive taxon with a unique megaspore ornamentation character that readily separates it from *I. howellii* (Figure 5).

The following describes the most significant physical characteristics of *I. minima*, based on our observations supplemented by the (sparse) literature addressing this and related taxa. The observations of Pfeiffer (1922) are used cautiously, however, as they included misidentified specimens (likely *I. howellii*) in their consideration of *I. minima* characteristics.

Gross form and leaves—The pale green plants emerge as tufts of 6–12, ~0.5–0.75-mm-wide leaves from a corm-like rootstock (Figure 1), which has been described as either three-lobed (Eaton 1898) or two-lobed (Pfeiffer 1922; our study). Freund *et al.* (2018) considered corm lobation to be of significant value in classifying some *Isoetes* taxa into clades, but their study did not include *I. minima*.

Most Canadian plants average 3–6 cm in height, but if there is sufficient available moisture toward the end of the April–June growing season, the plants can

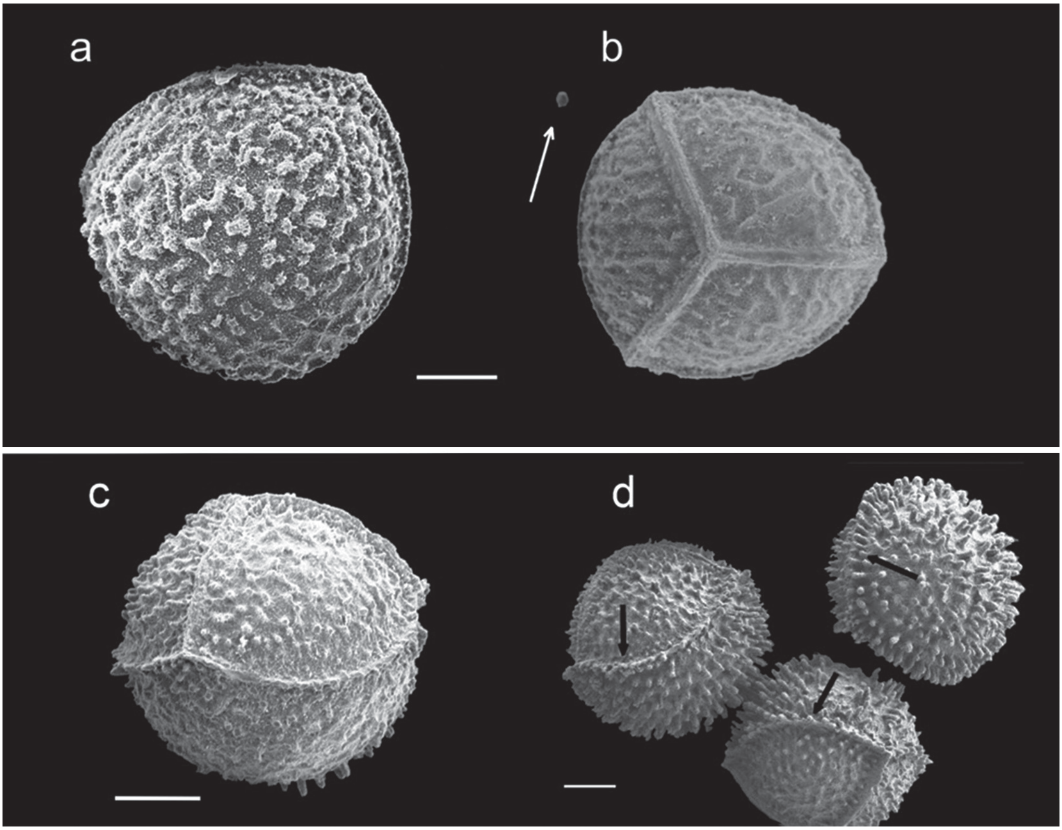


FIGURE 5. Howell's Quillwort (*Isoetes howellii*) and Columbian Quillwort (*Isoetes minima*) megaspores. a and b. *Isoetes howellii* open ornamentation pattern of low, broad, anastomosing muri (walls) with (a) distal side (*L.F. Henderson 2,894*, Moscow, Idaho [MO 200569]) and (b) proximal side with microspore [arrow] (*D.F. Brunton & K.L. McIntosh 10,855*, Akamina-Kishinena Provincial Park, BC [OAC]). c and d. *Isoetes minima* with (c) dense ornamentation pattern of thin tubercles on distal and proximal sides (*D.F. Brunton & K.L. McIntosh 17,243*, Salmo, BC [DFB]) and (d) diagnostic row of tubercles ("spokes of ship's wheel") [arrows] atop the equatorial ridge. Scale bars = 100 µm. Photos: a and b. D.M. Britton, University of Guelph, 1992. Used with permission. Photos: c and d. P. Sokoloff.

become much larger, with maximum height ranging between 11 and 20 cm (COSEWIC 2019a).

Sporangia containing either megaspores or microspores and set into the adaxial side of the swollen leaf bases are covered by a partial velum (tissue membrane). Velum coverage is substantial (Figure 6), ranging from an estimated 60 to 75% (Eaton 1898) and calculated to average 60.4% (n = 27) in a representative Canadian subpopulation (our study). This is substantially greater than the range of velum coverage documented for *I. howellii* (typically 25–40%: Brunton *et al.* 2020) and substantially less than the 100% coverage of *I. nuttallii* and *I. orcuttii* (Pfeiffer 1922; Taylor *et al.* 1993).

Megaspores—The globose, white megaspores (Figure 5c,d) are small, even in comparison with most other North American diploids, ranging from 320 to 420 µm in diameter (Taylor *et al.* 2003) with megaspores of Canadian plants ranging from 384 to 424 µm with an average of 406.9 µm (SD 18.0 µm, n = 80, two subpopulations) in our study. Contrary to the low pattern of broad muri (walls) evident in *I. howellii* (Figure 5a,b), *I. minima* megaspores are more or less uniformly covered by short, blunt, narrow tubercles (Figure 5a–c).

A distinctive—indeed diagnostic—feature of *I. minima* is the megaspore equatorial ridge, which is conspicuously "beset with polished spinules," as stated by Eaton (1898: 30; Figure 5d). No other North American (or global?) *Isoetes* has such a feature (D.F.B. pers. obs. 2020).

Microspores—Eaton (1898) accurately described the minute, white (*en mass*) microspores as ranging from 26 to 31 µm in length (mean 29.67 µm, n = 20, *D.F. Brunton & K.L. McIntosh 17,243*, 28 June 2008, Salmo, BC [DFB]) and being sparsely papillose or

Figure 6. Columbia Quillwort (*Isoetes minima*) inner basal leaves showing partial (~ 65%) coverage of light tan-coloured sporangia; megaspores are evident through unmarked, translucent sporangium walls (29 June 2014, Lloyd's Meadow, British Columbia). Photo: R. Batten.

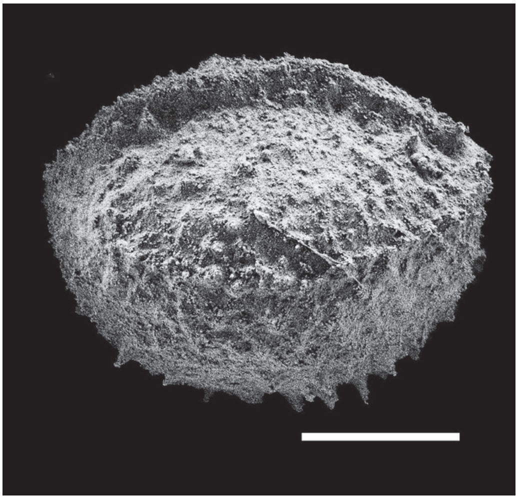


Figure 7. Columbia Quillwort (*Isoetes minima*) microspore (A. *Ceska & O. Ceska 19,754*, 30 June 1985, Ellenburg, Kittatis County, WA [DFB]). Scale bar = 10 µm. Photo: P. Sokoloff, August 2020.

coarsely echinate (Figure 7). Those of *I. howellii* are similar in size and ornamentation, but are somewhat more echinate. An apparently broad and conspicuous dorsal ridge on the latter may present a usefully distinctive feature in comparison to the inconspicuous and narrow dorsal ridge of *I. minima* microspores (Brunton *et al.* 2020), but this possibility requires further study.

Table 2 summarizes the distinctions between *I. minima* and the morphologically most similar taxa found in the Pacific northwest with which there could be confusion. Its most distinctive characteristics are its wet-meadow habitat, diminutive size, and unique megaspore ornamentation (particularly the diagnostic equatorial ridge feature).

Key—The following key to BC *Isoetes* species is based on mature plants with well formed (white, globose) megaspores. Data are from Britton and Brunton (1993, 1995, 1996) and the present study. Hybrids can be expected to occur sparingly in mixed populations of *Isoetes* and several have been described from BC (Britton and Brunton 1993, 1995, 1996). They are identified by spore size, cytology, and morphological features that are intermediate between their on-site putative parents. Sterile hybrids can be distinguished from fertile species (treated in the key) by their misshapened (not globose) form, variable (not uniform) size within a single sporangium, and spore ornamentation that expresses features of two (not a single) species.

1\. Spring to early summer (March–late June) maturing plants of ephemeral open vernal pools or seepage areas in upland forest glades or in shore meadows; megaspores 350–450 (500) µm in diameter **2**

– Summer to autumn (July [rarely late June]–September) maturing aquatic plants in permanently shallow to deep oligotrophic water of lakes, ponds, and rivers (or late-season emergent); megaspores 450–600 (720) µm in diameter **4**

2\. Velum coverage of sporangia complete (100%); megaspores with ± smooth ornamentation; in vernal pools along the Pacific coast ...... ***Isoetes nuttallii***

– Velum coverage of sporangia partial (25–75%); megaspores with ridged or tuberculate ornamentation; in forest glade seepages or shoreline meadows in interior **3**

3\. Short (<7 [rarely 15] cm tall) forest glade seepage plants; velum coverage of sporangia 60–75%; megaspores average 407 µm in diameter, ornamentation prominently densely tuberculate with diagnostic row of spinules along equatorial ridge; matures May and June in Canada .... ***Isoetes minima***

– Moderately (10–15 [rarely 30] cm) tall shore meadow plants; velum coverage of sporangia 25–40%; megaspores average 450 µm in diameter, ornamentation obscurely mounded or with broken

TABLE 2. Major morphological/ecological characteristics of Columbia Quillwort (*Isoetes minima*) and related taxa (particularly notable features in bold type); data from Cody and Britton (1989), Taylor *et al.* (1993), COSEWIC (2019a), Brunton *et al.* (2020), and the present study.

	Isoetes minima	Howell's Quillwort (*Isoetes howellii* Engelmann)	Orcutt's Quillwort (*Isoetes orcuttii* A.A. Eaton)	Nuttall's Quillwort (*Isoetes nuttallii* A. Braun ex Engelmann)
Habitat	Seasonal **seepage on bedrock slopes** with **unique** floristic associates	**Ephemeral wetlands** with widespread wetland associates	Ephemeral swales with **vernal pool** floristic associates	Ephemeral swales and vernal pools with **vernal pool** floristic associates
Plant size	**Exceptionally small** stature; **3–6 cm** (rarely to 20 cm)	Moderately robust; **10–15 cm** (up to 30 cm) long	Small stature; **<8 cm** long	Small to modest stature; **8–10 cm** (to 25 cm) long
Canadian distribution	Kootenay region	Interior west of Rocky Mountains	n/a	Pacific coast
Leaf form and colour	**Stiffly** erect; **green**	**Weak**, **arching to reflexed**; pale to **bright green**	Erect, **pliant**, pale green	Erect, **firm**, bright green
Velum coverage	60%	**25–40%**	100%	100%
Megaspores	Average 407 µm in diameter; densely fine-tuberculate pattern; **row of tubercles ("spinules") along equatorial ridge**	Average 450 µm; low, **broad anastomosing muri** or obscure mounds pattern; equatorial ridge plain	Average **320 µm**; smooth to obscurely tuberculate; equatorial ridge plain	Average 421 µm; smooth to tuberculate; equatorial ridge plain
Microspores	Smooth to coarsely low echinate; average ~30 µm long	Coarsely low echinate; average ~28 µm long	Smooth to papillose; 20–30 µm long	Papillose; 20–30 µm long

network of low muri; smooth-crested equatorial ridge; matures July (rarely late June)–August in Canada .... ***Isoetes howellii*** (in part)

4. Early summer (July [rarely late June]–August) maturing plants of shallow ponds and emergent shores; megaspores average 450 µm in diameter, ornamentation obscurely mounded or with broken network of low muri .... ***Isoetes howellii*** (in part)

– Mid-summer to late autumn (late July–September) maturing plants of deep to shallow permanent water (or mixed emergent-aquatic along shores in late season); megaspores >500 µm in diameter, ornamentation with pronounced echinate or ridged pattern **5**

5. Robust plants with thick, evergreen, dark green leaves in shallow to (typically) deep water; megaspores >600 µm in diameter, ornamentation coarsely papillate or with short muri in broken-reticulate pattern .... ***Isoetes occidentalis*** L.F. Henderson

– Plants thin to moderate, deciduous, bright to dull green leaves in shallow water (mixed emergent-aquatic in late season); megaspores <550 µm in diameter, with echinate ornamentation **6**

6. Bright green diploid plants with ascending to recurved leaves; megaspores 420–475 (510) µm in diameter, with densely echinate ornamentation of fine-tipped spines .... ***Isoetes echinospora*** M. Durieu

– Dull green to green tetraploid plants with ascending leaves; megaspores 500–550 (600) µm in diameter, with echinate ornamentation of thin tubercles and blunt-tipped spines .... ***Isoetes maritima*** L. Underwood

Discussion

We confirm that the obscure and long-overlooked lycophyte, *I. minima*, represents a distinct and rare native element of the North American flora. Its short growing season, small size, and isolated occurrences have resulted in limited investigations both in Canada and the United States (the furthest south population being within 800 km of the Canadian border). Accordingly, our understanding of basic aspects of its natural history, such as physical size, limitations to morphological variation, reproductive potential, and distributional vectors, are based on relatively limited data gathered over a short period (several decades). Many of the detailed morphological and ecological characteristics of this rare lycophyte, for example, are documented for the first time in our present study. As well, only preliminary genetic information is available concerning its relationship with associated species. Is it an ancient relict species or a newly developed evolutionary "experiment"? That and similar origin and relationship questions remain to be answered.

The four known Canadian subpopulations (Figure 4) constitute just over a quarter of the species' total global occurrences. Accordingly, the long-term stability and security of Canadian subpopulations of this Columbia Region endemic is of significant importance to the global survival of the species. Maintaining the rare pocket meadow seepage habitat is fundamental to the sustainability of this species as well as the other Species At Risk and regionally significant taxa that are entirely contained within it. The lack of suitable habitat across the landscape coupled with limited dispersal mechanisms is likely the cause for the rarity of *I. minima*.

Maintaining the ecological integrity of the habitat will require protecting upslope hydrology, limiting encroachment by trees and shrubs into the pocket meadows, and preventing the further spread of invasive, non-native plants. All of the known subpopulations are on provincial Crown land, which precludes impacts associated with land development (COSEWIC 2019a). However, Crown land remains subject to threats associated with recreational activities, logging, invasive species, and fire suppression.

All known subpopulations in Canada are accessible to the public and subject to varying levels of use. Fairview Meadow is a mountain biking area and near active all-terrain vehicle trails; bike tracks were observed within several metres of *I. minima* (COSEWIC 2019a). A new housing development adjacent to the site may increase future recreational impacts. Biking and hiking activities trample plants or can dislodge soil, trails can alter hydrology by diverting water flow from seepage areas, and tires and shoes can introduce and spread invasive non-native plants (COSEWIC 2019a). Recreational activities are more likely to create channels that increase water flow either by flooding or by drying the habitat, rather than expanding the seepage areas. Such activities in small amounts, however, may also create habitat by dispersing spores, decreasing competition from vascular plants, and altering hydrology in ways that could transport megaspores to new habitats.

Logging was planned for at least one of the sites; however, the logging company is now aware of the presence of rare species on the site. The company has agreed to leave a buffer of 30 m beside and below the meadow and any harvesting upslope will involve a detailed drainage plan using Lidar data to ensure that the hydrology of the site is not impacted (G. Cordeiro pers. comm. 18 July 2018). Logging and road building, even in areas adjacent to open meadows, can alter hydrology and erode the thin soils, damaging seepage areas (COSEWIC 2019a). The presence of heavy equipment in nearby areas can also spread invasive plants.

Non-native invasive plants, most notably Spotted Knapweed (*Centaurea stoebe* L.), are present at all sites. Although knapweed plants are small while *I. minima* is producing sporangia, later in the season knapweed dominates all Canadian sites. Knapweed may cause premature drying of seepages, potentially reducing reproductive success and rendering the habitat unsuitable for *I. minima* (COSEWIC 2019a).

The role of wildfire in maintaining the open pocket meadow habitat is unclear (COSEWIC 2019a). Imagery over the last 10 years shows shrub and tree encroachment along the edge of pocket meadow habitat. However, the specialized habitat has likely always been uncommon on the landscape limiting the distribution of *I. minima*. Encroachment may decrease the habitat available to *I. minima* by shading, while tree and shrub roots may absorb seepage flow and alter hydrology. With the increased fuel loading associated with decades of fire suppression, future wildfires may be more severe and may degrade habitat by causing erosion and altering hydrology (COSEWIC 2019a).

Isoetes minima will be impacted by climate change. Climate model projections (Pacific Climate Impacts Consortium's statistically downscaled climate scenarios) for the Kootenay Region suggest temperatures will increase across all seasons and all elevations, with worst-case scenarios predicting an increase in the average annual temperature of 1.6°C in the 2020s, 3.2°C in the 2050s, and 5.3°C by the 2080s (BC Agriculture and Food Climate Action Initiative 2019). Predictions suggest an increase in overall annual precipitation, with more extreme precipitation events, and a decrease in precipitation during the summer season (BC Agriculture and Food Climate Action Initiative 2019). Increased winter precipitation (coupled with warmer temperatures) is predicted to fall as rain rather than snow, resulting in decreased snowpack, more rapid snowmelt, and further reducing spring and summer flows (Province of BC 2016). These climatic changes are likely to reduce flow to seepages and may cause earlier drying of the habitat. If the window between snow melt and seepage drying is compressed, *I. minima* may not have sufficient time to produce mature sporophytes. Changes to flow patterns (decreased flow or extreme rain events) may interfere with effective spore dispersal.

Predicted climate changes may also result in an increased risk of wildfire, larger fluctuations of unpredictable seasonal conditions, and more extreme heat events (Province of British Columbia 2016; BC Agriculture and Food Climate Action Initiative 2019). All of these could potentially have a negative impact on *I.*

minima subpopulations.

From the limited surveys we conducted, at least three of the four Canadian subpopulations of *I. minima* appear to be self-sustaining because previously documented subpopulations have persisted for almost 25 years. A lack of previous rigorous plant counts, however, makes long-term population trends impossible to determine at present.

Although it appears that *I. minima* in Canada is currently self-sustaining, and other subpopulations could be found in the southern interior of BC, subpopulations of the species will always be vulnerable to declines resulting from direct or inadvertent human activity. To minimize the potential harm and loss from such negative impacts and to maximize the potential for recovery and sustainability, more knowledge of the natural history of this species is required. Further research is necessary to determine how *I. minima* and other associated rare species disperse to such isolated habitats within large stretches of unsuitable terrain. More information is required to understand whether *I. minima* is susceptible to impact from invading non-native plants and how invasive plants might alter hydrology. Further surveys and monitoring are essential for determining natural population fluctuations over time and to document other potential occurrences. Further research to understand taxonomic relationships, particularly with the closely related species *I. howellii* and *I. nuttallii,* will also help illuminate the diversity of *Isoetes* species globally and inform our understanding of evolutionary radiation and relationships in the genus.

Author Contributions

Conceptualization: C.Y.M.; Data Gathering & Curation: C.Y.M., R.B., and D.F.B.; Methodology: C.Y.M., D.F.B., R.B., and P.C.S.; Documentation Review: C.Y.M., D.F.B., R.B., and P.C.S.; Data Analysis: C.Y.M., D.F.B., and R.B.; Microscopic Imagery: P.C.S. and D.F.B.; Writing – Original Draft: C.Y.M.; Writing – Revision & Editing: C.Y.M., D.F.B., R.B., and P.C.S.; Cartography: P.C.S.

Acknowledgements

Our thanks to Frank Lomer (Vancouver, British Columbia [BC]), Hans Roemer (Victoria, BC), and Adolf Ceska (Victoria, BC) for sharing data and insights from their field investigations of *Isoetes minima* and related species in Canada and the adjacent United States. We also appreciate the cooperation and assistance of curators and collection managers in the examination of herbarium specimens under their care. We thank Walter Fertig (Washington Natural Heritage Program), Lynn Kinter (Idaho Natural Heritage Program), and Sue Vrilakas (Oregon Biodiversity Information Center) for providing information on the distribution of *I. minima* in the United States. This investigation benefited significantly from access to the extensive *Isoetes* SEM library of the late D.M. Britton (University of Guelph, Guelph, Ontario) who authorized the review and application of those images in various research projects. D.F.B. was aided during some of his field investigations, as always, by the expert observational skills of Karen L. McIntosh of Ottawa, Ontario. Thanks to Jenifer Penny for providing communication from Gerald Cordeiro regarding Kalesnikoff Timber plans for Lloyd's Meadow.

Notice: Some of the information used in this document is Crown Copyright, compiled on behalf of COSEWIC under a contract with Environment and Climate Change Canada. However, comments or conclusion made by the authors using this information do not necessarily reflect the opinions of Environment and Climate Change Canada or COSEWIC.

Literature Cited

BC Agriculture and Food Climate Action Initiative. 2019. Kootenay & boundary. Regional adaptation series. BC Agriculture and Climate Change, Victoria, British Columbia, Canada. Accessed 22 June 2020. https://www.bcagclimateaction.ca/wp/wp-content/media/RegionalStrategies-KootenayBoundary.pdf.

BC Conservation Data Centre. 2017. CDC occurrence 106021 — Columbia Quillwort. Ministry of Environment, Victoria, British Columbia, Canada. Accessed 15 May 2020. http://maps.gov.bc.ca/ess/hm/cdc/?attributeSearch=767,SHAPE_ID,106021.

BC Conservation Data Centre. 2020. BC species and ecosystems explorer. Ministry of Environment, Victoria, British Columbia, Canada. Accessed 15 May 2020. http://a100.gov.bc.ca/pub/eswp/.

BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development. 2018. BEC [Biogeoclimatic ecosystem classification] map (version 11). Forest Analysis and Inventory, Government of British Columbia, Victoria, British Columbia, Canada. Accessed 5 May 2020. https://catalogue.data.gov.bc.ca/dataset/f358a53b-ffde-4830-a325-a5a03ff672c3.

Britton, D.M., and D.F. Brunton. 1993. *Isoetes ×truncata*: a newly considered pentaploid hybrid from western North America. Canadian Journal of Botany 71: 1016–1025. https://doi.org/10.1139/b93-117

Britton, D.M., and D.F. Brunton. 1995. *Isoetes ×marensis*, a new interspecific hybrid from western Canada. Canadian Journal of Botany 73: 1345–1353. https://doi.org/10.1139/b95-146

Britton, D.M., and D.F. Brunton. 1996. *Isoetes ×pseudotruncata*, a new triploid hybrid from western Canada and Alaska. Canadian Journal of Botany 74: 51–59. https://doi.org/10.1139/b96-008

Britton, D.M., and J.P. Goltz. 1991. *Isoetes prototypus*, a new diploid species from eastern Canada. Canadian Journal of Botany 69: 277–281. https://doi.org/10.1139/b91-037

Brunton, D.F., and D.M. Britton. 2006. *Isoetes ×novae-angliae* (Isoetaceae), an additional hybrid quillwort from New England. Rhodora 108: 228–241. https://doi.org/10.3119/0035-4902(2006)108[228:iniaah]2.0.co;2

Brunton, D.F., M.A. Krichbaum, R.S. Krichbaum, and P.C. Sokoloff. 2020. Distribution and status of Howell's Quillwort (*Isoetes howellii*, Isoetaceae) in Canada and its relation to Bolander's Quillwort (*Isoetes bolanderi*). Canadian Field-Naturalist 134: 252–264. https://doi.org/10.22621/cfn.v134i3.2509

Brunton, D.F., P.C. Sokoloff, J.F. Bolin, and D.F. Fraser. 2019. *Isoetes laurentiana*, sp. nov. (Isoetaceae) endemic to freshwater tidal marshes in eastern Quebec, Canada. Botany 97: 571–583. https://doi.org/10.1139/cjb-2019-0037

Brunton, D.F., and A. Troia. 2018. Global review of recent taxonomic research into *Isoetes* (Isoetaceae), with implications for biogeography and conservation. Fern Gazette 20: 309–333.

Ceska, A. 2001. *Isoetes minima* A.A. Eaton (Isoetaceae): an overlooked terrestrial quillwort of the Pacific northwest. Botanical Electronic News 269, 2 June. Accessed 22 June 2020. https://www.ou.edu/cas/botany-micro/ben/ben269.html.

Cody, W.J., and D.M. Britton. 1989. Ferns and Fern Allies of Canada. Publication 1829/E. Research Branch, Agriculture Canada, Ottawa, Ontario, Canada. https://doi.org/10.5962/bhl.title.53784

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2019a. COSEWIC assessment and status report on the Columbia Quillwort (*Isoetes minima*) in Canada. COSEWIC, Ottawa, Ontario, Canada.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2019b. COSEWIC assessment and status report on the Dwarf Hesperochiron (*Hesperochiron pumilus*) in Canada. COSEWIC, Ottawa, Ontario, Canada.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2019c. COSEWIC assessment and status report on the Hairy Paintbrush (*Castilleja tenuis*) in Canada. COSEWIC, Ottawa, Ontario, Canada.

Demarchi, D.A. 2011. An introduction to the ecoregions of British Columbia. Ecosystem Information Section, Ministry of Environment, Victoria, British Columbia, Canada. Accessed 25 August 2020. https://tinyurl.com/yach7c8n.

Eaton, A.A. 1898. *Isoetes minima* n. sp. Fern Bulletin 6: 30.

Freund, F.D., W.A. Freyman, and C.J. Rothfels. 2018. Inferring the evolutionary reduction of corm lobation in *Isoëtes* using Bayesian model-averaged ancestral state reconstruction. American Journal of Botany 105: 1–12. https://doi.org/10.1101/212316

Klinkenberg, B. 2020 [continuously updated]. *Isoetes*, in E-flora BC: electronic atlas of the flora of British Columbia. Lab for Advanced Spatial Analysis, Department of Geography, University of British Columbia, Vancouver, British Columbia, Canada. Accessed 8 June 2020. https://tinyurl.com/2f57rk9j.

Larsén, E., and C. Rydin. 2016. Disentangling the phylogeny of *Isoetes* (Isoetales) using nuclear and plastid data. International Journal of Plant Sciences 177: 157–164. http://doi.org/10.1086/684179

NatureServe. 2004. Habitat-based plant element occurrence delimitation guidance. *In* Biotics5 Online Help. NatureServe, Arlington, Virginia, USA. Accessed 6 July 2020. https://tinyurl.com/465d58d5.

NatureServe. 2020. NatureServe Explorer, version 7.1. NatureServe, Arlington, Virginia, USA. Accessed 10 August 2020. http://explorer.natureserve.org.

Pfeiffer, N.E. 1922. Monograph of the Isoetaceae. Annals of the Missouri Botanical Garden 9: 79–233. https://doi.org/10.2307/2990000

Pigg, K.B. 2001. Isoetalean lycopsid evolution: from the Devonian to the present. American Fern Journal 91: 99–114. https://doi.org/10.1640/0002-8444(2001)091[0099:ileftd]2.0.co;2

Province of BC. 2016. Adapting natural resource management to climate change in the Kootenay Boundary Region: considerations for practitioners and government staff. Government of British Columbia, Victoria, British Columbia, Canada. Accessed 22 February 2020. https://tinyurl.com/cssf7p3w.

Schafran, P.W. 2019. Molecular systematics of *Isoëtes* (Isoëtaceae) in eastern North America. Ph.D. thesis, Old Dominion University, Norfolk, Virginia, USA. https://doi.org/10.25777/37tg-7846

Shorthouse, D.P. 2010. SimpleMappr, an online tool to produce publication-quality point maps. Accessed l5 July 2020. https://www.simplemappr.net.

Taylor, T.M.C. 1970. Pacific Northwest Ferns and Their Allies. University of Toronto Press, Toronto, Ontario, Canada.

Taylor, W.C., N.T. Luebke, D.M. Britton, R.J. Hickey, and D.F. Brunton. 1993. Isoetaceae. Pages 64–75 *in* Flora of North America North of Mexico, Volume 2: Pteridophytes and Gymnosperms. *Edited by* Flora of North America Editorial Committee. Oxford University Press, New York, New York, USA.

Taylor, W.C., N.T. Luebke, and A.R. Lekschas. 2003. Taxonomic status and evolutionary relationship of *Isoetes minima* A.A. Eaton (Isoetaceae) based on nuclear ribosomal DNA internal transcribed spacer sequences. Botanical Electronic News 304: 6 March. Accessed 16 July 2020. https://www.ou.edu/cas/botany-micro/ben/ben304.html.

Thiers, B. 2020 [continuously updated]. Index herbariorum. New York Botanical Garden, Bronx, New York, USA. Accessed 20 July 2020. http://sweetgum.nybg.org/science/ih/.

Troia, A., J.B. Pereira, C. Kim, and W.C. Taylor. 2016. The genus *Isoetes* (Isoetaceae): a provisional checklist of the accepted and unresolved taxa. Phytotaxa 277: 101–145. https://doi.org/10.11646/phytotaxa.277.2.1

Wood D., G. Besnard, D.J. Beerling, C.P. Osborne, and P.A. Christin. 2020. Phylogenomics indicates the "living fossil" *Isoetes* diversified in the Cenozoic. PLoS ONE 15: e0227525. https://doi.org/10.1371/journal.pone.0227525

Received 10 September 2020
Accepted 21 July 2021
Associate Editor: J.M. Saarela

The Canadian Field-Naturalist

Abundance and arboreal tendencies of slugs in forested wetlands of southwestern Nova Scotia, Canada

Hugo Reis Medeiros[1,*], **John E. Maunder**[2], **Sean Haughian**[1, 3], and **Karen A. Harper**[1]

[1]Biology Department, Saint Mary's University, Halifax, Nova Scotia B3H 3C3 Canada
[2]P.O. Box 250, Pouch Cove, Newfoundland and Labrador A0A 3L0 Canada
[3]Nova Scotia Museum, Halifax, Nova Scotia B3H 3A6 Canada
[*]Corresponding author: hugo.medeiros.r@gmail.com

Medeiros, H.R., J.E. Maunder, S. Haughian, and K.A. Harper. 2021. Abundance and arboreal tendencies of slugs in forested wetlands of southwestern Nova Scotia, Canada. Canadian Field-Naturalist 135(3): 305–316. https://doi.org/10.22621/cfn.v135i3.2677

Abstract

Non-native slugs, such as *Arion*, are becoming a concern for land managers in Nova Scotia, Canada, particularly in forested wetlands. They appear to have a highly diverse diet and may pose a particular risk to native slug species and to rare or at-risk lichens. We provide novel information on the distribution, abundance, arboreal tendencies, and seasonality of slugs in forested wetlands across southwestern Nova Scotia. We collected a total of 402 slugs representing seven species including two native species, Pale Mantleslug (*Pallifera dorsalis*) and Meadow Slug (*Deroceras laeve*), and five non-native *Arion* taxa. The three most abundantly caught taxa were Northern Dusky Arion (*Arion fuscus*), *D. laeve*, and Western Dusky Slug (*Arion subfuscus*). *Arion fuscus* and *D. laeve* were collected on the forest floor and on lichen-bearing trees, while *A. subfuscus* was collected only on the ground. All three taxa showed differences in collectability between July and September and low arboreal tendencies. We highlight that further studies are needed to better understand the biology and ecology of this largely neglected invertebrate group that seems to be dominated by non-native *Arion* species in the study region. Such information is crucial for conservationists and forest managers untangling the question of how non-native slugs affect native slug taxa and other groups including at-risk lichens.

Key words: *Arion fuscus*; biodiversity conservation; biological invasion; forested wetlands; slug community

Introduction

Gastropods are an ecologically important invertebrate group that constitute a considerable proportion of the forest floor biomass in northern forests (Hawkins *et al*. 1997; Jordan and Black 2012). They are important decomposers of forest litter, contributing directly to soil formation and nutrient recycling (Jennings and Barkham 1979; Oli and Gupta 2000; Meyer *et al*. 2013), and are important sources of food and calcium for several animal groups including invertebrates (Symondson *et al*. 2002) and birds and small mammals (Allen 2004). They also play a significant role in the dispersal of vascular plants (Lanta 2007), bryophytes (Boch *et al*. 2014), lichens (Boch *et al*. 2016), and even some small animals (Türke *et al*. 2018), mainly through endozoochory (i.e., dispersal of propagules via gut passage; McCarthy and Healy 1978; Boch *et al*. 2011). However, such roles may be significantly altered where non-native gastropods invade ecosystems (Buschmann *et al*. 2005; Holland *et al*. 2007; Strauss *et al*. 2009).

Biological invasions typically proceed in three steps: introduction, initial establishment, and subsequent spread (Robinson 1999; Suarez *et al*. 2001; Diez *et al*. 2008). Over any significant distance, such invasions are usually human-mediated (Hobbs 2000; Cowie and Robinson 2003; Ding *et al*. 2008; Capinha *et al*. 2015). Non-native slugs have become increasingly serious agricultural pests in most European countries where they are responsible for significant economic losses (Runham and Hunter 1970; Castillejo *et al*. 1996; Kozłowski 2012) and have serious negative impacts on natural biodiversity (Blattmann *et al*. 2013; Zemanova *et al*. 2018). Such effects are steadily becoming a worldwide problem. Since the arrival of Europeans in North America, several non-native slugs including a number of *Arion* species (Nekola 2014; Zemanova *et al*. 2018) have become distributed across the continent (even a coarse estimate of the number of taxa involved is difficult to determine because it depends upon varying interpretations of species complexes and cryptic taxa). Some of these slugs have become a great concern for land managers (Hammond and Byers 2002; Hahn *et al*. 2011). In Nova Scotia, Canada, non-native slugs are generally thought to increase grazing pressure on rare and at-risk lichens such as the Endangered Atlantic population of Boreal Felt Lichen (*Erioderma pedicellatum*; Cameron 2009; COSEWIC 2014; SARA Registry 2021). However, the prevalence and severity of slug grazing on lichen communities have not been well documented in North America.

In general, slugs have not been widely studied in North America and most of what we assume about their biology and ecology has been extrapolated from studies of non-native slugs in European agricultural environments (South 1992). Indeed, the ecological functioning of non-native slugs in agricultural landscapes in Europe may not be similar to that seen in forested landscapes in Atlantic Canada. Our aim is to provide new information on the occurrence, distribution, relative abundance, arboreal tendencies, and seasonality of slug species across forested wetlands in southwestern Nova Scotia. Such information is crucial for helping conservationists and forest managers to better conserve native biodiversity in Atlantic Canada.

Methods

Study sites

Slugs were collected in eight mixed-wood forested wetland sites (intact stands ≥6 ha that had not been harvested for at least 100 years) in southwestern Nova Scotia (Figure 1). Overall, southwestern Nova Scotia has a humid temperate maritime climate with mean daily temperatures of –5.5°C in January and 18.5°C in July and with annual average precipitation of 1350 mm with >80% as rain (Environment Canada 2017). The area falls within the Acadian Forest Region, which is characterized by abundant Red Spruce (*Picea rubens* Sargent), Balsam Fir (*Abies balsamea* L.), Yellow Birch (*Betula alleghaniensis* Britton), and maple (*Acer* spp.) trees (Rowe 1972). However, our study sites, chosen specifically for their association with rare lichens, are instead dominated by Red Maple (*Acer rubrum* L.), Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh), and Balsam Fir. Soils are poorly drained (remain wet all year) and support a dense cover of *Sphagnum* spp. and Cinnamon Fern (*Osmundastrum cinnamomeum* (L.) C. Presl). The study sites were chosen primarily

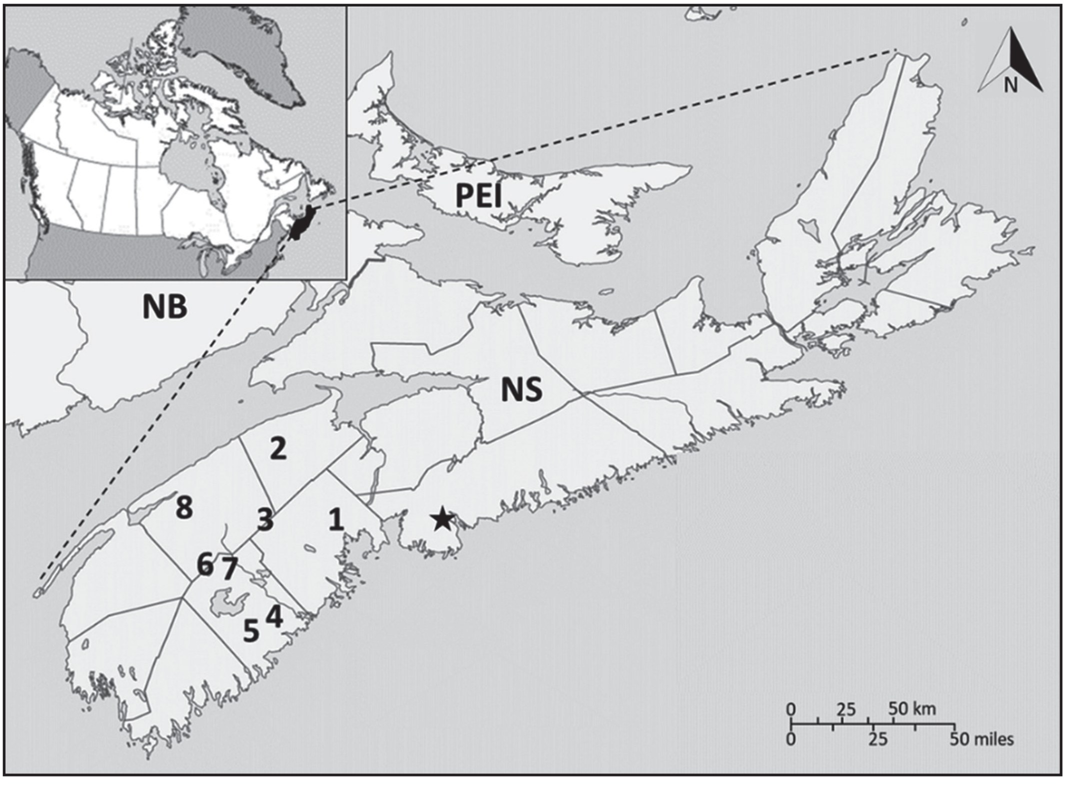


Figure 1. Location of slug study sites in Nova Scotia. The black star indicates Halifax. Sites are indicated by numbers. NS = Nova Scotia, NB = New Brunswick, PEI = Prince Edward Island.

for a long-term study on lichen community dynamics as they relate to logging and its interaction with slug grazing (S.H. and K.A.H. unpubl. data). Criteria for selecting study sites included: (a) presence of Red Maple and lowland-associated tree species in the canopy, according to provincial forest inventory data (Province of Nova Scotia 2021), (b) an intact forested portion of at least 6 ha, and (c) an estimated depth to water table of <0.5 m (Province of Nova Scotia 2007).

Slug surveys

Slugs were collected using pitfall traps. Initially we set out 224 traps in eight wetland forested sites. At each site, there were seven 5 × 50 m plots spaced 20 m apart with three tree traps (one trap per tree on canopy-height Red Maple; Figure 2) and one ground trap (1 m away from one of the trees) in each of the seven plots (8 sites × 7 plots × 4 traps = 224 traps). We had more tree traps than ground traps because we were more interested in potentially arboreal species, a requirement for grazing on epiphytic lichens. The efficacy of our tree pitfall traps was unknown compared with ground pitfall traps and cardboard sheet traps, which have been commonly used in previous studies of terrestrial slugs (e.g., Moss and Hermanutz 2010; Rodriguez-Cabal *et al*. 2015; Lucid *et al*. 2018; De Smedt *et al*. 2019). In addition to the initial 224 traps set out within the eight forested wetland study sites, we also placed one pitfall trap on the ground in an adjacent clearcut area to determine if additional species were present in the disturbed areas around these wetland forested sites.

All traps consisted of 100 ml plastic specimen jars (6 cm diameter openings), baited with ~20 ml of Budweiser beer (Anheuser-Busch, LLC [USA]/Labatt Brewing Company [Canada]). Pitfall traps on the ground were pressed into the duff layer and covered with a 30 × 20 cm cardboard sheet that acted as a protective roof. Slugs accessed the ground pitfall traps through a gap of at least 1.5 cm between the cardboard and the trap. Pitfall traps on trees were suspended from the rim of a wide hole in the bottom of a wooden box (15 × 15 × 20 cm) affixed to a tree trunk ~1.3 m above the ground (Figure 2). The inner side of each box was open to the tree trunk and positioned carefully so as to frame a targetted lichen thallus, most often Tree Lungwort (*Lobaria pulmonaria*). The outer side of the box swung open to allow collector access to the enclosed pitfall trap. A gap of 1.5 cm was provided between the inner edges of the wooden box and the bark of the tree to allow slugs to enter the box.

Trapping took place over two time periods in 2019: 11–29 July (19 days) and 23–27 September (five days). In July, the traps were typically emptied after nine days, allowing for two separate collecting events during the 19-day collection period. In September, there was only a single collecting event lasting five consecutive days. Once collected, the specimens were preserved in 70% ethanol.

Slugs were identified to the lowest taxonomic level practical by J.E.M. using standard references including, but not limited to Chichester and Getz (1973), Davies (1977, 1979), De Wilde (1983), De Winter (1984), Backeljau and Marquet (1985), Backeljau and van Beeck (1986), Backeljau and de Bruyn (1988), Garrido *et al*. (1995), Pinceel *et al*. (2004), Skujienė (2004), Jordaens *et al*. (2006), Rowson *et al*. (2014a,b), and Gural-Sverlova and Gural (2015). It should be noted that slug taxonomy is still very much in a state of flux. In recent years, ongoing refinements in both morphological and molecular knowledge have contributed to increasingly defensible species descriptions and delineations. However, these same refinements have also contributed to the discovery of many new "cryptic species" (two or more species formerly "classified as a single nominal species because they are at least superficially morphologically indistinguishable" [Bickford *et al*. 2007: 149]), and "genetically-defined forms", both of which are very difficult, if not impossible, to distinguish using traditional morphological methods.

All slugs resembling either "*Arion fuscus*" or "*Arion subfuscus*" were dissected and subsequently assigned to one of these two taxa on the basis of their distinct gonad morphologies (Garrido *et al*. 1995; Pinceel *et al*. 2004; Jordaens *et al*. 2006; Rowson *et al*. 2014b; Gural-Sverlova and Gural 2015). However, each of these two taxa has been found to include multiple cryptic forms (Pinceel *et al*. 2004, 2005a,b; Rowson *et al*. 2014a), so each should more properly be thought of as a "species complex" or a "species aggregate". Gastropod voucher specimens have been deposited in the Natural History collections of the Nova Scotia Museum in Halifax, Canada (accession number N020-018).

Statistical analyses

We compared specimen counts between tree and ground traps from the forested wetlands using a Mann-Whitney *U*-test in the software PAST (Hammer *et al*. 2001). The Mann-Whitney *U*-test is a non-parametric alternative used to examine significant differences between two groups of single variables with no specific distribution (McKnight and Najab 2010). Although the total number of traps was initially 224, several traps were damaged or destroyed by wildlife in both months and on both substrates. Moreover, the number of sampling days varied among study sites and the number of traps varied between substrates (168 tree and 56 ground traps). Therefore, for a fair comparison between trap types across study sites we

FIGURE 2. A tree trap used to collect slugs on lichen trees in southwest Nova Scotia. A plastic jar baited with beer was placed in the bottom of the trap. The inner side of the box was open, against the tree trunk. The outer side of the box served as a door to retrieve collected slugs and to rebait the traps.

used the number of slugs per trap per sampling day (x):

$$x = \frac{y}{ji}$$

where for each site, y = number of slugs, j = number of days traps were baited, and i = number of traps. We included all active traps including intact traps with zero slugs, but damaged and inactive traps were excluded. The number of undamaged traps was 165 in July and 152 in September.

We also performed a Mann-Whitney *U*-test to compare the occurrence of slug species between forested wetlands and adjacent clearcuts. For this analysis, we used the number of slugs per trap per sampling day in both forest and clearcut habitats. Only ground traps were used in this analysis.

Results

We collected 315 slugs in the forested wetlands (Table 1) and 87 slugs in adjacent clearcut areas (Table 2), for a total of 402 slugs of seven species. Of these seven, only two, Pale Mantleslug (*Pallifera dorsalis*; Nearctic) and Meadow Slug (*Deroceras laeve*; Holarctic) are native to North America, whereas the other five species are non-native *Arion* species: Northern Dusky Arion (*Arion fuscus*), Western Dusky Slug (*Arion subfuscus*), Forest Arion (*Arion* (*Carinarion*) cf. *silvaticus*), Orange-banded Arion (*Arion* (*Carinarion*) cf. *fasciatus*), and Dark-face Arion (*Arion* cf. *distinctus*). (Note: common names from Turgeon *et al.* [1998] except for dusky slugs and Northern Dusky Arion from Rowson *et al.* [2014b].) Although the single specimen of *Arion* (*Carinarion*) cf. *fasciatus* and the two specimens of *Arion* (*Carinarion*) cf. *silvaticus* were clearly members of the *Arion* (*Carinarion*) complex, they were in poor condition when examined and could therefore not be identified with certainty. The same should be noted for the single specimen of *Arion* cf. *distinctus*.

Arion fuscus was present in all eight forested wetland sites and was the most abundant taxon, representing half of all slugs collected. *Deroceras laeve* was also present in all forested wetland sites. However, *A. subfuscus* was present in only two forested wetland sites (Table 1) and in an additional adjacent clearcut (site 8; Table 2). Together, these three species represented the vast majority of slugs caught in both forested wetlands (Table 1) and adjacent clearcuts (Table 2). More *A. fuscus* and *A. subfuscus* were caught in July than in September in both forested wetland and adjacent clearcuts, whereas *D. laeve* showed the opposite pattern in forested wetlands, with more being caught in September than in July (Table 1). The exception was site 1 where 20 individuals were collected in July and only three were collected in September (Table 1). A total of six *D. laeve* were caught in adjacent clearcuts (Table 2). Of the two uncommon taxa, *A.* cf. *distinctus* was caught at a single forested wetland in July, while single *A.* cf. *silvaticus* were caught in both July and September in the same forested wetland site as was *A.* cf. *distinctus* (Table 1); neither species was caught in adjacent clearcuts (Table 2). Fifty-seven of the 66 individuals of *A. fuscus* and all individuals of *A. subfuscus*, *P. dorsalis*, and *A.* cf. *fasciatus* found in clearcuts were collected in July.

In forested wetlands, we recorded the native species *D. laeve* and the four non-native *Arion* species:

TABLE 1. Numbers for each species of slug caught at each of the eight forested wetland sites in July/September in southwest Nova Scotia. The number in each cell is total number of individuals per month for July/September, whereas the numbers in parenthesis are the total number of individuals collected per species summing all individuals collected in all the eight sites and in both months. Exact locations of the trapping sites are available upon request for approved users.

Slug species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Total
Arion cf. *distinctus* (Mabille, 1868), Dark-face Arion	1/0	—	—	—	—	—	—	—	1/0 (1)
Arion fuscus (O.F. Müller, 1774), Northern Dusky Arion	16/6	9/2	3/0	2/0	6/5	32/5	33/10	1/6	102/34 (136)
Arion subfuscus (Draparnaud, 1805), Western Dusky Slug	78/4	—	—	—	—	—	—	0/1	78/5 (83)
Arion (*Carinarion*) cf. *fasciatus* (Nillson, 1823), Orange-banded Arion	—	—	—	—	—	—	—	—	—
Arion (*Carinarion*) cf. *silvaticus* Lohmander, 1837, Forest Arion	1/1	—	—	—	—	—	—	—	1/1 (2)
Deroceras laeve (O.F. Müller, 1774), Meadow Slug	20/3	0/2	0/2	0/1	1/12	6/18	1/10	2/15	30/63 (93)
Pallifera dorsalis (A. Binney, 1842), Pale Mantleslug	—	—	—	—	—	—	—	—	—
Total	130	13	5	3	24	61	54	25	315

TABLE 2. Numbers for each species of slug caught in adjacent clearcuts in July/September in southwest Nova Scotia. Similar to Table 1, the column "Total" is the total number of individuals per month July/September and the numbers in parenthesis are the total number of individuals collected in all the eight sites and in both months.

Slug species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Total
Arion cf. *distinctus* (Mabille, 1868), Dark-face Arion	—	—	—	—	—	—	—	—	—
Arion fuscus (O.F. Müller, 1774), Northern Dusky Arion	—	11/4	3/0	—	4/1	7/0	1/0	31/4	57/9 (66)
Arion subfuscus (Draparnaud, 1805), Western Dusky Slug	5/0	—	—	—	—	1/0	—	5/0	11/0 (11)
Arion (*Carinarion*) cf. *fasciatus* (Nillson, 1823), Orange-banded Arion	—	—	—	—	—	—	—	1/0	1/0 (1)
Arion (*Carinarion*) cf. *silvaticus* Lohmander, 1837, Forest Arion	—	—	—	—	—	—	—	—	—
Deroceras laeve (O.F. Müller, 1774), Meadow Slug	1/0	1/0	—	—	0/1	1/0	1/0	0/1	4/2 (6)
Pallifera dorsalis (A. Binney, 1842), Pale Mantleslug	—	—	—	—	—	2/0	1/0	—	3/0 (3)
Total	6	16	3	0	6	11	3	42	87

A. fuscus, *A. subfuscus*, *A.* (*Carinarion*) cf. *silvaticus*, and *A.* cf. *distinctus*. *Arion fuscus* was the dominant species followed by, in order, *D. laeve* and *A. subfuscus*. *Arion fuscus, A.* cf. *silvaticus*, and *D. laeve* were caught on both the "tree" and the "ground" substrates. The abundance of *A. fuscus* was higher in ground traps (117 individuals) than in tree traps (19) with significant differences found between substrates (using the number of slugs per trap per sampling day) for July ($U = 7$; $P < 0.005$) and September ($U = 9$; $P < 0.004$; Table 3). *Deroceras laeve* was numerically more abundant in ground traps (81 individuals) than in tree traps (12), however significant differences between substrates were observed only in September ($U = 4$; $P < 0.001$; Table 3). *Arion subfuscus* and *A.* cf. *distinctus* were collected exclusively in ground traps.

In clearcuts, we collected a total of 87 slugs of five species: two native species *D. laeve* and *P. dorsalis*, and three non-native *Arion* species: *A. fuscus*, *A. subfuscus*, and *A.* (*Carinarion*) cf. *fasciatus* (Table 2). For *A. fuscus* (the only species that showed high abundance in both forested wetlands and adjacent clearcuts and which was, overall, the most numerous species caught), habitat comparisons were restricted to July because of very low capture rates in September. We did not find a significant difference in the abundance of *A. fuscus* between forested wetlands and adjacent clearcuts ($U = 23$; $P < 0.366$; ground traps only). We collected the most slugs and the most species of slugs in sites 1 and 8 (Tables 1 and 2).

Discussion

Understanding the life span and temporal cycles of reproduction is critical to making sense of the biology and ecology of slugs. Of the seven slug taxa we recorded, the three species that were commonly caught (*A. fuscus*, *D. laeve*, and *A. subfuscus*) varied in the number of captures between July and September. More *A. fuscus* and *A. subfuscus* were caught in July, while more *D. laeve* were caught in September in seven of the eight study sites. The lower numbers of *A. subfuscus* caught in July supports the generally held view that *A. subfuscus* adults lay eggs during late summer or early fall and die soon afterwards. This slug has a life span of less than one year and overwinters either as eggs or as newly hatched young (Taylor 1907; Barnes and Weil 1945; Ord and Watts 1949; Bett 1960; Chichester and Getz 1973; Jennings and Barkham 1975; Bless 1977; Beyer and Saari 1978; Hutchinson *et al*. 2017). The lower numbers of *A. fuscus* in July suggests a life cycle generally similar to that of *A. subfuscus*. Unfortunately, there appear to be no published seasonal data for slugs identified as *A. fuscus*—a taxon long confused with *A. subfuscus*.

In contrast with *Arion* spp., *D. laeve* was more abundantly caught in September. However, it is difficult to infer a seasonal pattern for this species because it has a life span of less than one year (Faberi *et al*. 2006; Mohamed and Ali 2011) and lays eggs continuously after maturity (Chichester and Getz 1973; Jordaens *et al*. 2006). All life stages of *D. laeve* can be found throughout the year, including winter, suggesting overlapping generations (Taylor 1907; Getz 1959; Quick 1960; Chichester and Getz 1973; Boag and Wishart 1982; Jordaens *et al*. 2006). Most *D. laeve* we caught in September were extremely small, indicating recent hatching. Approximately how many of these very small young slugs might have survived to

TABLE 3. Descriptive statistics for the three most abundantly caught species (Northern Dusky Arion [*Arion fuscus*], Meadow Slug [*Deroceras laeve*], and Western Dusky Slug [*Arion subfuscus*]) collected in the eight forested wetlands (adjacent clearcuts not included) in southwest Nova Scotia. We tested for significant differences in the number of slugs between tree and ground traps. Mann-Whitney values (*U*) and respective *P*-values are reported.

Slug species	Sampling month	# sites with detections	# traps with detections		% traps with detections per trap-day, mean ± SD		Number of slugs		Statistical test
			Tree	Ground	Tree	Ground	Tree	Ground	
A. fuscus	July	8	6	24	3%	43%	0.02±0.03	0.24±0.26	$U = 7$; $P < 0.005$
	Sept	6	1	18	1%	32%	0.003±0.008	0.17±0.12	$U = 9$; $P < 0.004$
D. laeve	July	6	6	13	4%	23%	0.01±0.02	0.03±0.04	$U = 36$; $P < 0.73$
	Sept	8	4	22	2%	39%	0.01±0.08	0.26±0.22	$U = 4$; $P < 0.001$
A. subfuscus	July	3	0	8	0%	13%	0	0.07±0.21	Absent in tree traps
	Sept	2	0	4	0%	9%	0	0.03±0.06	

maturity is unknown, because survivorship curves for slugs are not well reported.

So far, we have treated *D. laeve* as a native species in North America; however, there is some uncertainty with it being native or non-native throughout the continent. Pilsbry (1948) suggested that the species originated in Eurasia and arrived in the Americas by two routes: once via Beringia during the Pleistocene i.e., native and once more recently via human transport across the Atlantic Ocean from Europe. Preliminary genetic analysis (Araiza-Gómez *et al.* 2017) has identified at least three, more or less discrete groups of *D. laeve*, concentrated primarily in the United Kingdom, Ireland and Switzerland, and North America including Mexico. Rumi *et al.* (2010) had earlier found *D. laeve* to be additionally present, supposedly as introductions, throughout the Americas and elsewhere. Given the number of slug species thought to have been introduced to eastern North America from Europe in post-Columbian times (Chichester and Getz 1969; Nekola 2014; Zemanova *et al.* 2018) it is possible that at least some Nova Scotian populations of *D. laeve* are of European origin. Consequently, *D. laeve* could be considered to be both native and introduced within our region. Whether or not such a reality might lead to different ecological impacts is unknown because we do not know of any detailed comparative studies of habitat preferences, food preferences, or feeding behaviour involving both eastern North American and European *D. laeve* populations.

Most *Arion* species are generalists that feed on a wide variety of items including litter, herbs, ferns, bryophytes, fungi, and lichens (Beyer and Saari 1977, 1978; Asplund and Gauslaa 2010; Boch *et al*. 2013, 2016), as well as animals such as worms and small gastropods (Barker and Efford 2004). Some slug taxa, including *Arion* spp., have definite food preferences. For example, *A. subfuscus* and *D. laeve* have a significant preference for mushrooms (Chichester and Getz 1969, 1973; Beyer and Saari 1977; Maunder and Voitk 2010). The apparent preference of *A. fuscus*, *A. subfuscus*, and *D. laeve* for the forest floor may be associated with a high diversity of edible plants and fungi, coupled with a dense litter layer not available on trees. Dense understorey vegetation contributes to cool shade and abundant moisture, both of which can be particularly important for slugs that are highly susceptible to desiccation (Thompson *et al*. 2006; Nicolai and Ansart 2017), especially small immature individuals during hot summer days.

The history of *A. fuscus* in North America remains poorly known. It was first confirmed for the United States using molecular methods by Barr *et al.* (2009). L'Heureux (2016) and L'Heureux and Angers (2018) subsequently found it to be common in southern Quebec, Canada, and additionally reported the first Nova Scotia record from a single locality near Kempt in the southwestern part of that province. During the present study, we collected *A. fuscus* from eight additional localities in southwestern Nova Scotia, suggesting that it may be quite common in that region.

To our knowledge, our two specimens of *A.* (*C.*) cf. *silvaticus* represent the first likely records for Nova Scotia. However, additional sampling and better-preserved specimens are needed to confirm its presence. Although we did not record *P. dorsalis* within forested wetlands, we did find it in adjacent clearcuts.

Implications for biodiversity conservation

Non-native gastropods, such as *Arion* spp., can alter the structure and functioning of ecosystems and may contribute to the loss of native species (Brown and Gurevitch 2004; Zettler *et al*. 2004), including native gastropods. In Nova Scotia, Davis and Browne (1996) suggested that *Arion* species restrict the occurrence of the native *P. dorsalis* to forest habitats, but evidence for this is scant and we found *P. dorsalis* (*n* = 3) only in the adjacent clearcuts. Competition between non-native and native slugs in North America may not be as strong as has generally been thought; native gastropods also appear to be less abundant in urban areas which are dominated by non-native species (P.M. Catling and B. Kostiuk unpubl. data). Paustian and Barbosa (2012) examined food and microhabitat preferences of Carolina Mantleslug (*Philomycus carolinianus*) and Changeable Mantleslug (*Megapallifera mutabilis*), both native to North America, as well as of the non-native slug *A. subfuscus* (possibly *A. fuscus*), in Maryland, United States. They found that although the overlap in food use was greater between *A. subfuscus* and *P. carolinianus* than between *P. carolinianus* and *M. mutabilis*, the overlap may have been low enough to keep competition to a minimum.

Because *Arion* species, including *A. fuscus* and *A. subfuscus*, are known lichenivorous grazers (Asplund and Gauslaa 2010; Asplund *et al*. 2010; Asplund 2011), their spread into southwestern Nova Scotia might be expected to increase grazing pressure on at-risk tree lichen species including *E. pedicellatum*. Given that we collected *A. subfuscus* only on the ground, and that *D. laeve* prefers mushrooms and we found more of them on the ground than in the tree traps, it seems likely that most of the grazing pressure on tree lichens in southwestern Nova Scotia is attributable to *A. fuscus.* Additionally, *A. fuscus* was recorded in all eight study sites and is much larger in size than *D. laeve* (adults of *A. fuscus* are around 50–70 mm in length while *D. laeve* are 15–25 mm long; Rowson *et al*. 2014b). In Quebec, L'Heureux and Angers (2018) also found *A. fuscus* to be the most abundant and widely distributed slug species. While Cameron (2009) found "*Arion subfuscus*" to be commonly recorded on *E. pedicellatum* thalli in mixedwood forest remnants in central Nova Scotia, from his description, these slugs may well have been *A. fuscus*.

Due to limited mobility, non-native slugs probably use passive means to quickly colonize new sites. Forest roads are the main access for logging, monitoring, and management of forest resources but can also act as corridors that facilitate the introduction and dispersion of alien species by increasing human activities in previously inaccessible areas (Mortensen *et al*. 2009). Anthropogenic activities, such as clearcut harvesting, can also favour the colonization of non-native slugs including *Arion* species (Kappes 2006). This seems to be the case for *A. fuscus,* which did not differ in abundance between forest and clearcut habitats. As the eight forested wetlands were adjacent to 2–5 year-old clearcuts, the non-native species, particularly *A. fuscus*, may have been spread by anthropogenic vectors such as off-highway vehicles and forest harvesting equipment then spread to the intact forest. Haughian and Harper (2018) surveyed lichens in our eight study sites and found a higher proportion of gastropod grazing on lichens near clearcut edges than in the forest interior. Despite this evidence, additional examinations of the prevalence, abundance, and effects of *Arion* species on native slugs and lichens in undisturbed habitat are needed.

We have provided novel information on the ecology of slugs in Nova Scotia. There did not seem to be anything special about sites 1 and 8, where we captured the highest diversity and numbers of slugs, except that the traps were open for more days at these two sites than at the other six. Additional studies in different habitats and at multiple spatial and temporal scales are needed to better understand patterns of seasonality, food and habitat preferences, and dispersal capacity of this neglected group. Such information will enable a better understanding of how environmental factors regulate interactions between slug species and between slugs and other taxa, such as lichens and fungi, which will aid conservationists and forest managers to conserve native biodiversity and minimize the spread of non-native species.

Acknowledgements

H.R.M. received a Mitacs Accelerate Postdoctoral Fellowship in partnership between Mitacs and Port Hawkesbury Paper Inc. Funding was also provided by Nova Scotia Habitats Conservation Fund and the Natural Sciences and Engineering Research Council of Canada (NSERC Discovery Grant to K.A.H.). In-kind support was provided by Saint Mary's University, the Nova Scotia Department of Lands and Forestry, the Nova Scotia Museum, and the Mersey Tobeatic Research Institute. We thank Andrew Fedora for the support, Alex Setchell, Chad Simons, Cole Vail, and Rowan Kernaghan for field assistance, and Mindy-Lee Romo for the sorting the collected invertebrates. We also thank the valuable comments and suggestions from the editor Dr. Dwayne Lepitzki and the reviewers Dr. Paul Catling and Dr. Annegret Nicolai as well as a third, anonymous, reviewer.

Literature Cited

Allen, J.A. 2004. Avian and mammalian predators of terrestrial gastropods. Pages 1–36 *in* Natural Enemies of Terrestrial Molluscs. *Edited by* G.M. Barker. CABI Publishing, Wallingford, United Kingdom. https://doi.org/10.1079/9780851993195.0001

Araiza-Gómez, V., E. Naranjo-García, and G. Zúñiga. 2017. The exotic slugs of the genus *Deroceras* (Agriolimacidae) in Mexico: morphological and molecular characterization, and new data on their distribution. American Malacological Bulletin 35: 126–133. https://doi.org/10.4003/006.035.0205

Asplund, J. 2011. Chemical races of *Lobaria pulmonaria* differ in palatability to gastropods. Lichenologist 43: 491–494. https://doi.org/10.1017/s0024282911000387

Asplund, J., and Y. Gauslaa. 2010. The gastropod *Arion fuscus* prefers cyanobacterial to green algal parts of the tripartite lichen *Nephroma arcticum* due to low chemical defence. Lichenologist 42: 113–117. https://doi.org/10.1017/s0024282909990284

Asplund, J., P. Larsson, S. Vatne, and Y. Gauslaa. 2010. Gastropod grazing shapes the vertical distribution of epiphytic lichens in forest canopies. Journal of Ecology 98: 218–225. https://doi.org/10.1111/j.1365-2745.2009.01584.x

Backeljau, T., and L. de Bruyn. 1988. Notes on *Arion hortensis* s. l. and *A. fasciatus* s. l. in Denmark. Apex 4: 41–48.

Backeljau, T., and R. Marquet. 1985. An advantageous use of multivariate statistics in a biometrical study on the *Arion hortensis* complex (Pulmonata: Arionidae) in Belgium. Malacological Review 18: 57–82.

Backeljau, T., and M. van Beeck. 1986. Epiphallus anatomy in the *Arion hortensis* species aggregate (Mollusca, Pulmonata). Zoologica Scripta 15: 61–68. https://doi.org/10.1111/j.1463-6409.1986.tb00209.x

Barker, G.M., and M.G. Efford. 2004. Predatory gastropods as natural enemies of terrestrial gastropods and other invertebrates. Pages 279–403 *in* Natural Enemies of Terrestrial Molluscs. *Edited by* G.M. Barker. CAB International, Wallingford, United Kingdom. https://doi.org/10.1079/9780851993195.0279

Barnes, H., and J. Weil. 1945. Slugs in gardens: their numbers, activities and distribution. Part 2. Journal of Animal Ecology 14: 71–105. https://doi.org/10.2307/1386

Barr, N.B., A. Cook, P. Elder, J. Molongoski, D. Prasher, and D.G. Robinson. 2009. Application of a DNA barcode using the 16S rRNA gene to diagnose pest *Arion* species in the USA. Journal of Molluscan Studies 75: 187–191. https://doi.org/10.1093/mollus/eyn047

Bett, J.A. 1960. The breeding seasons of slugs in gardens. Proceedings of the Zoological Society of London 135: 559–568. https://doi.org/10.1111/j.1469-7998.1960.tb05865.x

Beyer, W.N., and D.M. Saari. 1977. Effect of tree species on the distribution of slugs. Journal of Animal Ecology 46: 697–702. https://doi.org/10.2307/3635

Beyer, W.N., and D.M. Saari. 1978. Activity and ecological distribution of the slug, *Arion subfuscus* (Draparnaud) (Stylommatophora), Arionidae). American Midland Naturalist 100: 359–367. https://doi.org/10.2307/2424835

Bickford, D., D.J. Lohman, N.S. Sodhi, P.K.L. Ng, R. Meier, K. Winker, K.K. Ingram, and I. Das. 2007. Cryptic species as a window on diversity and conservation. Trends in Ecology & Evolution 22: 148–154. https://doi.org/10.1016/j.tree.2006.11.004

Blattmann, T., S. Boch, M. Tuerke, and E. Knop. 2013. Gastropod seed dispersal: an invasive slug destroys far more seeds in its gut than native gastropods. PLoS ONE 8: e75243. https://doi.org/10.1371/journal.pone.0075243

Bless, R. 1977. Saisonal bedingte Abundanzverschiebungen einiger Schneckenarten des Naturparks Kottenforst-Ville. Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz 50: 65–68. https://doi.org/10.1007/bf02179525

Boag, D.A., and W.D. Wishart. 1982. Distribution and abundance of terrestrial gastropods on a winter range of bighorn sheep in southwestern Alberta. Canadian Journal of Zoology 60: 2633–2640. https://doi.org/10.1139/z82-338

Boch, S., M. Berlinger, M. Fischer, E. Knop, W. Nentwig, M. Türke, and D. Prati. 2013. Fern and bryophyte endozoochory by slugs. Oecologia 172: 817–822. https://doi.org/10.1007/s00442-012-2536-0

Boch, S., M. Fischer, E. Knop, and E. Allan. 2014. Endozoochory by slugs can increase bryophyte establishment and species richness. Oikos 124: 331–336. https://doi.org/10.1111/oik.01536

Boch, S., D. Prati, and M. Fischer. 2016. Gastropods slow down succession and maintain diversity in cryptogam communities. Ecology 97: 2184–2191. https://doi.org/10.1002/ecy.1498

Boch, S., D. Prati, S. Werth, J. Rüetschi, and M. Fischer. 2011. Lichen endozoochory by snails. PLoS ONE 6: e18770. https://doi.org/10.1371/journal.pone.0018770

Brown, K.A., and J. Gurevitch. 2004. Long-term impacts of logging on forest biodiversity in Madagascar. Proceedings of the National Academy of Sciences of the United States of America 101: 6045–6049. https://doi.org/10.1073/pnas.0401456101

Buschmann, H., M. Keller, N. Porret, H. Dietz, and P.J. Edwards. 2005. The effect of slug grazing on vegetation development and plant species diversity in an experimental grassland. Functional Ecology 19: 291–298. https://doi.org/10.1111/j.1365-2435.2005.00960.x

Cameron, R.P. 2009. Are non-native gastropods a threat to endangered lichens? Canadian Field-Naturalist 123: 169–171. https://doi.org/10.22621/cfn.v123i2.697

Capinha, C., F. Essl, H. Seebens, D. Moser, and H.M. Pereira. 2015. The dispersal of alien species redefines biogeography in the Anthropocene. Science 348: 1248–1251. https://doi.org/10.1126/science.aaa8913

Castillejo, J., I. Seijas, and F. Villoch. 1996. Slug and snail pests in Spanish crops and their economical importance. Pages 327–332 *in* Slug and Snail Pests in Agriculture. *Edited by* BCPC Symposium Proceedings. University of Kent, Canterbury, United Kingdom.

Chichester, L.F., and L.L. Getz. 1969. The zoogeography and ecology of arionid and limacid slugs introduced into northeastern North America. Malacologia 7: 313–346.

Chichester, L.F., and L.L. Getz. 1973. The terrestrial slugs of northeastern North America. Sterkiana 51: 11–42.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2014. COSEWIC assessment and status report on the Boreal Felt Lichen *Erioderma pedicellatum*, Boreal population and Atlantic population, in Canada. COSEWIC, Ottawa, Ontario, Canada.

Cowie, R.H., and D.G. Robinson. 2003. Pathways of introduction of nonindigenous land and freshwater snails and slugs. Pages 93–122 *in* Invasive Species: Vectors and Management Strategies. *Edited by* G.M. Ruiz and J.T. Carlton. Island Press, Washington, DC, USA.

Davies, S.M. 1977. The *Arion hortensis* complex with notes on *A. intermedius* Normand (Pulmonata: Arionidae). Journal of Conchology 29: 173–187.

Davies, S.M. 1979. Segregates of the *Arion hortensis* complex (Pulmonata: Arionidae) with the description of a new species, *Arion owenii*. Journal of Conchology 30: 123–127.

Davis, D.S., and S. Browne. 1996. Natural History of Nova Scotia. Nimbus Publishing, Halifax, Nova Scotia, Canada.

De Smedt, P., L. Baeten, E. Gallet-Moron, J. Brunet, S.A.O. Cousins, G. Decocq, M. Deconchat, M. Diekman, B. Giffard, O. Kalda, J. Liira, T. Paal, M. Wulf, M. Hermy, and K. Verheyen. 2019. Forest edges reduce slug (but not snail) activity density across western Europe. Pedobiologia 75: 34–37. https://doi.org/10.1016/j.pedobi.2019.05.004

De Wilde, J.J.A. 1983. Notes on the *Arion hortensis* complex in Belgium (Mollusca, Pulmonata: Arionidae). Annales de la Société Royale Zoologique de Belgique 113: 87–96.

De Winter, A.J. 1984. The *Arion hortensis* complex (Pulmonata: Arionidae): designation of types, descriptions, and distributional patterns, with special reference to the Netherlands. Zoologische Mededelingen 59: 1–17.

Diez, J.M., J.J. Sullivan, P.E. Hulme, G. Edwards, and R.P. Duncan. 2008. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. Ecology Letters 11: 674– 681. https://doi.org/10.1111/j.1461-0248.2008.01178.x

Ding, J., R.N. Mack, P. Lu, M. Ren, and H. Huang. 2008. China's booming economy is sparking and accelerating biological invasions. BioScience 58: 317–324. https://doi.org/10.1641/b580407

Environment Canada. 2017. Canadian Climate Normals 1981–2010. Ottawa, Ontario, Canada.

Faberi, A.J., A.J. López, P.L. Manetti, N.L. Clemente, and H.A. Álverez-Castillo. 2006. Growth and reproduction of the slug *Deroceras laeve* (Müller) (Pulmonata: Stylommatophora) under controlled conditions. Spanish Journal of Agricultural Research 4: 345–350. Accessed 21 October 2021. https://pdfs.semanticscholar.org/21fc/545c98c1bcc0643d6c8f9c7e4b876f282c53.pdf.

Garrido, C., J. Castillejo, and J. Iglesias. 1995. The *Arion subfuscus* complex in the eastern part of the Iberian Peninsula, with redescription of *Arion subfuscus* (Draparnaud 1805). Arkiv für Molluskenkunde 124: 103–118. https://doi.org/10.1127/arch.moll/124/1995/103

Getz, L.L. 1959. Notes on the ecology of slugs: *Arion circumscriptus*, *Deroceras reticulatum*, and *D. laeve*. American Midland Naturalist 61: 485–498. https://doi.org/10.2307/2422516

Gural-Sverlova, N.V., and R.I. Gural. 2015. Slugs from the complex *Arion subfuscus* (Arionidae) in the plain area of Ukraine. Ruthenica 25: 99–102. [In Russian]

Hahn, P.G., M.L. Draney, and M.E. Dornbush. 2011. Exotic slugs pose a previously unrecognized threat to the herbaceous layer in a midwestern woodland. Restoration Ecology 19: 786–794. https://doi.org/10.1111/j.1526-100x.2010.00710.x

Hammer, Ø., D.A.T. Harper, and P.B. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4: 1–9.

Hammond, R.B., and R.A. Byers. 2002. Agriolimacidae and Arionidae as pests in conservation-tillage soybean and maize cropping in North America. Pages 301–335 *in* Molluscs as Crop Pests. *Edited by* G.M. Barker. CABI Publishing, Wallingford, United Kingdom. https://doi.org/10.1079/9780851993201.0301

Haughian, S.R., and K.A. Harper. 2018. Distance of clearcut edge influence for epiphytic cyanolichens in old, wet, mixedwood forests of Nova Scotia: Year 1 of the L-ACER field study. Page 12 *in* Abstracts of the 9th bi-annual Eastern Canada-USA Forest Science Conference: Balancing Forest Production and Conservation. *Edited by* D.A. Maclean and N. Hay. Fundy Model Forest, Fredericton, New Brunswick, Canada. Accessed 14 September 2021. https://www.fundymodelforest.net/images/agenda_v1_abstractgs.pdf.

Hawkins, J.W., M.W. Lankester, R.A. Lautenschlager, and F.W. Bell. 1997. Length–biomass and energy relationships of terrestrial gastropods in northern forest ecosystems. Canadian Journal of Zoology 75: 501–505. https://doi.org/10.1139/z97-061

Hobbs, R.J. 2000. Land-use changes and invasions. Pages 55–64 *in* Invasive Species in a Changing World. *Edited by* H.A. Mooney and R.J. Hobbs. Island Press, Washington, DC, USA.

Holland, K.D., M.J. McDonnell, and N.S.G. Williams. 2007. Abundance, species richness and feeding preferences of introduced molluscs in native grasslands of Victoria, Australia. Austral Ecology 32: 626–634. https://doi.org/10.1111/j.1442-9993.2007.01749.x

Hutchinson, J.M.C., H. Reise, and G. Skujienė. 2017. Life cycles and adult sizes of five co-occurring species of *Arion* slugs. Journal of Molluscan Studies 83: 88–105. https://doi.org/10.1093/mollus/eyw042

Jennings, T.J., and J.P. Barkham. 1975. Slug populations in mixed deciduous woodland. Oecologia 20: 279–286. https://doi.org/10.1007/bf00347478

Jennings, T.J., and J.P. Barkham. 1979. Litter decomposition by slugs in mixed deciduous woodland. Holarctic Ecology 21–29. https://doi.org/10.1111/j.1600-0587.1979.tb00678.x

Jordaens, K., J. Pinceel, H. Krieckemans, and T. Backeljau. 2006. Accurate identification of cryptic slug taxa of the *Arion subfuscus/fuscus* complex by PCR-RFLP (Pulmonata: Arionidae). Journal of Molluscan Studies 72: 323–325. https://doi.org/10.1093/mollus/eyl012

Jordan, S.F., and S.H. Black. 2012. Effects of forest land management on terrestrial mollusks: a literature review. The Xerces Society for Invertebrate Conservation, Portland, Oregon, USA.

Kappes, H. 2006. Relations between forest management and slug assemblages (Gastropoda) of deciduous regrowth forests. Forest Ecology and Management 237: 450–457. https://doi.org/10.1016/j.foreco.2006.09.067

Kozłowski, J. 2012. The significance of alien and invasive slug species for plant communities in agrocenoses. Journal of Plant Protection Research 52: 67–76. https://doi.org/10.2478/v10045-012-0012-9

L'Heureux, É. 2016. Une invasion dans la discretion: repartition, origins, et expansion des limaces européennes du complexe d'*Arion subfuscus* s.l. au Québec. M.Sc. thesis, Université de Montréal, Montréal, Quebec, Canada.

L'Heureux, É., and B. Angers. 2018. A discreet invasion: distribution, origins, and expansion of the European slug complex *Arion subfuscus* s.l. in Quebec. Canadian Journal of Zoology 96: 325–331. https://doi.org/10.1139/cjz-2017-0171

Lanta, V. 2007. Effect of slug grazing on biomass production of a plant community during a short-term biodiversity experiment. Acta Oecologica 32: 145–151. https://doi.org/10.1016/j.actao.2007.03.013

Lucid, M., S. Ehlers, L. Robinson, and S. Cushman. 2018. Beer, brains, and brawn as tools to describe terrestrial gastropod species richness on a montane landscape. Ecosphere 9: e02535. https://doi.org/10.1002/ecs2.2535

Maunder, J.E., and A.J. Voitk. 2010. What we don't know about slugs and mushrooms. Fungi 3: 36–44.

McCarthy, P.M., and J.A. Healy. 1978. Field and study notes: dispersal of lichen propagules by slugs. Lichenologist 10: 131–134. https://doi.org/10.1017/s002428297800016x

McKnight, P., and J. Najab. 2010. Mann–Whitney U Test. Corsini Encyclopedia of Psychology 1. https://doi.org/10.1002/9780470479216.corpsy0524

Meyer, W.M., R. Ostertag, and R.H. Cowie. 2013. Influence of terrestrial molluscs on litter decomposition and nutrient release in a Hawaiian Rain Forest. Biotropica 45: 719–727. https://doi.org/10.1111/btp.12057

Mohamed, M.I., and R.F. Ali. 2011. Laboratory studies on the terrestrial marsh slug *Deroceras laeve* (Müller) (Agriolimacidae: Mollusca). Animal Biology Journal 2: 133–141.

Mortensen, D.A., E.S.J. Rauschert, A.N. Nord, and B.P. Jones. 2009. Forest roads facilitate the spread of invasive plants. Invasive Plant Science and Management 2: 191–199. https://doi.org/10.1614/ipsm-08-125.1

Moss, M., and L. Hermanutz. 2010. Monitoring the small and slimy – protected areas should be monitoring native and non-native slugs (Mollusca: Gastropoda). Natural Areas Journal 30: 322–327. https://doi.org/10.3375/043.030.0307

Nekola, J.C. 2014. Overview of the North American terrestrial gastropod fauna. American Malacological Bulletin 32: 1–35. https://doi.org/10.4003/006.032.0203

Nicolai, A., and A. Ansart. 2017. Conservation at a slow pace: terrestrial gastropods facing fast-changing climate. Conservation Physiology 5: 1–17. https://doi.org/10.1093/conphys/cox007

Oli, B.P., and P.K. Gupta. 2000. Land mollusc fauna of the Kumaon Himalayan forest and the role of snail in plant litter decomposition. Tropical Ecology 41: 247–250.

Ord, M.J., and A.H.G. Watts. 1949. New records for the distribution of certain land Mollusca in Nova Scotia. Proceedings of the Nova Scotia Institute of Science 22: 16–34.

Paustian, M.E., and P. Barbosa. 2012. Overlap of food and microhabitat preferences among some native and nonnative slugs in mid-Atlantic forests of eastern North America. Journal of Molluscan Studies 78: 92–99. https://doi.org/10.1093/mollus/eyr041

Pilsbry, H.A. 1948. Land Mollusca of North America (North of Mexico). Volume II, Part 2. Academy of Natural Sciences of Philadelphia. Philadelphia, Pennsylvania, USA.

Pinceel J., K. Jordaens, and T. Backeljau. 2005a. Extreme mtDNA divergences in a terrestrial slug (Gastropoda, Pulmonata, Arionidae): accelerated evolution, allopatric divergence and secondary contact. Journal of Evolutionary Biology 18: 1264–1280. https://doi.org/10.1111/j.1420-9101.2005.00932.x

Pinceel, J., K. Jordaens, N. van Houtte, G. Bernon, and T. Backeljau. 2005b. Population genetics and identity of an introduced terrestrial slug: *Arion subfuscus* s.l. in the north-east USA (Gastropods, Pulmonata, Arionidae). Genetica 125: 155–171. https://doi.org/10.1007/s10709-005-5816-3

Pinceel, J., K. Jordaens, N. van Houtte A.J. De Winter, and T. Backeljau. 2004. Molecular and morphological data reveal cryptic taxonomic diversity in the terrestrial slug complex *Arion subfuscus/fuscus* (Mollusca, Pulmonata, Arionidae) in continental north-west Europe. Biological Journal of the Linnean Society 83: 23–38. https://doi.org/10.1111/j.1095-8312.2004.00368.x

Province of Nova Scotia. 2007. Nova Scotia Wet Areas (GIS Data). Department of Natural Resources, Truro, Nova Scotia, Canada. Accessed 16 December 2020. http://www.novascotia.ca/natr/forestry/gis/wamdownload.asp.

Province of Nova Scotia. 2021. Forest Inventory - Current Forest Data (GIS Data). Department of Natural Resources, Truro, Nova Scotia, Canada. Accessed 15 December 2021. https://novascotia.ca/natr/forestry/gis/forest-inventory.asp.

Quick, H.E. 1960. British slugs (Pulmonata; Testacellidae, Arionidae, Limacidae). Bulletin of the British Museum (Natural History) Zoology 6: 105–228. https://doi.org/10.5962/bhl.part.26845

Robinson, D.G. 1999. Alien invasions: the effects of the global economy on non-marine gastropod introductions into the United States. Malacologia 41: 413–438.

Rodriguez-Cabal, M.A., T.C. Gibbons, P.M. Schulte, N.M. Barrios-Garcia, and G.M. Crutsinger. 2015. Comparing functional similarity between a native and an alien slug in temperate rain forests of British Columbia. Neobiota 25: 1–14. https://doi.org/10.3897/neobiota.25.8316

Rowe, J.S. 1972. Forest Regions of Canada. Fisheries and Environment Canada, Ottawa, Ontario, Canada.

Rowson, B., R. Anderson, J. Turner, and W.O.C. Symondson. 2014a. The slugs of Britain and Ireland: undetected and undescribed species increase a well-studied, economically important fauna by more than 20%. PLoS ONE 9: e91907. https://doi.org/10.1371/journal.pone.0091907

Rowson, B., J.R. Turner, R. Anderson, and B. Symondson. 2014b. Slugs of Britain and Ireland. Identification, Understanding and Control. FCS. National Museum of Wales, Cardiff, United Kingdom.

Rumi, A., J. Sánchez, and N.S. Ferrando. 2010. *Theba* *pisana* (Müller, 1774) (Gastropoda, Helicidae) and other alien land molluscs species in Argentina. Biological Invasions 12: 2985–2990. https://doi.org/10.1007/s10530-010-9715-x

Runham, N.W., and P.J. Hunter. 1970. Terrestrial Slugs. Hutchinson University Library, London, England.

SARA (*Species at Risk Act*) Registry. 2021. Species summary: Boreal Felt Lichen (*Erioderma pedicellatum*), Atlantic population. Accessed 10 May 2021. https://species-registry.canada.ca/index-en.html#/species/702-71.

Skujienė, G. 2004. *Arion distinctus* Mabille, 1868 (Gastropoda: Pulmonata: Arionidae) in Lithuania. Acta Zoologica Lituanica 14: 71–76. https://doi.org/10.1080/13921657.2004.10512582

South, A. 1992. Terrestrial Slugs: Biology, Ecology and Control. Chapman & Hall, London, England.

Strauss, S.Y., M.L. Stanton, N.C. Emery, C.A. Bradley, A.C. Dylan, R. Dittrich-Reed, O.A. Ervin, L.N. Gray, A.M. Hamilton, J.H. Rogge, S.D. Harper, K.C. Law, V.Q. Pham, M.E. Putnam, T.M. Roth, J.H. Theil, L.M. Wells, and E.M. Yoshizuka. 2009. Cryptic seedling herbivory by nocturnal introduced generalists impacts survival, performance of native and exotic plants. Ecology 90: 419–429. https://doi.org/10.1890/07-1533.1

Suarez, A.V., D.A. Holway, and T.J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. Proceedings of the National Academy of Sciences of the United States of America 98: 1095–1100. https://doi.org/10.1073/pnas.98.3.1095

Symondson, W.O.C., D.M. Glen, A.R. Ives, C.J. Langdon, and C.W. Wiltshire. 2002. Dynamics of the relationship between a generalist predator and slugs over five years. Ecology 83: 137–147. https://doi.org/10.1890/0012-9658(2002)083[0137:dotrba]2.0.co;2

Taylor, J.W. 1907. Monograph of the Land and Freshwater Mollusca of the British Isles. Testacellidae. Limacidae. Arionidae. Taylor Brothers, Leeds, England.

Thompson, J.M., A.G. Appel, J.L. Sibley, G.J. Keever, and W.G. Foshee. 2006. Comparative water relations of three sympatric terrestrial slugs (Stylommatophora: Agriolimacidae, Limacidae and Philomycidae). Journal of the Alabama Academy of Science 77: 181–192.

Turgeon, D.D., J.F. Quinn, Jr., A.E. Bogan, E.V. Coan, F.G. Hochberg, W.G. Lyons, P.M. Mikkelsen, R.J. Neves, C.F.E. Roper, G. Rosenberg, B. Roth, A. Scheltema, F.G. Thompson, M. Vecchione, and J.D. Williams. 1998. Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks. Second Edition. American Fisheries Society Special Publication 26, Bethesda, Maryland, USA.

Türke, M., M. Lange, and N. Eisenhauer. 2018. Gut shuttle service: endozoochory of dispersal-limited soil fauna by gastropods. Oecologia 186: 655–664. https://doi.org/10.1007/s00442-018-4058-x

Zemanova, M.A., O. Broennimann, A. Guisan, E. Knop, and G. Heckel. 2018. Slimy invasion: climatic niche and current and future biogeography of *Arion* slug invaders. Diversity and Distributions 24: 1627–1640. https://doi.org/10.1111/ddi.12789

Zettler, J.A., M.D. Taylor, C.R. Allen, and T.P. Spira. 2004. Consequences of forest clear-cuts for native and nonindigenous ants (Hymenoptera: Formicidae). Annals of the Entomological Society of America 97: 513–518. https://doi.org/10.1603/0013-8746(2004)097[0513:cofcfn]2.0.co;2

Received 9 December 2020
Accepted 14 July 2021
Editor: D.A.W. Lepitzki

The Canadian Field-Naturalist

Changes to the Book Reviews and New Titles Sections

Our Book Review Editor stepped down after publication of Volume 135, Issue 2. We have been unable to find a replacement to date; thus, this section will undergo several changes. Until we find a new editor, William Halliday (wdhalliday@gmail.com), our Online Journal Manager, will take over the New Titles list and Amanda Martin (canadianfieldnaturalistae@gmail.com), the Assistant Editor, will manage the Book Reviews. William Halliday will focus on titles of books that are available for review. Readers of this journal are invited to request titles they are willing to review from the list from William and, if still available, copies will be sent directly to them by the publisher. Readers will still be able to submit reviews of books they have on hand, provided that reviewed books have 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. Book reviews will be submitted through the online submission system https://www.canadianfieldnaturalist.ca/index.php/cfn/about/submissions. All received reviews will undergo editing, and prospective reviewers are encouraged to check our book review guidelines at https://www.canadianfieldnaturalist.ca/index.php/cfn/about/submissions. These changes will be fully in place as of Issue 135, Volume 3 and continue until a new Book Reviewer Editor is found.

We wish to thank each of you who has provided reviews in the past, and encourage all of you to continue to keep this section going. Lastly, are there any volunteers willing to assume the full role of the Book Reviewer Editor? If so, please contact the Editor-in-Chief (editor@canadianfieldnaturalist.ca) for more information.

Book Reviews

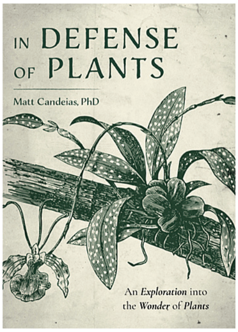
Book Review Editor's Note: *The Canadian Field-Naturalist* is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those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

In Defense of Plants: an Exploration into the Wonder of Plants

By Matt Candeias. 2021. Mango Publishing Group. 280 pages, 20.00 CAD, Hardcover. Also available as an E-book or Audiobook.



Written by the creator of the long-running (2015–present) podcast and blog of the same name, this semi-autobiographical work is an extension of the author's goal that the reader "see plants, even if for a moment, how I see plants" (p. 9). As the author of various print and online articles under the "In Defense of Plants" name, Candeias has considerable experience writing and talking about plants for a broad audience. Far from a dry textbook style, the writing comes alive through the author's obvious passion for plants and their ways.

Physically, this book is an odd size—at 13.5 cm wide and 19 cm tall, this is not your typical hardcover. It uses a small font which some readers may find challenging. The book is also printed on thin paper that allows type or images on the reverse side of a page to show through, giving it a grey tone and an almost newsprint-like feel. Combined with the small font, the paper transparency makes it a tougher than average read. (I have good eyesight and still found it a bit challenging in lower light.) The greyscale photos make for a mixed experience—several are very effectively balanced but some are not well suited to greyscale and appear overly dark, washed out, or murky.

Most chapters consist of a series of examples under a theme, typically accompanied by a few photos of the plants under discussion. The tone is very informal; often the author writes directly to the reader, using the first person and offering personal reflections and opinions. This casual tone is not a writing style that will appeal to all readers, but it does add personality to the writing. Following an oddly defensive Preface, the bulk of the work is interesting facts about various plants. Candeias explores a diversity of life stages and strategies, from pollination by seedsnipe birds to seed dispersal by fish. A personal favourite: bat pollination facilitated through specialized banner petals on the sea bean flower, adapted as a nectar guide for the frequency of the nectar feeding bat's echolocation. The really fun part is that once the flower has been visited, the banner petal shape changes and bats learn not to revisit spent nectar sources, thus increasing cross pollination (pp. 90–94). The final chapter, The Problems Plants Face, is a brief treatise on the various threats to plant diversity and populations accompanied by actionable steps readers can take to help.

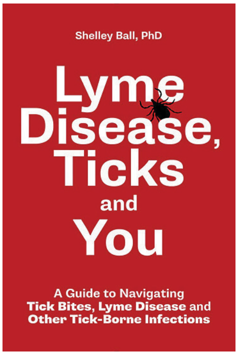
Overall, *In Defense of Plants* has the feel of listening to someone really interested in plants tell you all about them, a sort of highlight reel of weird and wonderful facts organized around a theme by chapter. While the intended audience is the broad public, this book will likely appeal most to those who already hold an interest in plant ecology, diversity, life histories, cultivation, etc. Although I found it tougher to get through than I anticipated, if your eyesight is good and you enjoy learning new things about the world around you, this book is a solid collection of interesting plant miscellany written by an author who knows their stuff.

HEATHER CRAY
Halifax, NS, Canada

ENTOMOLOGY AND ARACHNOLOGY

Lyme Disease, Ticks and You: a Guide to Navigating Tick Bites, Lyme Disease and Other Tick-Borne Infections

By Shelley Ball. 2021. Firefly Books. 128 pages, 19.95 CAD, Paper.



Any naturalist or person who works outdoors in temperate North America, particularly in hotspots for ticks, is likely already aware of ticks and perhaps has even had Lyme Disease or knows someone who has had it. For those still unfamiliar with Lyme Disease, it is caused by the bacterium *Borrelia burgdorferi* as well as other species within the genus *Borrelia* and is transmitted to humans via ticks such as black-legged ticks (*Ixodes* spp.). Once infected with *Borrelia* bacteria, humans can start to display a number of symptoms of Lyme Disease, including the iconic "bulls-eye rash" (*Erythema migrans* rash), fatigue, and flu-like symptoms. If *Borrelia* bacteria remain undetected or untreated in humans, then chronic symptoms may occur, although chronic Lyme Disease remains a contentious issue among medical professionals. Hotspots for ticks in Canada, and in North America as a whole, seem to be getting worse as the hotspots are expanding into new regions, and Lyme Disease is becoming more prevalent.

Lyme Disease, Ticks and You serves as an excellent overview for all aspects of Lyme Disease, including a history of Lyme Disease, the ecology of ticks and transmission of Lyme Disease, how to mitigate the risks of tick bites, what to do if you get a tick bite, and more information on the medical side related to acute and chronic Lyme Disease. This book serves as a really great crash course for anyone interested in many of the basics of Lyme Disease and ticks. Lyme Disease is not simple. It is transmitted to humans via tick species that have complex life cycles, including multiple host species at different life stages. Similarly, once *Borrelia* bacteria enter the blood stream of a human, the resulting symptoms are not necessarily predictable. Dr. Ball takes these relatively complex topics and describes them in a straightforward, logical fashion using fairly plain language. Readers with a basic understanding of science should find this book easy to digest and follow. Perhaps one of the most important take-home messages from this book is that ticks are becoming more common on the landscape and there is likely no way to remove this threat from the ecosystem. Rather than fearing the outdoors, we must learn to co-exist safely with ticks. This can be achieved through a number of simple steps, many of which are laid out in this book, including the use of repellants and tick checks (i.e., searching your body for ticks).

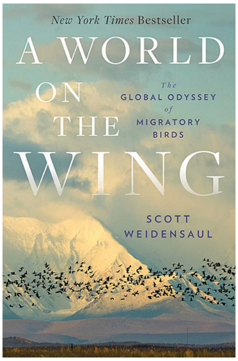
The author of this book is a biologist and educator. Dr. Ball lives in a hotspot for Black-legged Tick in Ontario, and she suffers from chronic Lyme Disease. Dr. Ball weaves together her expertise in ecology with her experience as someone who suffers from Lyme Disease to bring this book together. The preface is quite personal: it lays out Dr. Ball's history with Lyme Disease and describes why she thought it was necessary to write this book. One of the main goals of her book was to help educate people on Lyme Disease and its risks, and that goal has certainly been met. I highly recommend this book to any naturalist, student, or person getting into the outdoors for work or pleasure who does not know much about Lyme Disease and staying safe while in tick country.

WILLIAM D. HALLIDAY
Wildlife Conservation Society Canada,
Whitehorse, YT, Canada and
School of Earth and Ocean Sciences,
University of Victoria, Victoria, BC, Canada

ORNITHOLOGY

A World on the Wing: the Global Odyssey of Migratory Birds

By Scott Weidensaul. 2021. W.W. Norton & Company. 385 pages, 37 illustrations, and 15 maps, 42.00 CAD, Cloth.



In early October 2021, we travelled to the heart of the Central Flyway in central Saskatchewan, to spend a few days watching the annual spectacle of hundreds of thousands of migrating geese, ducks, and cranes. At times the swirling cacophony almost overwhelmed the senses, but for many species such seemingly large numbers are a fraction of what they used to be before market hunting, habitat destruction, and human-caused climate change. We wondered: Where are they coming from? Where are they going? How do they find their way? In *A World on the Wing*, Scott Weidensaul captures the stories of a few migrant species that help answer some of these questions. Weidensaul has a clear, engaging writing style, building stories from his experiences following researchers around the world. *A World on the Wing* is a collection of 10 chapters, sometimes focussing on single species, other times weaving a broader story about migration.

In Chapter 1 (Spoonies) Weidensaul uses the precarious existence of Spoon-billed Sandpiper (*Calidris pygmaea*) at stopover sites on the mudflats of China's Yellow Sea to discuss broader issues that shorebirds face, not only on the East Asian–Australasian Flyway, but around the world: loss of shoreline and wetland habitat, loss of sediment from dams, illegal hunting. In Chapter 2 (Quantum Leap), Weidensaul highlights the extraordinary physiological abilities that enable birds to migrate over stunningly long distances, especially shorebirds. Many adaptations are variations on a "binge-bulk-and-shrink" strategy (p. 69) involving huge weight gains, followed by extreme atrophy of digestive organs that are not needed during days of nonstop flight. This is done twice annually for years or even decades, with no ill effects. Recent research into how birds navigate has uncovered quantum entanglement, which allows birds to sense magnetic fields through electrons in their eyes.

The proliferation of new technology and the miniaturization of electronics, which Weidensaul discusses in Chapter 3 (We Used to Think) and Chapter 4 (Big Data, Big Trouble), have truly revolutionized the study of bird migration. Tracking technology is now showing that different populations of a species may have different migration routes and wintering areas, which is critical information for conservation. Doppler radar forecasts could even be used to alert cities to turn off excess lights to reduce building strikes during migration.

Weidensaul uses the plight of Kirtland's Warbler (*Setophaga kirtlandii*) in Chapter 5 (Hangover) to discuss carry-over effects, those consequences on the breeding grounds that are carried forward from the wintering area. One example is drought reducing food resources such that birds may delay departing or arrive in poor condition. Climate change (Chapter 6, Tearing Up the Calendar) is already having big impacts on migratory birds, causing changes in precipitation, sea level rise, shifting wind patterns, increasing storm strength, loss of habitat, phenological mismatch with food resources, and new diseases and parasites. Short-distance migrants may be more resilient and better positioned to alter their timing than long-distance migrants.

In Chapter 7 (Aguiluchos Redux) Weidensaul relates the story of Swainson's Hawk (*Buteo swainsoni*), which faced precipitous population declines in the 1990s because they ingested pesticides along with their prey on their wintering grounds in Argentina ("Aquiluchos" is Spanish for harriers). The good news is that a quick campaign to switch to less-toxic chemicals worked, and the hawk population rebounded.

In Chapter 8 (Off the Shelf) Weidensaul switches to pelagic seabirds, discussing not only declining populations and tracking of species that range around the globe, but also the conservation implications of taxonomic changes—a rare, cryptic species might need more protection than a more secure, widespread one. Is it a rare, cryptic species or a more secure, widespread one?

Conflicts between bird conservation and traditional use are the focus of Chapter 9 (To Hide from God). For example, many species of songbirds are still slaughtered for food in the tens of millions, particularly along the shores of the Mediterranean where they are considered traditional delicacies. Weidensaul suggests that education of younger generations may reduce this practice. Chapter 10 (Eninum) also provides hope that conflicts between conservation and traditional practices can be reduced. The local people in northeastern India have stopped shooting Amur Falcons (*Falco amurensis*), convinced that they can earn more money from tourists coming to see them in the hundreds of thousands at their stopover roosts. ("Eninum" is the local name for the falcon, meaning "two-love" because of how the birds perch together.)

Each chapter is supported by excellent maps of relevant migration routes. The 21-page References section includes not only references for works quoted or cited in each chapter (by page number) but also a select bibliography for each chapter. It would have been useful to have a list of common and scientific names of birds mentioned in the text.

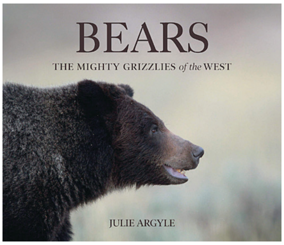
It is obvious that Weidensaul holds great reverence for the creatures written about, for their "endurance and tenacity" (p. 347).

CYNDI M. SMITH
Canmore, AB, Canada

ZOOLOGY

Bears: the Mighty Grizzlies of the West

By Julie Argyle. 2021. Gibbs Smith. 224 pages, 50.00 USD, Cloth.



Bears is a beautiful coffee table book that contains an impressive 190 glossy, colour pictures of Grizzly Bears (*Ursus arctos horribilis*) from Yellowstone National Park. It is a large (26.0 × 2.4 × 30.6 cm), heavy (4 pounds [just under 2 kg]) book that is meant to be gazed at in admiration. *Bears* gives us the pleasure of peeking into the detailed lives of these remarkable animals. Fans of Yellowstone, nature, bears, the western USA, national parks, and predators will enjoy reading about this iconic bruin, which is a symbol of wilderness and brute strength.

I have had the recent privilege of reading very personal accounts of Gray Wolves (*Canis lupus*) in Yellowstone (e.g., Way 2019, 2020). This tome follows that trend for Brown Bears—as the species is officially referred to, with Grizzly Bear denoting the *horribilis* subspecies—in one of the world's first national parks. This great bear can live up to 34 years in the wild (p. 45), and many have become local celebrities over the course of their lifetime. Each bear has a distinct personality and, as is the case with people, they have unique and distinguished identities (p. 123).

Accordingly, many of the chapters in *Bears* focus on individuals, and show awe-inspiring images of them. We get to know Raspberry, 791, Snow, Snaggletooth, and The Obsidian Sow in full photographic detail. Raspberry is Argyle's favourite and she dedicates the book to that ursid. The sow, born in 2007 (p. 125), still inhabits the northern shores of Yellowstone Lake. She has raised cubs in full view of people, including one called Snow. She—and other female bruins—often do that, people speculate, to avoid male bears, who stay away from the roads and people (p. 125). Male bears—also referred to as boars—sometimes kill cubs that aren't theirs, so there is an acute reason for the females to circumvent them. I enjoyed reading Argyle's personal stories of the bears, and seeing prints emanating from those accounts was really cool. For instance, watching Raspberry walking along the shore of Yellowstone Lake was amazing, especially because I have driven by there so many times (without seeing a bear on the shoreline). Seeing Snaggletooth's genetic defect (pp. 190–191), the missing part of his mouth, was bizarre. Observing the large, 500-pound (227-kg) boar 791 on a large bull Elk that he killed was awesome, especially because the incident made international news in 2020 (pp. 153–156). Lastly, gazing at the many images of the very adorable and light-coloured female bear named Snow (pp. 163–189) was special, and tear-jerking for Argyle to watch as the adolescent transitioned to living on her own when Raspberry chased her away at 3.5 years of age.

In addition to focussing on individual bruins, Argyle discusses bear relationships with Native Americans. Many tribes view the grizzly as a sacred animal and consider them brothers (p. 17). They were offended by calls to have them hunted and shot as trophies when they were removed from the list of species protected under the *Endangered Species Act* (ESA; p. 21). Rather, they believe the grizzly is a great and powerful spirit who is a gift to Mother Earth and her people (p. 18). Some tribes even have a bear dance, which they believe brings the spirits of their ancestors back (p. 18).

Grizzly Bears have made a remarkable recovery and are considered a success story (p. 30). Stable populations exist in the Greater Yellowstone Ecosystem and around Glacier National Park. But there are still many factors that influence their survival, so it is fortunate that judges have kept Grizzly Bears on the ESA despite numerous attempts to remove them from being federally protected. A fraction of the original 50

000 bears in the western USA still inhabit this country (p. 75), and being listed under the ESA currently prevents states from instituting hunting seasons on the great beasts. This has also allowed their population and range to continue to increase, albeit tenuously (pp. 55–56). However, there are still long-term issues associated with fluctuating and diminishing food sources, climate change, and the potentially harsh treatment of these bears by western states outside of national parks. The majority of bear deaths are human-caused (pp. 79, 193), which means that we must remain vigilant to ensure their populations stay sustainable.

We learn in *Bears* that grizzlies are super-hibernators, because their breathing slows down greatly and their heart rate drops significantly during their five month long fasting period where they do not eat, drink, defecate, or urinate (p. 91). Remarkably, cubs are born in the den in January to February, while the females are still sleeping (p. 93). This is an extraordinary adaption to survive harsh winters. As food sources become available, grizzlies awaken in the spring with boars leaving first and females with cubs last (p. 93).

Bears: the Mighty Grizzlies of the West was very easy to read. There is not much text in this book. I started it on a Saturday afternoon and read over half of it within a couple of hours, then finished it the next morning in even less time. I didn't mind how quick of a read it was, because the purpose of the book is to be a photo-essay of this powerful species. There are only minor typos in the book. One complaint I have is that there are no maps. Showing the current range of the Grizzly Bear in the USA would have been helpful to the average reader. The bears were historically found throughout the western USA, but most bears currently live in a couple of large, core populations situated within Glacier, Yellowstone, and Grand Teton National Parks, with isolated and much smaller numbers outside of those protected areas. Framing where the author took the pictures compared to the species' overall range would have been insightful. Also, the book was relatively pricey, at $50 USD. However, this price might be expected given the book's large dimensions, length (over 200 pages), and paper quality, using 100% glossy paper for all sheets.

Overall, I greatly enjoyed the book. It was well worth my time. Then again, it is difficult for me to not like something that is Yellowstone-based, especially when it involves animals, and specifically a large powerful predator like the Grizzly Bear. I will continue to follow Argyle's work, which can be found on social media and through her photography business (Wild Love Images), as well as in published materials.

Literature Cited

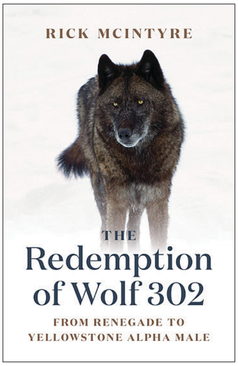
Way, J. 2019. [Book Review] The Rise of Wolf 8: Witnessing the Triumph of Yellowstone's Underdog, by Rick McIntyre. Canadian Field-Naturalist 133: 180–181. https://doi.org/10.22621/cfn.v133i2.2407

Way, J. 2020. [Book Review] The Reign of Wolf 21: The Saga of Yellowstone's Legendary Druid Pack, by Rick McIntyre. Canadian Field-Naturalist 134: 392–393. https://doi.org/10.22621/cfn.v134i4.2739

JONATHAN (JON) WAY
Eastern Coyote/Coywolf Research,
Osterville, MA, USA

The Redemption of Wolf 302: from Renegade to Yellowstone Alpha Male

By Rick McIntyre. 2021. Greystone Books. 290 pages, 34.95 CAD, 26.95 USD, Cloth.



The Redemption of Wolf 302, the third book in Rick McIntyre's Alpha Wolves of Yellowstone series, picks up where *The Reign of Wolf 21* (2020, Greystone Books) left off (Way 2020). It is another fascinating and epic read by McIntyre that will enthrall fans of nature, wolves and carnivores, wildlife, and national parks, especially Yellowstone. Wildlife biologists, teachers, and other professionals will be inspired by the unprecedented first-hand information provided on a wild species which, I hope, will help readers see wolves as the clever (p. 45), humorous (pp. 46–47), sentient (pp. 170, 237, and throughout book), intelligent (e.g., pp. 173, 226), playful (e.g., pp. 212–213), and ecologically important beings that they are. These attributes contrast with the way they are treated with the long hunting seasons that they experience in the Rocky Mountain states surrounding Yellowstone.

This book transitions smoothly from the second book, with introductory pages that enable the reader to recall what happened in McIntyre's previous volumes, sort of like a two-minute recap before a television series starts a new season. It also allows one to read this edition without reading the previous books in the series. The introduction includes two, two-page maps of the main wolves studied in the park from 2004 to 2009, the timeframe of this tome, as well as where those packs lived. There is also a four-page section, Principal Wolves, which nicely summarizes the positions of the wolves in their respective packs. Lastly, there is a nice three-page summary that describes previous events in Yellowstone, as well as a bit of McIntyre's background to put everything in context for this current book.

The Redemption of Wolf 302 is organized by year into six parts, making it easy to keep track of where you are during the ongoing saga of the park wolves. It can be overwhelming to keep track of the different wolves at times, but McIntyre does a very formidable job of making it manageable to digest without leaving out too many details. In fact, it was like reading about a real-life television soap opera (p. 214). I personally liked the way McIntyre described individual wolves such as 642, 693, 527, 569, Light Gray, Dark Gray, Big Blaze, Medium Gray, Small Blaze, Big Brown, and, of course, 302. These descriptions revealed their unique and distinct personalities.

At the end of *The Reign of Wolf 21*, the world-famous breeding male of the Druid pack, 21 had just passed away in mid-summer 2004 following the loss of his long-time mate, 42, earlier that year. In the beginning of *The Redemption of Wolf 302*, we find 302 and a younger black male nephew of his, 480, trying to join the Druid Peak wolf pack during summer 2004. It took 302 and 480 a few months to integrate into the pack because one of 21's sons (253) claimed the dominant role in the pack until he left at the end of the summer, likely because he was too related to the females in that group (see Chapters 1 and 2). McIntyre provides amazing levels of detail throughout this very easy to read tome. His direct observations of the park's wolves, including of 302's and 480's interaction in the Druid pack, make McIntyre's book series unprecedented. 480, despite his youth, was much more aggressive and took over the alpha male role in the pack. Unlike his nephew, 302 would often run and avoid confrontations with rival wolves (e.g., p. 26). In fact, before the two males were accepted into the pack, 302—to avoid getting attacked himself—once even ganged up on 480 with the Druids and bit him during a fight (pp. 5–6). 480 was a yearling when he became an alpha, yet he held the dominant position in the formidable Druid pack until the end of the book in October 2009. However, the stress of leading a pack wore on 480. He had to constantly deal with the antics of 302 trying to mate females in his pack, as well as in outside packs (p. 163), and the competition for territory with rival wolves, most notably the Slough Creek pack to their west. His black pelage started to turn grey before the age of two, and McIntyre wondered if this anxiety caused him to prematurely age (p. 37)!

We see that Wolf 480 ruled the pack in a benevolent way like Wolves 8 (Way 2019) and 21 (Way 2020) did before him; he didn't kill rival wolves and let them go unharmed during pack interactions (pp. 3–4, 14, 22–23, 143). The only exception was for packs, like the Slough Creeks, that previously killed one of their own (e.g., pp. 144–147, 195–196). His benevolence was a consistent theme throughout the book, even when he fought the rival Mollie's wolves in "The Battle of Mount Norris" (pp. 115–119). During that interaction, 480 defeated the larger pack with just pups of the year helping him. He repeatedly charged at the opposition, knocked them down, then ran after other individuals, ultimately driving off Mollie's wolves.

Wolf 302's behaviour was less predictable. McIntyre watched 302, resting about a mile away near an old Moose carcass during The Battle of Mount

Norris. He was befuddled that an adult male wolf would choose to ignore the calls of an invading pack and spend the day napping (p. 118). In addition to this event, McIntyre also watched as 302 received regurgitations from pups (pp. 112–113) to avoid approaching bull Elk carcasses, which he was clearly scared of. McIntyre deemed him a lost cause and never thought he would be able to lead a pack of his own (p. 118). In the second half of the book, however, 302 started to prove his worth which impressed McIntyre and caused the author to reconsider the "most unorthodox wolf I had ever known" (p. 147). He started to provide for his pack by helping kill Elk, a main food source (pp. 142, 163–164). Then he became an active participant to force the Slough wolf pack out of their Lamar Valley territory (p. 147). Around that time in December 2007, 302 became the most famous wolf in the world when a major television documentary, *In the Valley of Wolves*, premiered (p. 151). That documentary, and successive ones (e.g., p. 152), featured him. Many people, including politicians, came to the park to see 302 (e.g., p. 152). 302 by that point was even chasing out the single males Light Gray and Dark Gray, which were attempting to breed females in the Druid pack (pp. 153–154). It is ironic that this sort of behaviour made 302 famous, given that he did the same thing throughout 21's reign, causing 21 to chase him out of Druid territory many times (Way 2020). During the 2008 denning season, as throngs of wolf watchers visited the park, 302 could be seen regurgitating food for breeding females (p. 173) and letting them have priority at carcasses (p. 176), stealing Elk calves from Grizzly Bears (p. 177), helping pups cross roads and rivers (pp. 188–189), protecting pups from Grizzly Bears (pp. 192–193), and feeding pups (p. 192).

By late fall 2008, 302 started his own pack, dubbed the Blacktails, with some yearling males from the Druid pack and some females from the nearby Agate pack (p. 201). This area was where 302 was born 8.5 years previously so his story had come full circle. We learn how 302 took care of pregnant females (p. 217) and his pack's six pups in 2009 (p. 223). He was like a benevolent patriarch (p. 225); despite 302 being the father of some of the pups (p. 212), he took almost a grandfatherly role of babysitting (p. 227) while younger wolves went out hunting. In fall 2009, the Blacktails expanded their range to find vulnerable prey. They soon encountered a pack to their west and, after all of 302's adventures with rival wolves in his 9.5 year life, he was fatally injured (p. 237). This was a very sad moment for all who knew him during his long tenure in Yellowstone (p. 241). McIntyre believed that so many people loved 302 because he was relatable—he was an imperfect, flawed individual which turned his life around (p. 242). In fact, fighting the rival pack during his last moments of his life probably saved his sons and daughters; to McIntyre, there was no greater accomplishment than this, placing him in the pantheon of great alpha wolves even if it took him a long time to get there (p. 244).

I continue to be enthralled with Rick McIntyre's Alpha Wolves of Yellowstone book series which, to date, has covered the first 15 years of wolves in Yellowstone: 1995–2009. The books are riveting and easy to follow. The only complaint I have, which is a very minor one, is that there are sometimes abrupt transitions that bring one paragraph into a totally different scene than a previous one. This seems to occur because McIntyre wants to include important observations from his detailed notes, while also maintaining a chronological organization. I don't disagree. Once one accepts these seemingly non-sequitur moments (e.g., on p. 174 we go from heart touching moments about a mother wolf interacting with her pup, to an Osprey and Bald Eagle confrontation, to a Grizzly Bear approaching wolves), the book is an absolute joy to read. In the Epilogue (p. 245), we are set up with the fourth installation of the series with the '06 Female', a master hunter (p. 211) and alpha of alpha female wolves. I surmise that next book will pick up in 2009 when this one leaves off. I can't wait for it!

Literature Cited

Way, J. 2019. [Book Review] The Rise of Wolf 8: Witnessing the Triumph of Yellowstone's Underdog, by Rick McIntyre. Canadian Field-Naturalist 133: 180–181. https://doi.org/10.22621/cfn.v133i2.2407

Way, J. 2020. [Book Review] The Reign of Wolf 21: The Saga of Yellowstone's Legendary Druid Pack, by Rick McIntyre. Canadian Field-Naturalist 134: 392–393. https://doi.org/10.22621/cfn.v134i4.2739

JONATHAN (JON) WAY
Eastern Coyote/Coywolf Research,
Osterville, MA, USA

NEW TITLES

Prepared by William Halliday

Please note: All books listed are available for review at the time of this publication. Please contact William Halliday (wdhalliday@gmail.com) if you are interested in reviewing any of these or any other new book.

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

BOTANY

A Generic Classification of the Thelypteridaceae. By Susan Fawcett and Alan R. Smith. 2021. BRIT Press. 112 pages, 25.00 USD, Paper.

A Guide to the Flora of the Sierra de San Pedro Mártir. By Alan Harper, Sula Vanderplank, and Jon Rebman. 2021. BRIT Press. 320 pages, 35.00 USD, Paper.

The Hidden Kingdom of Fungi: Exploring the Microscopic World in Our Forest, Homes, and Bodies. By Keith Seifert. 2022. Greystone Books. 288 pages, 34.95 CAD, Hardcover.

Lichen Field Guide for Oklahoma and Surrounding States. By Shelia A. Strawn. 2021. BRIT Press. 131 pages, 30.00 USD, Paper.

Mistletoes of the Continental United States. By Robert L. Mathiasen. 2021. BRIT Press. 220 pages, 25.00 USD, Paper.

A Systematic Vademecum to the Vascular Plants of Saba. By Franklin S. Axelrod. 2021. BRIT Press. 122 pages, 25.00 USD, Paper.

CONSERVATION AND CLIMATE CHANGE

The Carbon Footprint of Everything. By Mike Berners-Lee. 2022. Greystone Books. 312 pages, 24.95 CAD, Paper.

The Declaration of Interdependence: a Pledge to Planet Earth. Special 30th Anniversary Edition. By Tara Cullis and David Suzuki. 2022. Greystone Books. 80 pages, 20.00 CAD, Hardcover.

Tree Thieves: Crime and Survival in North America's Woods. By Lyndsie Bourgon. 2022. Greystone Books. 304 pages, 36.95 CAD, Hardcover.

A Trillion Trees: Restoring Our Forests by Trusting in Nature. By Fred Pearce. 2022. Greystone Books. 344 pages, 36.95 CAD, Hardcover.

ENTOMOLOGY

Ants: the Ultimate Social Insects. By Richard Jones. 2022. Bloomsbury Wildlife. 368 pages, 61.00 CAD, Hardcover.

ORNITHOLOGY

RSPB Spotlight: Eagles. By Mike Unwin. 2022. Bloomsbury Wildlife. 128 pages, 25.00 CAD, Paper.

ZOOLOGY

The Hair Scale Identification Guide to Terrestrial Carnivores of Canada. By Justin Kestler. 2022. Pelagic Publishing. 128 pages, 30.00 GBP, Paper.

OTHER

Best Hikes and Nature Walks With Kids In and Around Southwestern British Columbia. By Stephen Hui. 2022. Greystone Books. 248 pages, 24.95 CAD, Paper.

Forest Walking: Discovering the Trees and Woodlands of North America. By Peter Wohlleben and Jane Billinghurst. 2022. Greystone Books. 240 pages, 24.95 CAD, Paper.

The Hiking Book from Hell. By Are Kalvø. 2022. Greystone Books. 328 pages, 24.95 CAD, Paper.

How to Catch a Mole: Wisdom from a Life Lived in Nature. By Marc Hamer. 2022. Greystone Books. 208 pages, 22.95 CAD, Paper.

An Illustrated Coastal Year: the Seashore Uncovered Season by Season. By Celia Lewis. 2022. Bloomsbury Wildlife. 192 pages, 40.00 CAD, Hardcover.

Mary Strong Clemens, a Botanical Pilgrimage: Her Glorious Mission from here to the Outback via Southeast Asia. By Nelda B. Ikenberry. 2021. BRIT Press. 462 pages, 45.00 USD, Paper.

In Praise of Paths: Walking Through Time and Nature. By Torbjørn Ekelund. 2022. Greystone Books. 240 pages, 22.95 CAD, Paper.

Reading the Water: Fly Fishing, Fatherhood, and Finding Strength in Nature. By Mark Hume. 2022. Greystone Books. 288 pages, 34.95 CAD, Hardcover.

Urban Wild: 52 Ways to Find Wilderness on Your Doorstep. By Helen Rook. 2022. Bloomsbury Wildlife. 224 pages, 38.00 CAD, Hardcover.

The Canadian Field-Naturalist

News and Comment

Compiled by Amanda E. Martin

Upcoming Meetings and Workshops

Society for Integrative & Comparative Biology Annual Meeting

The annual meeting of the Society for Integrative & Comparative Biology to be held 3–7 January 2022 at the Phoenix Convention Center, Phoenix, Arizona. SICB+ to be held 14–31 January 2022 as an online meeting. Registration is currently open. More information is available at http://burkclients.com/sicb/meetings/2022/site/.

Stewardship Network Conference

The Stewardship Network Conference to be held as an online meeting 26–28 January 2022. Registration is currently open. More information is available at https://conference.stewardshipnetwork.org/.

Society for Range Management Meeting

The 75th annual meeting of the Society for Range Management to be held 6–10 February 2022 at the Albuquerque Convention Center, Albuquerque, New Mexico. The theme of the conference is: 'Sustainability through Culture and Innovation'. Registration is currently open. More information is available at http://annualmeeting.rangelands.org/.

Forests Ontario Annual Conference

The annual conference of Forests Ontario to be held as an online meeting 9–11 February 2022. The theme of the conference is: 'Strength in Biodiversity'. Registration is currently open. More information is available at https://forestsontario.ca/en/event/annual-conference.

Midwest Fish & Wildlife Conference

The 82nd Midwest Fish & Wildlife Conference to be held 13–16 February 2022 as a hybrid event, with online content and an in-person meeting in Des Moines, Iowa. The theme of the conference is: 'Fish & Wildlife Stewardship in Working Landscapes'. Registration is currently open. More information is available at https://www.midwestfw.org/.

Wetland Science Conference

The Wetland Science Conference to be held 15–17 February 2022 as a hybrid event, with online content and an in-person meeting at the Holiday Inn Hotel & Convention Center, Stevens Point, Wisconsin. Registration is currently open. More information is available at https://conference.wisconsinwetlands.org/announcing-the-2022-wetland-science-conference/.

Entomological Society of America, Eastern Branch Meeting

The annual Eastern Branch Meeting of the Entomological Society of America to be held 19–21 February 2022 at the Bellevue Hotel, Philadelphia, Pennsylvania. The theme of the meeting is: 'Contribute/Collaborate/Connect'. Registration is currently open. More information is available at https://www.entsoc.org/eastern/branch-meeting.

CCFFR-SCL 2022

CCFFR-SCL 2022, the Canadian Conference for Fisheries Research, to be held 24–27 February 2022 at the JW Marriott Parq Hotel, Vancouver, British Columbia. The theme of the conference is: 'Aquatic Systems Stewardship: Crisis, Change, and Cooperation'. Registration is currently open. More information is available at https://ccffr-scl2022.acadiau.ca/home.html.

VOL. XXXIV. No. 9. DECEMBER, 1920.

THE CANADIAN FIELD-NATURALIST

PUBLISHED BY
OTTAWA FIELD-NATURALISTS' CLUB

ISSUED MAY 12, 1921.

Entered at Ottawa Post Office as second class matter.

The cover of Volume 34, Number 9, showing the earliest cover design for *The Canadian Field-Naturalist* (CFN). A version of this cover design first appeared on issues of *The Ottawa Naturalist* starting with Volume 32, April 1918; it was updated when CFN replaced *The Ottawa Naturalist* in 1919. The cover seen here graced the issues of CFN until 1929.

Table of Contents (*concluded*)

Book Reviews

News and Comment

Upcoming Meetings and Workshops

Mailing date of the previous issue 135(2): 15 November 2021

The CANADIAN FIELD-NATURALIST

VOLUME 135, NUMBER 3 • 2021

(continued inside back cover)

ISSN 0008-3550