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COVER: An adult, female Gyrfalcon (*Falco rusticolus*), one of several large falcons that have been hunting Rock Pigeon (*Columba livia*) at an urban grain terminal in Edmonton, Alberta, during the winter for at least the past two decades. See the article in this issue by Lynds *et al.* pages 205–209. Photo: Gord Court.

The Canadian Field-Naturalist

Large winter falcons and their Rock Pigeon (*Columba livia*) prey at an urban grain terminal in Edmonton, Alberta: an update

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Abstract

In winter, Gyrfalcon (*Falco rusticolus*) and Prairie Falcon (*Falco mexicanus*) frequent a 96-year-old grain terminal, in Edmonton, Alberta, hunting Rock Pigeon (*Columba livia*). This phenomenon was reviewed shortly after it was first noticed by others in 1998 and, since then, we have observed hunting success and methods of Gyrfalcons and Prairie Falcons that were similar but not identical to earlier observations, with success rates of 21.0% and 10.6%, respectively, compared with 10.6% and 26.0% earlier. The most frequently observed hunting strategy for both species was a repeated upward attack on swirling Rock Pigeon flocks, resulting in success rates of 10.7% and 11.4%, respectively. Notably, 50% of downward dive hunts made by Gyrfalcon were successful, although only eight hunts using this method were recorded. The falcons were mildly selective with respect to pigeon colour morphs, with an apparent preference for pied colouration. Contrary to previous interpretations, Rock Pigeon do not appear to eat spilled grain on the building to any great extent; instead, the terminal may simply provide abundant roosting sites, which attain surface temperatures roughly 10°C warmer than ambient on sunny days and at temperatures below −20°C when the building is warmed internally.

Key words: Gyrfalcon; Prairie Falcon; Rock Pigeon; *Falco rusticolus*; *Falco mexicanus*; *Columba livia*; grain terminal; predation; colour preference; thermoregulation; Alberta

Introduction

The Alberta Grain Terminal in Edmonton, Alberta (53.5846°N, 113.5480°W) is home to a large population of Rock Pigeon (*Columba livia*), which in turn attract raptors of several species. The Canadian National rail corridor serves the terminal, and the building has been in operation for 96 years (Lamb 2015). The terminal is now operated by Cargill Inc., who removed the older name and modernized the interior of the facility. We retain the name Alberta Grain Terminal here, for continuity with previous literature and local usage.

Dekker and Lange (2001) investigated the hunting methods and success rates of Gyrfalcon (*Falco rusticolus*) and Prairie Falcon (*Falco mexicanus*) at the terminal, shortly after this phenomenon was first noticed. Since then, numerous additional insights have emerged, and this study summarizes our own observations at the terminal over 14 years. As well, we examined possible preferences of the falcons among pigeon colour morphs, because observers at the terminal had suggested that dark pigeons were preferred targets for predation and easier to see against the light sky or snow-covered ground. We also investigated the role of the building as an internally warmed and/or sun-warmed roost, using thermal imaging. Dekker and Lange (2001) proposed that the terminal was both a roost and a food source, but they emphasized the importance of spilled grain and canola seeds on the roof of the grain-loading annex as the major attractant for pigeons at the terminal.

Frequently, we also observed Merlin (*Falco columbarius*) at the terminal and, less frequently, Peregrine Falcon (*Falco peregrinus*), Bald Eagle (*Haliaeetus leucocephalus*), Northern Goshawk (*Accipiter gentilis*), Cooper's Hawk (*Accipiter cooperii*), and Rough-

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legged Hawk (*Buteo lagopus*), but we do not include data from these species here. Since we gathered our data, Bald Eagles have become more common and the large falcons less so, perhaps as a consequence. The terminal represents a rare opportunity to observe these raptors in an urban, albeit industrial, setting, and the terminal is also unusual because of the abundance of perches it provides on its south face, in part because of its age. In our experience, more modern terminals lack such perches, and are not as attractive to pigeons or raptors.

Methods

Observations of raptor hunting

We observed falcons at the terminal, opportunistically but usually at mid-day, during the winters of 1996–1997, 2002–2004, 2011–2013, and 2015–2018. We also took photos, with metadata, of hunting falcons during the winters of 2013–2018. We made additional observations in 2019–2020, but these were not included in the analyses that follow. Following Dekker and Lange (2001), we classified a hunt as a visible prey-capture attempt, including multiple sequential attempts, considered terminated when the falcon either perched or flew away. We observed from a parking lot about 100 m south of the terminal, at about 130 Street and 126 Avenue NW (for a map of the location see Acorn *et al.* 2018). Hunting methods were classified *post hoc*, and six hunting categories were established: attack on pigeon on ground, downward pass through swirling pigeons, upward pass through swirling pigeons, downward dive from the top of the terminal, level flight attack, and upward pursuit of an individual pigeon. All records included the species involved, but only some specified the type of hunt, because this was sometimes difficult to determine in the moment. Success rates and frequencies of hunting-method use were compared between the two falcon species.

Falcon preferences with respect to pigeon colouration

Photographs of large pigeon flocks (n = 1821) taken in 1999, 2012, 2015, and 2016, were used to determine the frequencies of colour type (wild type, lighter than wild type, darker than wild type, brown, and pied) and to test the assumption that pigeon morph frequencies remained roughly stable over time. Photographs of large falcons grasping or obviously targetting pigeons with their talons (n = 81 for Gyrfalcon, n = 18 for Prairie Falcon), including many obtained from amateur photographers and birders, were also scored for pigeon colour morph. All pigeon images were scored for wing and body colouration separately. G-tests were used to test for differences between expected and observed frequencies of morphs among the four years, and of pigeon morphs chosen as prey by falcons. G-tests were performed in the statistical program R, version 0.99.36 (R Core Team 2019).

Thermal characteristics of the building

To quantify the thermal profile of the terminal, we took infrared photographs of the south face, using a Reveal RW (Seek Thermal, Santa Barbara, California, USA) handheld thermal imager, between November 2018 and February 2019. The imager provides temperature information for a central point on the sensor, in real time, and we attempted to capture the average temperature of the brick wall on the upper face of the building while avoiding any reflective hotspots from windows. We imaged only the south face, because pigeons were rarely if ever seen on the other sides of the building, which also lack ledges or other perches. Simultaneously, the built-in thermometer in a 2016 pickup truck (Ford F-150, Ford, Dearborn, Michigan, USA), parked in the location described above, was used to measure ambient temperature. Conditions were classified as either sunny or cloudy, to assess direct insolation of the building. During February 2019, images of a bare, south-facing cliff, approximately as high as the terminal and located along the valley of the North Saskatchewan River, were also obtained.

Results and Discussion

Hunting methods and success rates for large falcons

We observed falcons at the terminal only from about mid-November to mid-March. We recorded 128 successful and unsuccessful hunting attempts, including 62 for Gyrfalcons and 66 for Prairie Falcons (summarized in Figures 1 and 2). Hunting success rates were the reverse of those observed by Dekker and Lange (2001): 21.0% for Gyrfalcon and 10.6% for Prairie Falcon compared with 10.6% and 26.0%, respectively, reported by Dekker and Lange. Dekker and Lange's data were collected over two winters and were, therefore, based on a small number of individual falcons, whereas our findings were based on multiple additional individuals, over 13 winters. Placed in the context of the extensive dataset gathered by Dekker

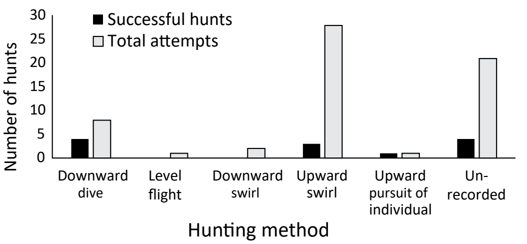

FIGURE 1. Hunting methods used by Gyrfalcon (*Falco rusticolus*) at the Alberta Grain Terminal in Edmonton, Alberta, Canada.

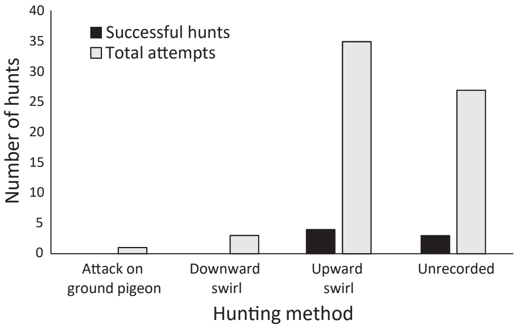

FIGURE 2. Hunting methods used by Prairie Falcon (*Falco mexicanus*) at the Alberta Grain Terminal in Edmonton, Alberta, Canada.

(2009), the average hunting success for large falcons at the terminal fell within the general range reported for Gyrfalcons and Prairie Falcons in other situations, Peregrines in a variety of situations, and Merlins hunting passerines and shorebirds, but lower than those for an experienced breeding pair of Peregrines hunting mostly immature gulls from the stack of a power plant on an Alberta lake (30.3%) or for Peregrines hunting Dunlin (*Calidris alpina*) over the saltmarsh shore zone along the Pacific coast (44%).

With respect to hunting method, the most common method used by both falcon species was a repeated upward attack on swirling pigeon flocks: 28 and 35 hunts, respectively, with success rates of 10.7% and 11.4%. No other raptors observed at the terminal used the upward swirling attack method. Dekker and Lange (2001: 397) also found this to be the preferred hunting method for Gyrfalcon and Prairie Falcon, which they described as "repeated attacks on pigeon flushes". This method is unusual for Gyrfalcon, which generally pursue one prey item for up to several kilometres through the air (Bent 1938; Potapov and Sale 2005).

Gyrfalcon also employed a downward dive from the top of the terminal, resulting in a 50% success rate in the eight hunting attempts observed. This method involves pursuit of an individual pigeon, and, although a high success rate reveals that it is efficient, it is not the most frequent method used by raptors hunting at the terminal. Perhaps specific factors, such as injured or weak pigeons, influence Gyrfalcon to use this hunting method. Rarely, Prairie Falcon have been observed using the downward dive hunting method at the terminal; however, all three Prairie Falcon hunts of this type we observed were unsuccessful. Dekker and Lange (2001) found that Prairie Falcon use this method successfully.

Unfortunately, hunting method was not apparent for 39.2% of the observed hunts. With up to a thousand birds in flight at a time it is often difficult to track the movements of the falcons and to adequately observe the moment when a pigeon has been taken. It was not unusual to suddenly notice a large falcon carrying prey. As well, hunts reported to us by birders and photographers often failed to indicate the method. Overall, however, our results indicate that Gyrfalcon and Prairie Falcon have such similar hunting styles and success rates that they are functionally equivalent in their ecological effects at the terminal, differing only insofar as Gyrfalcon can generally displace Prairie Falcon when both are present.

Falcon preferences with respect to pigeon colouration

Analysis of pigeon images showed no significant differences in frequency of colour morphs among years, supporting the assumption that morph ratios have remained relatively constant. Morph ratios among pigeons targetted by falcons (Figure 3, Table 1) were similar to those in the overall population, except for pied pigeons, which appeared to be overrepresented among the prey in the pooled Gyrfalcon and Prairie Falcon data. We pooled data for both falcon species to increase the sample size for analysis and because the birds appeared to use similar hunting techniques.

The notion among birders and photographers at the terminal that falcons can track dark pigeons more easily against a light background does not appear to be supported by our data, but a slight tendency for falcons to prefer pied pigeons could conceivably be influenced by the same mechanism. It is perhaps noteworthy that Rock Ptarmigan (*Lagopus muta*), which have colouration roughly comparable to pied-winged pigeons, are frequent prey for Gyrfalcons at higher latitudes and make up 50–95% of their diet biomass throughout the circumpolar region (Nielsen and

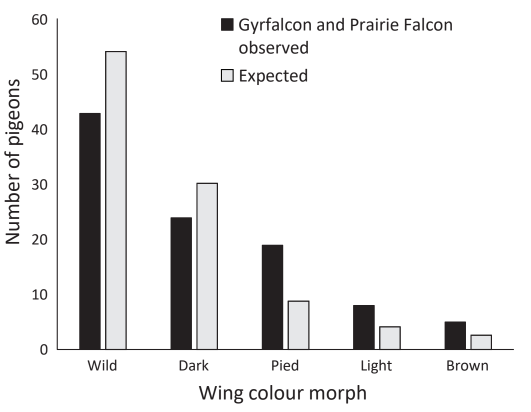

FIGURE 3. Combined Gyrfalcon (*Falco rusticolus*; $n = 81$) and Prairie Falcon (*Falco mexicanus*; $n = 18$) kills of Rock Pigeon (*Columba livia*), by colour morph, at the Alberta Grain Terminal in Edmonton, Alberta, Canada.

TABLE 1. Rock Pigeon (*Columba livia*) colour morphs targetted by Gyrfalcon (*Falco rusticolus*) and Prairie Falcon (*Falco rusticolus*) at the Alberta Grain Terminal in Edmonton, Alberta, Canada. *P* values in bold type indicate a significant difference ($P < 0.05$) between proportion of targetted prey and proportion in the general population.

Colour morph	*G*-test results (*P* values)					
	Wild	Dark	Pied	Light	Brown	All other
Wild		5.50E-06 (0.998)	5.113 **(0.024)**	2.062 (0.151)	1.338 (0.247)	2.325 (0.127)
Dark			4.352 **(0.037)**	1.894 (0.169)	1.264 (0.261)	0.905 (0.341)
Pied				0.021 (0.884)	0.016 (0.900)	4.548 **(0.033)**
Light					7.37E-06 (0.998)	1.380 (0.240)
Brown						0.837 (0.360)
All other						

Pétursson 1995; Booms *et al.* 2008). Potapov and Sale (2005) suggest that Gyrfalcons are the selective agents responsible for polymorphism in *Lagopus* spp. In general, however, falcons at the terminal were only mildly selective with respect to pigeon colour morphs and do not appear to be driving changes in pigeon polymorphism at this location.

Thermal characteristics of the building

Our observations do not corroborate the suggestion that pigeons feed on spillage on the roof of the grain-loading annex, and perhaps the source of spillage has been repaired. We observed only occasional groups of pigeons feeding at roof or ground level and then almost always inside the grain loading bays of the annex at times when workers and rail cars were not present. Although some grain does spill from the bottom of hopper cars, there is no longer reason to expect spillage higher in the terminal infrastructure.

On cloudy days warmer than −20°C ($n = 24$) the mean surface temperature of the south face of the terminal was only 1.2°C warmer than mean ambient temperature (Figure 4). However, on cloudy days when ambient temperatures dropped below −20°C ($n = 5$), the terminal surface temperature was 7–10°C warmer than ambient, likely because the terminal releases heat internally, presumably in response to cold outdoor conditions. On sunny days ($n = 5$), terminal surface temperatures were on average 13.8°C warmer than ambient, and maximally 23°C warmer than ambient, presumably as a result of direct insolation of the south face of the terminal.

Pigeons in natural situations are often found roosting on cliffs and nesting in crevices on such cliffs (Peterson *et al.* 1966). In Edmonton, the 22-story terminal (Lamb 2015) towers above the surrounding warehouses and neighbourhoods and offers a thermally comparable structure (Figure 5), with pipes, brackets, windowsills, and various other complex horizontal surfaces suitable for roosting. Solar and internal warming of the south face seems to attract pigeons, but an abundance of pigeons on days when the south face is at ambient temperature demonstrates that

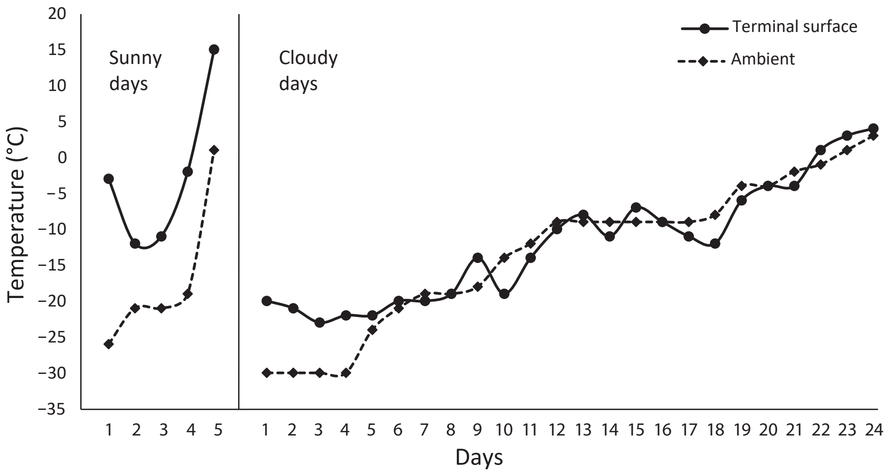

FIGURE 4. Surface and ambient temperature of the south face of the Alberta Grain Terminal in Edmonton, Alberta, Canada, on sunny ($n = 5$) and cloudy ($n = 24$) days in winter, 2019.

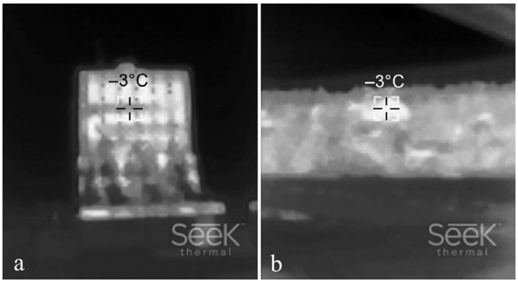

FIGURE 5. a. Thermal image of the south face of the Alberta Grain Terminal in Edmonton, Alberta, Canada, on a sunny day (9 February 2019), with a surface temperature of −3°C and ambient temperature of −26°C. b. Thermal image of a bare cliff face on the North Saskatchewan River (12 February 2019) on a sunny day with a surface temperature of −3°C and ambient temperature of −21°C.

elevated temperatures are not essential to the birds. The attraction of the terminal to pigeons is, therefore, a complex matter of roosting surfaces, ground-level food, and temperature, which together attract pigeons despite the risk of predation by large falcons.

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Note

First verified sighting of a Western Fence Lizard (*Sceloporus occidentalis*) in British Columbia, Canada

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Abstract
Western Fence Lizard (*Sceloporus occidentalis*) is known from Baja California, Mexico, north to north-central Washington State, including Puget Sound, where scattered populations extend from the Cherry Point area south to Tacoma and along the west side of Puget Sound to Port Townsend. On 6 June 2020, a single juvenile *S. occidentalis* was photographed in a Cloverdale area garden, Surrey, British Columbia, representing the first verified sighting of this species in Canada. No other *S. occidentalis* were sighted in the area, and we could not determine how the specimen entered the province.

Key words: British Columbia; first sighting; Western Fence Lizard; *Sceloporus occidentalis*

Western Fence Lizard (*Sceloporus occidentalis*) is known from several islands off Baja California, Mexico, and California, USA, and on the North American continent from northern Baja California through California, Nevada, western Utah, Idaho, Oregon, and Washington (Storm *et al.* 1995; St. John 2002; Stebbins and McGinnis 2018). An isolated observation of one *S. occidentalis* in Rosebud County, and eight reports in Sanders County, Montana, represent introduced lizards (Anonymous 2020). Davis and Verbeek (1972) noted that *S. occidentalis* frequented coastal localities throughout the species' latitudinal range, including east and west sides of Puget Sound, Washington, where it is found on log-littered shorelines. Brown (1992) introduced *S. occidentalis* in Puget Sound beyond its native range, and, as noted by Kraus (2009), the four experimental translocations from just north of Everett, Washington, to Clayton Beach (in 1986 and again in 1990), Oyster Creek (in 1990), and Cherry Point (also in 1990) resulted in breeding populations. On the west side of Puget Sound, *S. occidentalis* ranges north to Port Townsend (Stebbins and McGinnis 2018). Owen (1940) also mentioned that *S. occidentalis* occurred in the Cape Flattery area, Clallam County, Washington, although this location is not included in recent field guides and the population may not persist today. Given its proximity to the Canadian border, Matsuda *et al*. (2006) listed *S. occidentalis* as a potential immigrant, and, here, we document the first sighting of *S. occidentalis* in British Columbia.

A single juvenile *S. occidentalis* (Figure 1) was photographed by R.F. on 6 June 2020, at 1150, 49.103868°N, 122.719329°W, in the Cloverdale area

Figure 1. The single juvenile Western Fence Lizard (*Sceloporus occidentalis*) found in the Cloverdale area of Surrey, British Columbia, Canada, 6 June 2020. Total length estimated at 50 mm. Photo: R. Farrell.

of Surrey, British Columbia (Figure 2), but was not captured. The photograph was forwarded to the Royal British Columbia Museum to confirm identification. The dorsal colouration of the lizard was unusual for *S. occidentalis* (A. St. John pers. comm. 9 June 2020), but was similar to that of a specimen photographed at Teddy Bear Cove, Washington (https://inaturalist.ca/observations/47077052). Furthermore, the pale yellow-orange tint to the rear surfaces of fore and hind limbs is diagnostic, distinguishing *S. occidentalis* from Sagebrush Lizard (*Sceloporus graciosus*), which is also found in Washington (Storm *et al*. 1995; St. John 2002; Stebbins and McGinnis 2018). The tail of the lizard was almost entirely missing, but was regenerating. It was a juvenile, with total length estimated at 50 mm based on dimensions of deck boards in the photograph.

Latitude and longitude for the locality were generated from photograph metadata. The location is bordered on the north by 56th Avenue (British Columbia Highway 10) and urban housing and on the south by a semi-rural environment of undeveloped fields and blueberry farms with limited commercial development stretching to the international border. The area between Cloverdale and the border is interrupted by railroad tracks and the Redwood Park housing district; there are no major roads to impede dispersal. Perhaps the only significant barrier to northward dispersal in this region is the Nicomekl River, which is a low-gradient stream south of Cloverdale, ranging

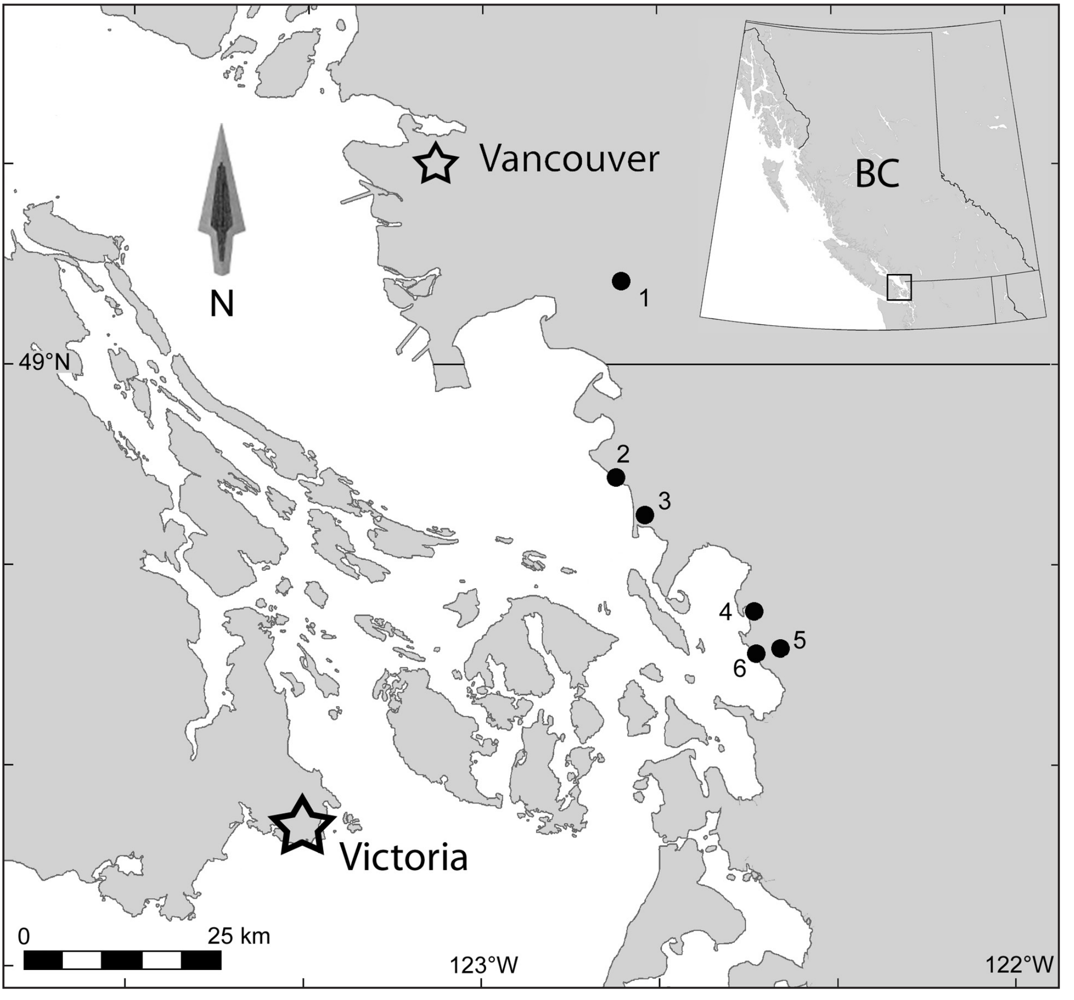

FIGURE 2. Location of the Western Fence Lizard (*Sceloporus occidentalis*) photographed in the Cloverdale area of Surrey, British Columbia (1) and nearest records in Washington: 2. Cherry Point; 3. the Ferndale area, based on Storm *et al*. (1995); 4. Teddy Bear Cove–Chuckanut Mountain (https://inaturalist.ca/observations/47077052); 5. Oyster Creek; 6. Clayton Beach. Populations at 2, 5, and 6 intentionally introduced and studied by Brown (1992).

from 22 m to about 4 m wide. This semi-rural habitat continues south of the border, with scattered woods and farmland south to the Cherry Point area where *S. occidentalis* is known to exist.

In the Puget Sound area of Washington, *S. occidentalis* is known from scattered locations, with the northernmost population introduced at Cherry Point, Washington (Figure 2; Brown 1992; Storm *et al*. 1995). The species also is recorded in iNaturalist from the coast at Teddy Bear Cove–Chuckanut Mountain, south of Fairhaven and Bellingham, and from there south to the Tacoma area. The population at Cherry Point is about 27 km south of where the Cloverdale specimen was photographed. The Cloverdale specimen represents the first verified sighting of a free-ranging *S. occidentalis* in Canada. In addition to this record, *S. occidentalis* was reported on iNaturalist on 29 April 2019, at MacNeill Secondary School, Richmond, British Columbia (https://www.inaturalist.org/observations/23960841), but the report cannot be verified because neither the specimen nor photograph is available. Given other iNaturalist records at that location, the lizard may be in captivity in a classroom. It is possible that the Cloverdale specimen was transported by human activity, as was a single *S. occidentalis* that appeared in cargo at Apra Harbor, Guam, in 1992 (Wiles 2000; Kraus 2009), or it could be an escaped pet.

Author Contributions

Writing – Original Draft: G.H.; Writing – Review & Editing: G.H. and D.V.; Species Identification: R.F., G.H., and D.V.

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Note

New records of grasshoppers (Orthoptera) from the Northwest Territories

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Abstract
We provide information on two additions to the fauna of Northwest Territories, Canada: Two-striped Grasshopper (*Melanoplus bivittatus*) and Huron Short-winged Locust (*Melanoplus huroni*). We suspect that both are long established but were overlooked in the past as a consequence of general rarity.

Key words: Orthoptera; grasshoppers; distribution; ecology; Northwest Territories; new records; range extensions; Two-striped Grasshopper; *Melanoplus bivittatus*; Huron Short-winged Locust; *Melanoplus huroni*

Recent updating of information on Northwest Territories (NWT) grasshoppers has included (1) a 700-km extension to the northwest of the range of Graceful Sedge Grasshopper (*Stethophyma gracile* (Scudder, 1862)) which was reported in Catling *et al*. (2017), and (2) unexpected range extensions into the tundra for Northern Grasshopper (*Melanoplus borealis* (Fieber, 1853)), Bruner Spur-throated Grasshopper (*M. bruneri* Scudder, 1897), Club-horned Grasshopper (*Aeropedallus arcticus* Hebard, 1935), and Crackling Grasshopper (*Trimerotropis verruculata* (Kirby, 1837)), all outlined by Catling *et al.* (2018a). Here we report the addition of Two-striped Grasshopper (*Melanoplus bivittatus* (Say, 1825)) and Huron Short-winged Locust (*Melanoplus huroni* Blatchley, 1898) to the NWT fauna. Both of these species were expected to be found in the NWT (Working Group on General Status of NWT Species 2016) and were described and included in the key of Catling (2008). The names and subfamily classification follow Cigliano *et al.* (2020).

Acrididae
Melanoplinae

Melanoplus bivittatus (Say, 1825), Two-striped Grasshopper

The first locations in the NWT for this large grasshopper are 425 km to the north-northwest of the nearest site to the south at Fort McMurray, Alberta. These Slave River sites were in native prairies (Catling *et al.* 2018b) dominated by either graminoids, such as Wheat Sedge (*Carex atherodes* Sprengel), Kentucky Bluegrass (*Poa pratensis* L.), Canada Wildrye (*Elymus canadensis* L.), and/or reedgrasses (*Calamagrostis* spp.), or by forbs including Biennial Ragwort (*Artemisia biennis* Willdenow), Yellow Avens (*Geum aleppicum* Jacquin), Blue Lettuce (*Mulgedium pulchellum* (Pursh) G. Don), Silverweed (*Potentilla anserina* L.), and Common Dandelion (*Taraxacum officinale* F.H. Wiggers). A drier site (Figure 1) was dominated by Clustered Field Sedge (*Carex praegracilis* W. Boott), Balsam Groundsel (*Packera paupercula* (Michaux) Á. Löve & D. Löve), and Kentucky Bluegrass (*Poa pratensis* L.).

At both the Grande Detour Prairie and Kim's Bison Prairie sites (see *Voucher specimens*), Red-legged Grasshopper (*Melanoplus femurrubrum* DeGeer, 1773) was very abundant with up to 100 flying up with each step we took. Migratory Grasshopper (*Melanoplus sanguinipes* (Fabricius, 1798)) and Two-striped Grasshopper were much less common, with fewer than 50 confirmed at each of the two sites.

The pair of pale dorsal lines is distinctive. The male cerci with a ventral lobe resulting in a boot-shape is a characteristic possessed only by two other

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FIGURE 1. Habitat (foreground) of Two-striped Grasshopper (*Melanoplus bivittatus*) in a drier portion of Kim's Bison Prairie in the Slave River Lowland, Northwest Territories, Canada. The site has a boundary of Trembling Aspen (*Populus tremuloides* Michaux) and the open foreground is dominated by Clustered Field Sedge (*Carex praegracilis*), Balsam Groundsel (*Packera paupercula*), and Kentucky Bluegrass (*Poa pratensis*). Photo: P.M. Catling.

species of *Melanoplus,* both found in eastern Canada (Vickery and Kevan 1985).

Melanoplus huroni Blatchley, 1898, Huron Short-winged Locust (Figure 2)

The first location for this species in the NWT is ~675 km north of the nearest location in the Peace River Prairies of Alberta. It is in an area of more or less burned Jack Pine (*Pinus banksiana* Lambert) parkland with prairie glades (Figure 3) that include disjunct plants and animals from the Canadian prairie region far to the south as well as some elements from unglaciated Beringia to the northwest. The dominant plants here include Cut-leaved Anemone (*Anemone multifida* Poiret), Common Bearberry (*Arctostaphylos uva-ursi* (L.) Sprengel), Purple Reedgrass (*Calamagrostis purpurascens* R. Brown), Downy Lymegrass (*Elymus innovatus* (Beal) Pilger), and Northern Bedstraw (*Galium boreale* L.).

Among the grasshoppers, Speckle-winged Rangeland Grasshopper (*Arphia conspersa* Scudder, 1875) of the Canadian prairies and unglaciated Beringia (Vickery and Kevan 1985) shares this unusual habitat in the NWT.

Key features in identifying the Huron Short-winged Locust include the short wings (to third or fourth abdominal segment) with the outer wings (tegmina) spotted, male subgenital plate (rear view) with a pointed apical tubercle, male cerci becoming slender apically, and male furculae small and blunt (Vickery and Kevan 1985: figs. 449, 486, 522; Otte 2012: 146).

We suspect that both species reported here are long established in the NWT, but were overlooked in the past as a consequence of their local occurrence and limited search effort for orthopteroid insects in the north. Both occur in largely isolated patches of northern prairie and are likely to be absent from forested landscapes between the newly discovered sites and the previous northernmost records. Two-striped Grasshopper thrives in non-native vegetation and is readily transported by vehicles (Catling 2008). It moves along roads and may also be transported in hay, which was introduced in the Slave River lowlands (Catling *et al.* 2018b: 7–8). Sites where Two-striped Grasshopper was found in the Slave River lowlands do not have concentrations of introduced plants and are not known sites of hay introduction, nor are they connected to roads. Thus, we favour native status for this grasshopper. However, we anticipate that Two-striped Grasshopper will become more continuously distributed in the northern prairie prov-

FIGURE 2. Huron Short-winged Locust (*Melanoplus huroni*) from a native prairie glade in Jack Pine (*Pinus banksiana*) parkland northwest of Great Slave Lake, Northwest Territories, Canada. Photo: P.M. Catling.

FIGURE 3. Habitat of Huron Short-winged Locust (*Melanoplus huroni*) in Jack Pine (*Pinus banksiana*) parkland that was burned four years previously northwest of Great Slave Lake, Northwest Territories, Canada. Photo: P.M. Catling.

inces and southern NWT as a result of human activity. Its status in the NWT will then be "native and introduced". Huron Short-winged Locust, as a native prairie specialist, is much less likely to increase its range substantially, but it will probably be found in other prairies of the Great Slave Lake region.

Voucher specimens

Melanoplus bivittatus (Say, 1825)—CANADA, NORTHWEST TERRITORIES: Slave River Lowland, Grande Detour Prairie, 60.4036°N, 112.7291°W, 28 July 2018, *P.M.C., B.K., T.A.* Canadian National Collection of Insects (CNC 1009518); Kim's Bison Prairie, 60.9951°N, 112.8103°W, 28 July 2018, *P.M.C., B.K., T.A.* Canadian National Collection of Insects (CNC 1009519).

Melanoplus huroni Blatchley, 1898—CANADA, NORTHWEST TERRITORIES: open prairie-like glade in Jack Pine parkland on Hwy. 3 south of Rae/Edzo, 62.3842°N, 116.4989°W, 6 July 2019, *P.M.C., B.K.* Canadian National Collection of Insects (CNC 1009517).

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Note

A case of a Pustulated Carrion Beetle (*Nicrophorus pustulatus*, Coleoptera: Silphidae) burying live Tree Swallow (*Tachycineta bicolor*, Passeriformes: Hirundinidae) nestlings under the nest

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Abstract
The ecology of Pustulated Burying Beetle (*Nicrophorus pustulatus*, Coleoptera: Silphidae) appears distinct among *Nicrophorus* species, with evidence of it parasitizing snake eggs and foraging primarily above the ground and into the forest canopy. Here we document an extension of its aberrant ecology and behaviour: a case of *N. pustulatus* burying 2-day-old live and dead nestlings of Tree Swallow (*Tachycineta bicolor*, Passeriformes: Hirundinidae) under the nest, behaviour consistent with the early stages of breeding in *N. pustulatus*. Based on different levels of decomposition, we suspect that *N. pustulatus* responded to one dead swallow nestling in the brood of five and went on to bury all of the nestlings at the bottom of the nest box. The observation provides the first evidence, to our knowledge, of *Nicrophorus* burying live vertebrates.

Key words: Burying beetle; *Nicrophorus pustulatus*; Tree Swallow; *Tachycineta bicolor*; evolutionary ecology

Pustulated Carrion Beetle (*Nicrophorus pustulatus* Herschel, Coleoptera: Silphidae) has a broad distribution across the eastern United States and Canada (Anderson and Peck 1985; Ringrose *et al.* 2019), and yet its ecology has remained puzzling. Early observations suggested that this species was rare throughout its range because few were captured in ground traps that typically attract burying beetles (Wilson *et al.* 1984; Anderson and Peck 1985; Trumbo 1990; Robertson 1992). However, observations of *N. pustulatus* coming in to lights at night hinted that it may be more common than ground trapping has revealed (Anderson and Peck 1985; Robertson 1992; Lingafelter 1995).

In captivity, *N. pustulatus* readily bred on vertebrate carcasses >100 g, suggesting that this species may specialize in larger carcasses, unlike many other *Nicrophorus* species that typically use small vertebrate carrion for breeding (Trumbo 1990; Robertson 1992). Experiments in the lab further demonstrated that *N. pustulatus* was unique among coexisting *Nicrophorus* in its ability to raise up to 187 young in a single reproductive bout (one female) on larger carcasses (up to 260-g Black Rat [*Rattus rattus*]), sometimes even rejecting smaller carcasses (<20 g) for breeding (Trumbo 1992). The scarcity of *N. pustulatus* captured in the field, even on larger carcasses, was perplexing (Wilson *et al.* 1984; Trumbo 1992). Also, observations of *N. pustulatus* acting as a brood parasite of Roundneck Sexton Beetle (*Nicrophorus orbicollis* Say) in captivity provided evidence of more complexity in its breeding biology (Trumbo 1994).

The discovery of *N. pustulatus* regularly parasitizing oviparous snake eggs (Blouin-Demers and Weatherhead 2000; Keller and Heske 2001; Smith *et al.* 2007; LeGros *et al.* 2010) documented a remarkable evolutionary shift for burying beetles. *Nicrophorus* were only known to reproduce on the carcasses of vertebrates (Scott 1998), and thus larvae entering and parasitizing live, developing vertebrate eggs and causing their mortality was unique (Blouin-Demers and Weatherhead 2000). The suggestion that

N. pustulatus could be a snake egg specialist, however, was at odds with (i) its capture at traps baited with rat (Trumbo 1990; Ulyshen *et al.* 2007), chicken (Wettlaufer *et al.* 2018), goose (Ringrose *et al.* 2019), fish (White Sucker [*Catostomus commersonii*]; Anderson 1982), and ground beef (Robertson 1992); (ii) its willingness to breed on vertebrate carcasses in captivity (Robertson 1992; Rauter and Moore 2002; Trumbo 2007; Rauter and Rust 2012); (iii) its similarity to other *Nicrophorus* in terms of breeding biology in the lab, including burying, removing fur, and preparing mouse carcasses (Robertson 1992); and (iv) its occurrence outside of the range of oviparous snakes (Ringrose *et al.* 2019), although beetles could potentially parasitize turtle eggs in some of these areas (Blouin-Demers and Weatherhead 2000; Smith *et al.* 2007). Although the use of vertebrate carcasses could represent an ancestral trait that had not yet been lost (Blouin-Demers and Weatherhead 2000; Smith *et al.* 2007), evidence suggested that *N. pustulatus* would still likely use vertebrate carrion as a resource for reproduction in nature.

The capture of *N. pustulatus* in passive insect traps in the forest canopy (Ulyshen *et al.* 2007), followed by repeated successful trapping of this species using baited traps set above the ground (Ulyshen *et al.* 2007; LeGros and Beresford 2010; Low and Lauff 2012; Dyer and Price 2013; Brown and Beresford 2016; Wettlaufer *et al.* 2018), provided new evidence that this species could be a specialist on vertebrate resource opportunities above the ground. In most populations, *N. pustulatus* was more common in traps set above the ground than on it (Ulyshen *et al.* 2007; LeGros and Beresford 2010; Dyer and Price 2013; Wettlaufer *et al.* 2018) and represented the only carrion beetle species to be more abundant in the canopy than on the ground (Ulyshen *et al.* 2007; LeGros and Beresford 2010; Wettlaufer *et al.* 2018).

If *N. pustulatus* is uniquely common above the ground, then what resources does it use for breeding, and how does it prepare or bury its resources for breeding? One hypothesis is that *N. pustulatus* specializes in nesting vertebrates, such as birds, snakes, and mammals, taking advantage of mortality associated with reproduction, in addition to live snake eggs (LeGros and Beresford 2010; Wettlaufer *et al.* 2018). Observations of *N. pustulatus* in the nests of cavity-nesting birds, including cases of it burying dead nestlings in the nests, are consistent with these ideas (Phillips *et al.* 1983; Low and Lauff 2012; Wettlaufer *et al.* 2018).

Here we report an extension of these observations: a case of *N. pustulatus* burying nestlings of the cavity-nesting Tree Swallow (*Tachycineta bicolor*, Hirundinidae), including at least one live nestling, under the nest.

At 1440 on 10 June 2019, K.V.B.D. was checking nests of Tree Swallows at the Massassauga Tree Swallow nest box grid at the Queen's University Biological Station in southeastern Ontario (44°34′38.9″N, 76°23′07.9″W, 150 m elevation), where 54 artificial nest boxes were part of a long-term Tree Swallow monitoring project (Cox *et al.* 2019). Nest checks are conducted every three days throughout May and June and into July, to monitor the progress of nest building and record information on important breeding events, such as first egg, incubation start, and hatch. During nest checks, K.V.B.D. came across a failed nest, ~35 m from the forest, and ~1.5 m above the ground, that had contained five eggs on 7 June. The first egg in this nest was laid on 21 May, and the female Tree Swallow began incubating on 25 May, the day she laid the final egg. The estimated hatch date was 8 June (calculated as 14 days after the beginning of incubation).

On 10 June, the nest was expected to contain two-day old nestlings; however, K.V.B.D. found the nest empty. When a nest that is expected to contain eggs or nestlings is empty, it usually means that it has been subject to predation. In such cases, the nest is removed from the box by researchers so that a new pair of birds can use it. When K.V.B.D. lifted the nest to remove it, she found five nestlings on the wooden floor of the nest box: four dead and one alive. One large *N. pustulatus*, identified later in photos and video by P.R.M. (following Anderson and Peck 1985; voucher photographs deposited in the Canadian National Collection of Insects, Arachnids and Nematodes, https://cnc.agr.gc.ca/taxonomy/Specimen.php?id=2520115), was also present in the box, carrying or pulling two of the nestlings across the bottom of the box. The *N. pustulatus* then went to the back corner of the box and attempted to hide under some of the nest material that was still present. Photos and videos of *N. pustulatus* and the nestlings, as well as the nest and nest box, are archived in the Macaulay Library, Cornell Lab of Ornithology, and are available online (https://macaulaylibrary.org/asset/173174091, 173174111, 173174121, 488626, 488627, 488628). The live nestling (far right in the photos and video) had a fresh faecal sac stuck to its cloaca and was moving. Three of the four dead nestlings looked fresh, with normal colouration and no signs of decomposition. The fourth dead nestling (far left in photos and video) was yellowish, with a darker colouration of the abdomen under the skin, consistent with decomposition. No odour of decomposition was noticed by K.V.B.D. The developmental stage of the nestlings (see Gates 2019) was consistent with their having hatched on 8 June. We did not weigh the nestlings, but a Tree Swallow nestling of similar age and developmental stage typically weights 2–5 g (Zach and Mayoh 1982; Quinney *et al.* 1986).

The adult Tree Swallows did not appear to be active at the nest. When a nest is being cared for by adults, they typically become agitated when someone approaches the nest and will dive-bomb (Winkler *et al.* 2011; K.V.B.D. pers. obs.). Because this did not occur during the several minutes that K.V.B.D. observed the nestlings, it is likely that the adults had already abandoned the nest. The cause of death of the nestlings is unknown, and there was no mortality at any of the other 53 boxes at the site in the days leading up to or following the death of these nestlings. The nestlings showed no signs of damage or physical trauma, and the faecal sac stuck to the live nestling is consistent with recent feeding by the adults.

Following the observation, K.V.B.D. left the nestlings and the beetle in the box (with the nest); when she returned to the grid on 13 June 2019, the nestling carcasses had decayed, suggesting that the beetle had abandoned them.

We provide evidence of *N. pustulatus* burying live Tree Swallow nestlings under the nest, consistent with the early stages of preparation for breeding on vertebrate carrion in this species (Robertson 1992). We suspect that the beetle was attracted to the nest by one dead nestling in the nest box, and that it proceeded to bury the remaining live nestlings as well. Although we did not witness *N. pustulatus* burying the nestlings, we surmise that this occurred because (i) *N. pustulatus* regularly bury vertebrate carcasses in captivity (Robertson 1992), (ii) the *N. pustulatus* was observed moving two dead nestlings in the nest box suggesting that it was treating the nestlings as a resource, (iii) adult Tree Swallows have never been recorded burying nestlings despite extensive study (Winkler *et al.* 2011), (iv) nestling Tree Swallows at that developmental stage have little coordinated movement beyond raising their heads during begging (Winkler *et al.* 2011), (v) Tree Swallow nestlings have never been recorded burrowing into the nest on their own (Winkler *et al.* 2011), and (vi) the Tree Swallow nest was composed of densely interwoven grasses and other materials (https://macaulaylibrary.org/asset/173174121), making the passive movement of all nestlings to the bottom of the nest box almost impossible, even while *N. pustulatus* was burying a dead nestling. Given their developmental stage, the nestlings would likely be unable to resist being moved by *N. pustulatus*. We saw no evidence that the beetle injured or killed the dead nestlings; however, once buried, the nestlings would not be fed or retrieved by the adult Tree Swallows, and thus would likely starve. The faecal sac present on the one remaining live nestling suggests that it had been fed by the adults sometime earlier that day. *Nicrophorus pustulatus* are typically nocturnal when foraging (Anderson 1982; Anderson and Peck 1985) and, thus, likely entered the nest box the previous night when adult females usually brood young nestlings (Winkler *et al.* 2011).

Nicrophorus pustulatus has been found previously in Tree Swallow nest boxes at our study site, always associated with dead nestlings. In 2017, *N. pustulatus* was found in a nest box with a brood of Tree Swallow nestlings that had all died when they were 8–12 days old (A. Cox pers. comm. August 2019). On 14 June 2016, a male–female pair of *N. pustulatus* was found with five, week-old dead nestlings buried at the bottom of a nest box, suggesting that the pair was beginning to breed (A. Schizkoske unpubl. data 2016 as cited in Wettlaufer *et al.* 2018). Before 2016, researchers on the Tree Swallow grids had also noticed carrion beetles in boxes associated with nestling mortality (both American Carrion Beetle [*Necrophila americana* L.] and *Nicrophorus* spp.); however, the beetles were not identified to species (F. Bonier pers. comm. August 2019).

Tree Swallows are extremely sensitive to cold and rainy weather because they rely on flying insects for food, and insects are less likely to fly during poor weather (Winkler *et al.* 2011, 2013; Cox *et al.* 2019). When cold, rainy weather events coincide with the nestling period for Tree Swallows, nestlings suffer high mortality (Winkler *et al.* 2013; Cox *et al.* 2019) creating a potentially abundant resource for burying beetles. This resource may be limited by adult Tree Swallows removing dead nestlings in response to partial brood mortality (Chek and Robertson 1991) and by researchers removing dead nestlings during nest checks. In addition to Tree Swallow nests, *N. pustulatus* has also been found in the nests of two other cavity-nesting birds: Northern Saw-whet Owl (*Aegolius acadicus*; Phillips *et al.* 1983) and American Kestrel (*Falco sparverius*; Low and Lauff 2012). Both of these species will accumulate excess prey remains in the nest (Smallwood and Bird 2002; Rasmussen *et al.* 2008) that could be food for *N. pustulatus*, and American Kestrels often suffer nestling mortality and partial brood loss when prey is scarce (Smallwood and Bird 2002).

The burying of live vertebrates has not, to our knowledge, been described previously in the genus *Nicrophorus* (Anderson and Peck 1985; Scott 1998). Although we suspect that the behaviour was accidental, associated with a beetle responding to a dead nestling, it represents an interesting intermediate step between scavenging and predation that might be expected in the evolution of predatory behaviour. Such a transition was suggested for the origins of snake egg parasitism, which may have begun with *N. pustulatus* responding to ruptured or spoiled eggs that failed to hatch, and progressed to parasitoid behaviour (Blouin-Demers and Weatherhead 2000; Smith *et al.* 2007). Although burying live nestlings may be a rare occurrence, most nest box researchers clean out the nest boxes after the end of the nesting season (Gates 2019), and, thus, cases of live burial would not likely be discovered. Also, any nestling alive at the time of burial would likely starve soon after and would, therefore, be dead on discovery by researchers.

The burial behaviour of *N. pustulatus* in this and previous nests suggests that dead nestlings of birds are used for breeding, adding new perspectives to *N. pustulatus* ecology. Overall, *N. pustulatus* appears most common off the ground and in the canopy and seems extremely flexible in its ability to use different resources, including resources of different sizes (Trumbo 1992). The use of snake eggs, particularly in cavity nests above the ground (Blouin-Demers and Weatherhead 2000), has parallels with observations of *N. pustulatus* in bird nests. Collectively, carrion and other sources of food arising from vertebrate reproduction may provide an important resource for *N. pustulatus* largely ignored by ground-breeding burying beetles.

Author Contributions

Discovery, Observations, Photos, and Video: K.V.B.D.; Investigation: K.V.B.D. and P.R.M.; Writing – Original Draft Preparation: K.V.B.D. and P.R.M.; Writing – Review & Editing: K.V.B.D. and P.R.M.

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Freshwater turtle by-catch from angling in New Brunswick, Canada

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Abstract
Turtles are among the most threatened vertebrate taxa, with populations especially vulnerable to any increase in adult mortality. By-catch from freshwater angling, as a potential cause of turtle mortality is poorly documented and little understood. Here we document cases of turtle by-catch by recreational anglers in an urban park in New Brunswick and among the wider angling communities in the province. We also consider factors that may influence rates of hooking. Although we are unable to estimate turtle hooking frequency for the provincial recreational angling community as a whole, five of 75 (~7%) anglers interviewed in the urban park reported interactions with a turtle, with most reported incidents (75%) involving hooking. Snapping Turtles (*Chelydra serpentina*) seem to be more prone to hooking than Eastern Painted Turtles (*Chrysemys picta picta*). Although we conclude that turtle hooking by recreational anglers appears to be generally uncommon in New Brunswick, even apparently low by-catch rates may be sufficient to lead to population declines at heavily fished sites. The collection of additional data on turtle by-catch in the recreational fishery in Canada is warranted.

Key words: Angling by-catch; *Chelydra serpentina*; *Chrysemys picta picta*; *Glyptemys insculpta*; fishing; New Brunswick; Eastern Painted Turtle; Snapping Turtle; Wood Turtle; Red-eared Slider; threats; *Trachemys scripta*

Introduction
Turtle populations have declined worldwide. Globally, 62% of turtle species are at risk of extinction (IUCN 2020). Numerous investigations have focussed on mitigating threats to turtles, which include roads (e.g., Gibbs and Shriver 2002; OMNRF 2016), agriculture (e.g., Saumure and Bider 1998; Tingley *et al.* 2009; Erb and Jones 2011), and subsidized predators (Ratnaswamy *et al.* 1997; Browne 2003; Browne and Hecnar 2007; Wirsing *et al.* 2012). Although it is known that freshwater turtles are accidentally caught by recreational anglers (Nemoz *et al.* 2004; Enge *et al.* 2013; Steen *et al.* 2014), little information is available about rates of turtle by-catch in recreational fisheries; survival rates for hooked, injured, and released turtles; or impacts on populations. Where oral structures are affected (Figure 1), a hooked turtle may die following release, even if the hook has been removed.

The extirpation of Eastern Musk Turtle (*Sternotherus odoratus*) around the city of Hamilton, Ontario, is believed to have been the result of angling combined with habitat modification (Lamond 1994 cited in COSEWIC 2012). Steen and Robinson (2017) demonstrate that in settings where recreational fishing pressure is intense, hooking by anglers could have a great enough impact to affect populations. Steen *et al.* (2014) x-rayed over 600 turtles from five rivers in the southeastern United States and found that the prevalence of ingested fish hooks ranged from 0% to 33% depending on species, sex, age class, and site; the highest rate, 33%, was for adult female Snapping

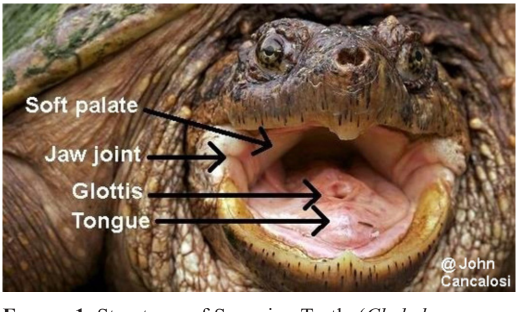

Figure 1. Structures of Snapping Turtle (*Chelydra serpentina*) mouth that are sensitive to hooking. Although hooks in the mouth are generally considered a lower risk than swallowed hooks, when penetrated by a hook, the glottis, jaw joint, soft palate, and tongue are prone to infection. If the glottis is damaged, water may drip into the lungs of a released turtle and may cause pneumonia and eventual death (Parga 2012). Photo: John Cancalosi.

Turtle (*Chelydra serpentina*). Steen and Robinson (2017) estimated that the probability of an individual turtle ingesting a hook and dying was 1–11%, depending on the species and the population, and was sufficient to cause declines in simulation models.

Here we suggest that hooking by recreational anglers may be a greater cause of turtle mortality at some sites than is recognized. We document turtle by-catch by recreational anglers in New Brunswick, assess frequency, and consider factors that may influence rates of hooking. We then present an approach to mitigating hooking mortality in the recreational fishery applied in New Brunswick. Most of our data were collected in a heavily fished urban park, but we also collected data more broadly in the province using a social media survey. All native freshwater turtles in New Brunswick are near the northeastern limit of their range, and populations often appear to be small and isolated (McAlpine 2010), leaving them particularly susceptible to even apparently minor incidents of anthropogenic mortality.

Methods

Study area and Rockwood Park turtle communities

Rockwood Park (RWP), Saint John, New Brunswick, (45°17′29.0″N, 66°03′14.1″W) is one of the oldest (established in 1896) and largest (~695 ha) urban parks in Canada. Ten lakes (1.4–10.3 ha) and several ponds (≤1.0 ha) lie within RWP boundaries. Several RWP lakes, including Lily Lake and Fisher Lakes are located in a designated recreation zone that is heavily used by the public, including recreational anglers (Figure 2). Although we do not have data on the number of anglers in RWP, angling was rare at remote sites but common at easily accessible sites. Crescent Lake is adjacent to the Rockwood Park golf course and supported an aquatic driving range from 1973 to 2013; the driving range was closed from 2014 to 2017, but reopened in 2018. Angling was not permitted at Crescent Lake when the aquatic driving range was in operation (S. Koval pers. comm. 2014), but did occur during the years it was closed. The remaining lakes are in a designated wilderness area and are less used by the public. We conducted visual and trap surveys for turtles at all 10 lakes in RWP, five ponds located in the RWP recreational zone, and one wetland in the wilderness zone (Table 1).

FIGURE 2. Annual fishing derby in Rockwood Park, Saint John, New Brunswick. Fishing derbies in urban parks can concentrate recreational anglers in turtle habitat and threaten freshwater turtles. Photo: Acadia Broadcasting.

Four species of turtles have been reported in RWP, although only one appears to form a self-sustaining population. Eastern Painted Turtle (*Chrysemys picta picta*) is resident at Crescent Lake with some use of an adjacent small pond in the golf course during summer (Golf Course Pond 1). A single Eastern Painted Turtle, originally marked at Crescent Lake and recaptured at Harrigan Lake, appears to have been dispersing. In 2015, using mark–recapture and the Jolly-Seber method (Krebs 1999), the population of Eastern Painted Turtles at RWP was estimated at 55 individuals (95% CI 48–74), including 17 females (95% CI 17–17), nine males (95% CI 9–9), and 29 juveniles (95% CI 22–48; C.L.B. and S.A.S. unpubl. data). Snapping Turtles appear to be widely distributed in RWP. From 2005 to 2016, members of the public submitted eight Snapping Turtle observations that were confirmed by photo evidence or expert identification and 12 unconfirmed observations (descriptions matched Snapping Turtle). Nonetheless, trapping only produced three Snapping Turtles, indicating that few individuals are present (Tables 1 and 2). It is not known whether the Snapping Turtles in RWP are the remnants of a previously larger population, are dispersers from populations in the Saint John River system, or are human releases. In 2016, we caught one Wood Turtle (*Glyptemys insculpta*) at A-frame Pond; we believe this was a human release, as suitable habitat to support a resident Wood Turtle population does not appear to be present in RWP. Red-eared Slider (*Trachemys scripta elegans*) is present in RWP, but this species is non-native and of pet trade origin. In 2014–2016, we caught and removed two Red-eared Sliders from Lily Lake and four from First Arch Pond and found one dead individual in Fisher Lakes.

During our trapping efforts and surveys, we noted any injuries to turtles potentially attributable to hooking events. Eastern Painted Turtle and Snapping Turtle are both assessed as Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2018a and 2008, respectively) with Snapping Turtle listed in the *Species at Risk Act* as Special Concern (SARA Registry 2019a); Wood Turtle is assessed (COSEWIC 2018b) and listed as

TABLE 1. Turtle species* documented and angler presence recorded at lakes in Rockwood Park, Saint John, New Brunswick.

Site	Size of lake, ha	Sampling dates†	No. trap-days	Turtle species captured	No. days visited in 2016	Angler recorded in 2016
Lily Lake‡	10.32	21 July–9 Sept. 2016 (basking)	50	RES	51	Y
Harrigan Lake	7.78	27 July–10 Aug. 2015	84	0	—	—
Harrigan Lake	7.78	27 July–3 Aug. 2016	125	EPT	8	N
Crescent Lake‡	7.60	25–29 Aug., 31 Aug.–12 Sept. 2014	96	EPT	—	—
Crescent Lake‡	7.60	13 May–17 June 2015	210	EPT/ST	—	—
Crescent Lake‡	7.60	25 Aug.–12 Sept., 15–27 Sept. 2015	180	EPT	—	—
Crescent Lake‡	7.60	17 May–15 June 2016	174	EPT	30	Y
Fisher Lakes‡	6.31	18–25 Aug. 2015	42	RES§	—	—
Fisher Lakes‡	6.31	22–29 June 2016	126	0	8	Y
Long Lake	5.37	13–27 July 2016	180	0	15	Y
Mayflower Lake	2.78	15–22 June 2016	42	0	8	Y
Owen Lake	2.10	14–20 July 2016	63	0	7	N
TCT Wetland	1.90	24–30 June 2015	36	0	—	—
Frying Pan Lake	1.63	6–13 July 2016	126	0	8	N
Crystal Lake	1.52	18–22 Aug. 2014	24	ST	—	—
Crystal Lake	1.52	29 June–6 July 2016	126	ST	8	N
Little Harrigan Lake	1.44	10–18 Aug. 2015	48	0	—	—
Little Harrigan Lake	1.44	3–10 Aug. 2016	84	0	8	N
First Arch Pond‡	0.93	16–18 July, 20–25 July, 5–8 Aug. 2014	51	RES	—	—
First Arch Pond‡	0.93	24 June–21 July 2016 (basking)	27	RES	28	Y
A-Frame Pond‡	0.43	11–15 Aug. 2014	24	WT¶	—	—
Golf Course Pond 1‡,**	0.27	17–24 June 2015	25	EPT	—	—
Golf Course Pond 1‡,**	0.27	3–10 Aug. 2016	35	EPT	8	—
A-Frame Picnic Pond‡	0.12	27 July–1 Aug. 2014	30	0	—	—
Golf Course Pond 2‡,**	0.09	17–24 June 2015	5	0	—	—
Golf Course Pond 2‡,**	0.09	3–10 Aug. 2016	7	0	8	—

*EPT = Eastern Painted Turtle, RES = Red-eared Slider, ST = Snapping Turtle, WT = Wood Turtle.
†Note: Hoop traps used, unless "basking" traps noted (see Browne and Hecnar 2005).
‡Located in designated Rockwood Park recreational zone.
§Found dead on 21 May 2015.
¶Captured opportunistically on 21 May 2016.
**Not open to angling during the time of this study.

TABLE 2. Number of Eastern Painted Turtles (*Chrysemys picta picta*; EPT) and Snapping Turtles (*Chelydra serpentina*; ST) marked in 2014–2016, Red-eared Sliders (*Trachemys scripta elegans*; RES) captured and removed in 2014–2016, and number of angling incidents/potential interactions reported in 2016* in Rockwood Park, Saint John, New Brunswick.

Site	No. EPT marked	No. EPT with mouth injuries	No. ST marked	No. ST hooked or (nibble)	No. RES caught and removed	No. RES hooked or (nibble)
Crescent Lake	53	3	1	0	0	0
Fisher Lakes	0	0	0	1 (1)	0	0
First Arch Pond	0	0	0	0	4	5
Crystal Lake†	0	0	2	0	0	0
Lily Lake	0	0	0	0	2	(1)

*Incidents occurred in 2013–2016.
†Crystal Lake flows into Fisher Lakes; the main waterbodies are ~130 m apart; thus, ST observed at these two sites could be the same individual.

Threatened (SARA Registry 2019b). Red-eared Slider is now considered invasive in many parts of its introduced range (Kikillus *et al.* 2010) and a potential vector for disease in native turtle populations, including those in parts of southern Canada (Galois and Ouellet 2007). Red-eared Sliders captured in RWP in early spring suggest successful overwintering, although that has yet to be demonstrated for this species in New Brunswick.

Turtle hooking survey

We documented interactions between anglers and freshwater turtles by conducting interviews with 75 adult anglers encountered fishing in RWP from 20 May to 13 July 2016. Anglers were encountered when we visited lakes and ponds in RWP for turtle surveys and during other incidental travel. If a turtle was reported to have attempted to take bait from a hook or was reported hooked, we requested the following information: species involved or a description; date; location; hook type; bait type; nature of hooking event (e.g., hook swallowed, caught on leg); and outcome (e.g., hook removed and turtle released, released with hook embedded).

Social media survey

On 14 May 2017, we also assessed turtle hooking rates elsewhere in New Brunswick by soliciting information on turtles accidentally caught during angling from the New Brunswick fishing forum (http://www.NewBrunswickFishing.com/forums/).

To reduce turtle by-catch mortality among recreational anglers in New Brunswick, we developed a list of actions for anglers to follow once a turtle is hooked and delivered this information via social media (New Brunswick Museum Facebook post on 26 May 2017) and in the annual fishing regulations booklet for the province.

Results

Turtle hooking survey

Five of the 75 adult recreational anglers we encountered (6.7%) reported interactions with turtles in RWP in 2013–2016. Eight interactions, of which six (75%) involved hooking, were reported by five anglers (Table 3). Two of the interactions were with Snapping Turtles, both in Fisher Lakes, and both involving hooks baited with fish. In 2014, one Snapping Turtle attempted to consume fish on a line, but it was not hooked, and so was unharmed. In the second case, the fish was consumed and the line with hook was cut at a distance from the turtle. Six additional interactions, which we believe involved Red-eared Sliders, were reported in RWP. These occurred in Lily Lake and First Arch Pond, where only Red-eared Sliders were observed during our study. One turtle interaction occurred in Lily Lake in 2013 or 2014, in which a turtle consumed Pumpkinseed Sunfish (*Lepomis gibbosus*) bait without being hooked. The remaining five turtles were hooked by two anglers in one evening in

TABLE 3. Summary of interactions between turtles and anglers in New Brunswick, 2013–2016.

Turtle species	No. turtles	Year	Location	Gear	Interaction	Outcome
Snapping Turtle (*Chelydra serpentina*)	1	Unknown (“recent” in 2016)	Fisher Lakes, RWP	Hook baited with fish	Swallowed hook	Line cut, turtle released with ingested hook
Snapping Turtle (*Chelydra serpentina*)	1	2014	Fisher Lakes, RWP	Hook baited with fish	Bait taken	Unharmed
Red-eared Slider (*Trachemys scripta elegans*)	5	2014	First Arch, RWP	Small barbless J hooks and earthworm bait	Swallowed hook	Line cut, turtle released with ingested hook
Red-eared Slider (*Trachemys scripta elegans*)	1	2013–2014	Lily Lake, RWP	Hook baited with *Lepomis gibbosus* (Pumpkinseed Sunfish)	Bait taken	Unharmed
Eastern Painted Turtle (*Chrysemys picta picta*)	1	2014	Grand Lake	Unknown	Hooked at edge of shell/leg	Hook easily removed, turtle released
Wood Turtle (*Glyptemys insculpta*)	1	2016	New Brunswick*	Hook baited with a worm	Hooked in mouth by beak	Hook easily removed, turtle released
Wood Turtle (*Glyptemys insculpta*)	1	Unknown	New Brunswick*	Fly fishing	Hooked in tail	Hook easily removed, turtle released

RWP = Rockwood Park.
*Precise location on file at the New Brunswick Museum, but not disclosed here to protect a species at risk.

2014 at First Arch Pond. The anglers reported the five turtles as different individuals of the same species, which we were able to confirm as Red-eared Slider based on a photo. Small barbless J hooks and earthworm bait were in use. Each of these turtles swallowed the hook, and anglers cut the line and released the turtles. We do not know the fate of these individuals. Swallowed hooks are believed to lead to high risk of mortality in marine turtles (Parga 2012). In an attempt to gain more information, in 2019, we radiographed two Red-eared Sliders that were caught and removed from First Arch Pond in 2014 and had since been held in captivity at the RWP interpretation centre; no hooks were present.

Although our angler survey did not reveal any reports of interactions with Eastern Painted Turtles, during our population estimate we did observe injuries to this species consistent with hook-inflicted angling. For example, one adult male Eastern Painted Turtle had a penetrating wound between the lower mandibles (possible site of a hook removal; Figure 3) and two juvenile painted turtles (estimated to be two years old based on size and growth lines) had severe infections of the internal tissue of the throat/mouth (characteristic of hook injuries, S. Gillingwater pers. comm. 9 September 2015). Viewed in subsequent captures, the wound of the adult male appeared to be healing well. One of the juvenile turtles was taken to a local wildlife rehabilitation centre with a turtle program (Atlantic Wildlife Institute, Cookville, New Brunswick), but it did not survive. Necropsy results could not determine whether the infection was from a hook injury. The other juvenile was not recaptured during subsequent sampling.

The distribution of Eastern Painted Turtles, Red-eared Sliders, and Snapping Turtles and angling effort differed among sites. We encountered anglers most frequently at lakes and ponds that were easily accessible. Therefore, we cannot easily assess whether risk differed among species by comparing turtle capture numbers to number of angling interactions (Table 2). However, our data suggest that Snapping Turtles and Red-eared Sliders are more likely to swallow hooks than Eastern Painted Turtles.

Social media survey

Our post to the New Brunswick fishing forum received 1331 views and nine responses: five anglers reported never having hooked a turtle, two had hooked turtles outside New Brunswick, and two had hooked turtles in New Brunswick. An Eastern Painted Turtle was hooked under the edge of the shell by a leg. One Wood Turtle was hooked in the beak on 26 July 2016 when attracted to an earthworm on a hook. A third case, submitted independently to C.L.B., involved a Wood Turtle accidentally hooked in the tail during casting by a fly fisherman. In each of these cases, hooks were successfully removed and the turtles released without significant injuries. Nonetheless, we found that anglers, both those responding to our social media survey and those interviewed at RWP, were generally uncertain how to deal with a hooked turtle.

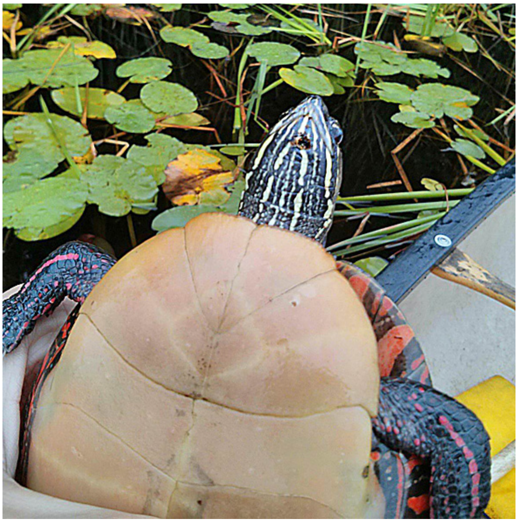

FIGURE 3. Probable hooking injury in an adult male Eastern Painted Turtle (*Chrysemys picta picta*) captured in Crescent Lake, Rockwood Park, Saint John, New Brunswick, on 11 September 2015. The injury penetrated the lower mandible and oral cavity. Photo: Sean Andrew Sullivan.

Our social-media-delivered guidelines for anglers who hook turtles reached 24 185 people and was shared 237 times, while a 14 May 2017 post in New Brunswick fishing forum's conservation section (http://www.NewBrunswickFishing.com/forums/index.php/forum/23-conservation/) received 1714 views by 9 October 2020. We were also able to place our guidelines (Figure 4) in the fishing regulations booklet for the province of New Brunswick (Browne 2018, 2019, 2020), which is distributed online and in hard copy at no cost through local Fish and Wildlife Branch offices and retail outlets that sell angling licenses.

Discussion

We documented instances of freshwater turtle bycatch by recreational anglers in New Brunswick for all three native species and one non-native turtle. Although we did not receive any reports of Eastern Painted Turtles being hooked in RWP, we did document one instance in New Brunswick outside RWP, and we observed Eastern Painted Turtles in RWP with injuries consistent with hooking. Hooking incidents, including swallowed hooks, have been documented for painted turtles elsewhere in Canada (S. Carstairs pers. comm. 4 March 2019). Mortality from hooking

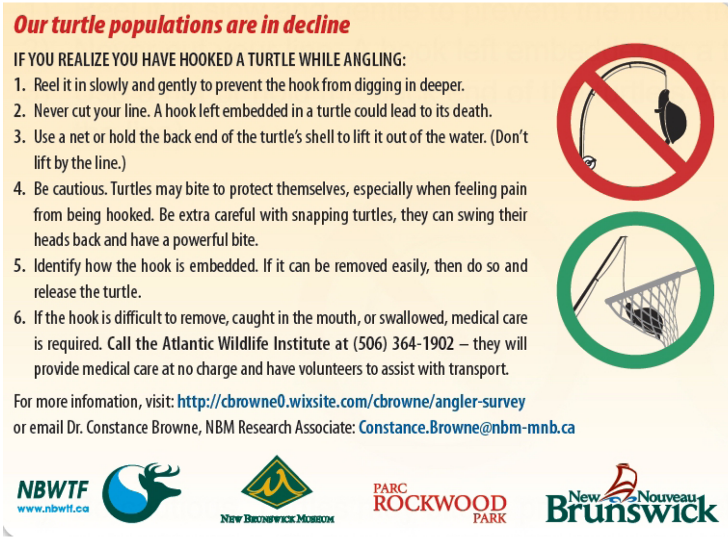

FIGURE 4. Guidelines instructing anglers how to deal with hooked freshwater turtles (Browne 2020).

is difficult to quantify, and is likely underestimated for many populations, as the remains of turtles that have died as a result of hooking are rarely encountered and available for examination.

We suspect that Eastern Painted Turtles were hooked less frequently in RWP than other species because anglers seldom fish the sections of Crescent Lake most heavily used by painted turtles. An intensive mark–recapture study conducted during 2014–2016 captured all adult painted turtles from the Crescent Lake population (>95% confidence that all were captured). The population was estimated to include 27 adults (10 males, 17 females) in spring 2015 and 26 (nine males, 17 females) in late summer 2015 (C.L.B. and S.A.S. unpubl. data). Of the adult turtles, only one male was unaccounted for in 2016.

Snapping Turtle populations may suffer greater impact from angling than other turtle species, as their larger size may allow them to swallow bait and hook more easily. Snapping Turtles admitted to the Ontario Turtle Conservation Centre have higher frequencies of ingested hooks than other turtle species (S. Carstairs pers. comm. 4 March 2019), and the highest hooking rates reported in Steen *et al.* (2014) were for Snapping Turtles. Post-release mortality estimates for sea turtles injured by hooks range from 19% to 82% (Swimmer *et al.* 2014). A swallowed hook, with line left trailing, is associated with the lowest survival rate (Parga 2012).

Target fish species may play a role in turtle by-catch rates in New Brunswick and elsewhere in Canada. Brook Trout (*Salvelinus fontinalis*) is the species most frequently fished recreationally in New Brunswick. This is a cold-water fish with a temperature preference of 10–18°C (Smith 1962). The four turtles present in RWP prefer temperatures of 20–30°C (Gatten 1974; Graham and Hutchison 1979; Schuett and Gatten 1980; Dubois *et al.* 2008). Thus, the microsites used by turtles and trout in RWP likely differ. However, Smallmouth Bass (*Micropterus dolomieu*), which is also a target species for anglers in RWP and elsewhere in New Brunswick, is a warm-water fish with a summer temperature preference of 30°C (Coutant 1977). This species is invasive in Maritime Canada and has been expanding its range, most recently in response to climate change (Sharma *et al.* 2009). Smallmouth Bass catch rates have been increasing in New Brunswick, whereas Brook Trout catch rates have declined (C. Connell unpubl. data). This difference may have implications for turtle by-catch rates in the future and is an example of how invasive species, climate change, and human recreational activities can interact to impact native species in ways that are difficult to predict.

Survey results from RWP cannot be extrapolated to infer rates of by-catch outside the park. We received only nine responses from anglers in other parts of New Brunswick, which represents <0.02% of the 57 025 angling licences (salmon excepted) issued in 2016 (C. Connell unpubl. data) limiting our ability to assess angling by-catch rates outside of RWP. Angling pressure undoubtedly varies across water bodies, and the overlap of turtles and anglers may be higher or lower than in RWP. Responses to our New Brunswick fishing forum query suggest that, currently, turtle by-catch by recreational anglers is generally uncommon in New Brunswick. Furthermore, the Atlantic Wildlife Institute has not received any New Brunswick turtles confirmed injured as a result of angling (P. Novak pers. comm. 1 May 2018). However, in each of the New Brunswick cases confirmed as by-catch that we did document, the turtle was released, including six high-risk cases where the hook was swallowed.

Where recreational fishing pressure is particularly intense, it may add a cumulative element to natural mortality and other anthropogenic deaths (i.e., road mortality) that may lead to population decline. Recreational fishing has been demonstrated to exert negative pressure on turtle populations in the United States (Steen and Robinson 2017). If similar pressures are present in Canada, impacts could be even greater because age of maturity is greater and clutch frequency reduced in northern climates (Galbraith *et al.* 1989; Iverson and Smith 1993; Iverson *et al.* 1997), increasing the importance of adult survivorship. At range margins, populations are often fragmented or isolated (Cook 1984), limiting immigration. However, even in connected habitats, long-lived species are slow to recover following impacts, and some populations may fail to recover even after survivorship rates improve (Keevil *et al.* 2018).

Freshwater turtle by-catch in the recreational fishery is still poorly documented in Canada, although we readily collected evidence of its occurrence in both urban and non-urban settings in New Brunswick. How significant recreational hooking may be overall to freshwater turtle mortality remains unclear. However, given that increased adult mortality of as little as 2–3% can, if chronic, result in marked declines in turtle populations (Congdon *et al.* 1994; Cunnington and Brooks 1996), we suggest that the issue requires greater scrutiny.

Author Contributions

Conceptualization: C.L.B.; Methodology: C.L.B.; Investigation: C.L.B. and S.A.S.; Data Curation: C.L.B. and S.A.S.; Writing – Original Draft: C.L.B.; Writing – Review & Editing: C.L.B., S.A.S., and D.F.M.; Visualization: C.L.B. and D.F.M.; Funding Acquisition: C.L.B. and D.F.M.

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Disjunctions of Needle-leaved Sedge (*Carex duriuscula*) and Thread-leaved Sedge (*Carex filifolia*) in the Husky Lakes area of Northwest Territories—first records for the Canadian true Arctic and possible Pleistocene relicts

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Abstract
Disjunctions are reported for Needle-leaved Sedge (*Carex duriuscula*) and Thread-leaved Sedge (*Carex filifolia*) into the Arctic region of Northwest Territories at the Husky Lakes south of Tuktoyaktuk. These are significant additions to the Canadian Arctic flora and may be part of a group of relicts of the Arctic vegetation of the Pleistocene, specifically the Tundra-steppe. The occurrence of relict vegetation east of the Mackenzie Delta is east of its frequently cited eastern limit in North America.

Key words: Cyperaceae; *Carex duriuscula*; *Carex filifolia*; phytogeography; relict; Tundra-steppe; Beringia; Northwest Territories

Introduction

The opening of the Tuk Highway (Inuvik to Tuktoyaktuk, also called the ITH), Northwest Territories (NWT) in 2018 allowed easier access to this remote region of the Canadian Arctic. Previous botanical explorations of this area were limited but included those by Mackay (1958, 1963), Cody (1965), and Corns (1974). We travelled the ITH during the summer of 2018 with the aim of improving the understanding of vascular plant diversity in the adjacent Shrub Tundra habitats. Herein we report substantial range disjunctions for two native sedges and discuss our discovery in the context of Arctic flora research. We also consider if the disjunctions are post-glacial or if they are Beringian or Pleistocene relicts.

Methods

As part of an exploration of diverse habitats, we surveyed dry slopes (P.M.C. and B.K. unpubl. data) identified with the help of aerial photography and accessed by road and foot. Our general survey protocol included walking back and forth across delineated areas of a particular vegetation type using parallel transects 2 m apart. Species were identified with the aid of Cody (1965, 2000) and Porsild and Cody (1980) and recorded. Collections were made as necessary and vouchers were deposited in the Canadian Museum of Nature and are cited below. The scientific and common names of plants are from Brouillet *et al.* (2010+). General information on plants is from the literature and relevant herbaria: University of Alaska (ALA), Bruce A. Bennett collection (BABY), Agriculture and Agri-Food Canada (DAO), and Canadian Museum of Nature (CAN). Online databases including both human observations and preserved specimens were also consulted, including GBIF (2020), ARCTOS (2020), and the Consortium of Pacific Northwest Herbaria (2020).

For the listing of Beringian taxa found in the largely unglaciated region west of the Mackenzie Delta, we accepted those: (1) Beringian species (largely confined to unglaciated northwestern North America); (2) Beringian and extending east of the Mackenzie Delta and becoming progressively more isolated eastward, in some cases extending to the region of Amundsen Gulf, but not reaching to Hudson Bay; (3) Beringian or mostly Beringian species with occurrences also in the southwestern Arctic islands; (4) Beringian species disjunct into the montane region of southwestern Alberta as well extending eastward, but not to Hudson Bay; and (5) largely Beringian and also present in the prairie region of central North America.

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

The major source for distributions was Porsild and Cody (1980), but we also examined maps and distributional information for all species noted in the more recent works of Aiken *et al.* (2007), Gillespie *et al.* (2015), and Saarela *et al.* (2013, 2017, 2020). These latter works contribute to a more accurate and current representation of the distribution of vascular plants in the Arctic islands and the adjacent mainland, areas included within our definition of "Beringian taxa east of the Mackenzie delta".

Results

On the dry-tundra slopes in the Husky Lakes area (also known as Imaryuk, Inuvialuktun, and the Eskimo Lakes, ~68.8704°N, 133.5331°W) south of Tuktoyaktuk, NWT we discovered substantial range disjunctions for two native sedges: Needle-leaved Sedge (*Carex duriuscula* C.A Meyer; *Carex* sect. Divisae) and Thread-leaved Sedge (*Carex filifolia* Nuttall var. *filifolia*; *Carex* sect. *Filifoliae*). The Husky Lakes area is a series of larger lakes, lowlands, and adjacent hills extending southwest of Liverpool Bay toward Inuvik. It is a loosely defined area identified by Cody (1965, opposite p. 1) and Natural Resources Canada (2006). It is within the Reindeer Grazing Preserve studied by Cody (1965), an area of ~6 million ha for which 420 species of vascular plants were recorded and for which the actual total may be 450 including more recent collections.

The two sedges are distinctive and easily distinguished from other sedge species and each other (Figure 1). The rhizomatous *C. duriuscula* has compound spikes (3–5) forming a capitate head, and the pistillate flowers have two stigmas. The tussock-forming *C. filifolia* has long solitary spikes and the pistillate flowers have three stigmas.

Both species are characteristic and often dominant in dry prairie and are widespread in the Canadian prairie regions of southern Alberta, Manitoba, Saskatchewan, and British Columbia, as well as in unglaciated Beringia including parts of Alaska, Yukon, and NWT (Vetter 2000; Mastrogiuseppe 2002; Reznicek and Catling 2002).

Discussion

Extent of disjunction

Being on the north side of the Husky Lakes, *C. duriuscula* and *C. filifolia* are north of treeline and within the Tuktoyaktuk Coastal Plain ecoregion (no. 33) of the Low Arctic Ecozone (Ecological Stratification Working Group 1996) and within, although near to the edge of, the true Arctic (CAVM Team 2003; Walker *et al.* 2005). These disjunctions (Figures 2 and 3) are therefore relevant to Canada's contribution to an understanding of circumpolar Arctic flora. Although they are the northernmost records for these species in Canada, the Holarctic *C. duriuscula* extends further north in Eurasia, reaching a northern limit on Wrangel Island (71.1948°N, 179.6549°W), off the north coast of Siberia in the Chukchi Sea (Polozova 1982). The Husky Lakes record of the exclusively North American *C. filifolia* is the northernmost in Canada and shares the title of northernmost and only Arctic occurrence in North America with two collections from coastal Alaska from slightly further north: https://www.gbif.org/occurrence/2005980149 and https://www.gbif.org/occurrence/2005980170. These specimens are not currently available for examination and are not shown on Sawtell's map (Sawtell 2012: Figure 4, p. 51). The nearest sites for both species to the disjunctions in the Husky Lakes are 350 km southwest along the "south-facing steppe bluffs" of the Porcupine River in Alaska west of the Yukon border (supported by *C. filifolia*: *D.F. Murray et al. 12107*, at 66.98°N, 142.82°W, ALA 18384; and *C. duriuscula*: *D.F. Murray et al. 12109*, at 66.98°N, 142.82°W, ALA 18386, 18391, *M.K. Reynolds s.n.* 95-586, at 66.98°N, 142.82°W, ALA

FIGURE 1. a. Needle-leaved Sedge (*Carex duriuscula*), b. Thread-leaved Sedge (*Carex filifolia*) from the Husky Lakes area of Northwest Territories. Photos: P.M. Catling.

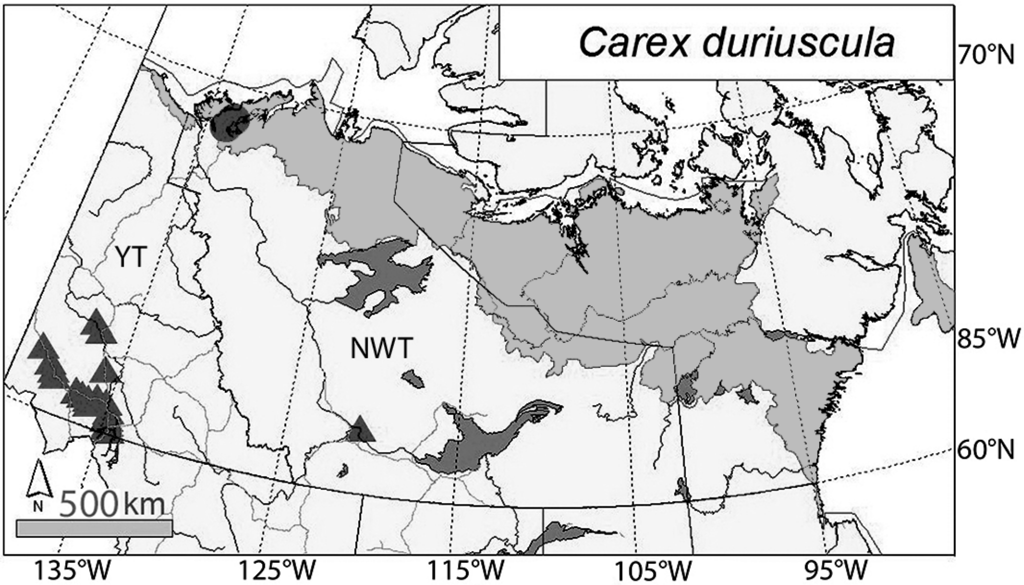

FIGURE 2. Distribution of Needle-leaved Sedge (*Carex duriuscula*) in northwestern Canada including Yukon Territory (YT) and Northwest Territories (NWT). Dots show occurrence of *C. duriuscula* in the Husky Lakes area. Triangles show occurrences elsewhere in northwestern Canada, based on Porsild and Cody (1980) and Cody (2000) and on specimens in CAN and DAO. Both types of symbols are centred on locations. The Southern Arctic Ecozone, as defined by the Ecological Stratification Working Group (1996), is shown in grey shading.

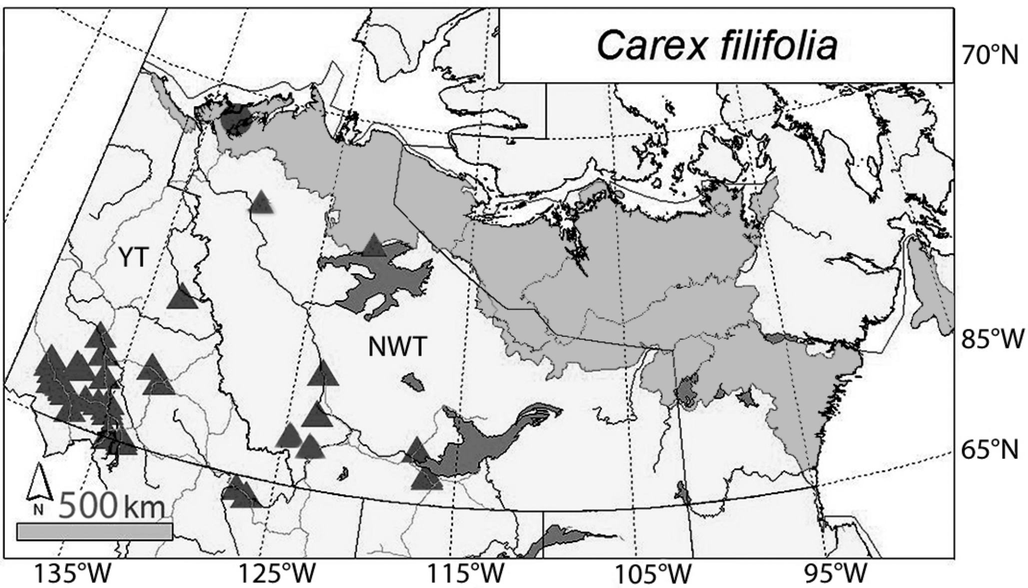

FIGURE 3. Distribution of Thread-leaved Sedge (*Carex filifolia*) in northwestern Canada including Yukon Territory (YT) and Northwest Territories (NWT). Dot shows occurrence of *C. filifolia* in the Husky Lakes area. Triangles show occurrences elsewhere in northwestern Canada, based on Porsild and Cody (1980) and Cody (2000) and on specimens in CAN and DAO. Both types of symbols are centred on locations. The Southern Arctic Ecozone, as defined by the Ecological Stratification Working Group (1996), is shown in grey shading.

13566, *R. Havenstein & J. Boron s.n.* at 66.98°N, 133.08°W, ALA 131318).

At the Husky Lakes, *C. duriuscula* is ~1000 km northwest of the only previous report in NWT near Fort Simpson (Porsild and Cody 1980 *sub Carex stenophylla* subsp. *eleocharis* (L.H. Bailey) Hultén; *W.J. Cody and K. Spicer 11450* at 61.78°N, 120.70°W, DAO, US 2456388), ~750 km north of the nearest location in Yukon on the east side of Kluane Lake (*B.A. Bennett et al. 06-0084* at 61.17°N, 138.44°W, BABY). *Carex filifolia* in the Husky Lakes is 250 km northwest of nearest locations in NWT on the east side of the Mackenzie River east of Tsiigehtchic (*DeCarlo and Kershaw s.n.* at 67.16°N, 129.97°W, CAN 10036734—a previously unpublished record) and 570 km from a site on the north arm of Great Bear Lake (Cody and Talbot 1978; Porsild and Cody 1980; whereabouts of supporting specimen[s] unclear). Other NWT sites are indicated in maps by Cody and Talbot (1978) and Sawtell (2012).

Although *C. filifolia* is shown in the Husky Lakes area by Cook and Roland (2002: 222, map 46), this *C. filifolia* map is identical to the map of *Carex eburnea* Boott (map 45) directly above it. The *C. eburnea* map (45) correctly depicts its range with the single occurrence in Yukon shown by Cody (2000: 148) and the location in the Husky Lakes shown in Porsild and Cody (1980: 178, map 231). The *C. filifolia* map (map 46) does not depict the range of *C. filifolia*, which is extensive in southwestern Yukon (Cody 2000: 149). The earlier mapping of *C. filifolia* from the Husky Lakes by Cook and Roland (2000) is thus an error based on a repeated map representing *C. eburnea*, and the report herein of *C. filifolia* from the Husky Lakes is the first.

Glacial relict or Recent (Holocene)

Habitats of *C. duriuscula* and *C. filifolia* in the Husky Lakes are small 200–5000 m^2 southwest (SW)-facing slopes of 30–45° dominated by a rich herb and graminoid cover (Figure 4). They are anomalies in a landscape strongly dominated by Shrub Tundra, wetlands, and lakes. During the period of climate changes between 4500 and 9500 years ago (Ritchie 1977, 1984), the extensive dry ground herb and graminoid cover is believed to have shrunk to these very small and widely scattered remnants. Shrub Tundra became predominant on higher ground as climate stabilized. The sloping habitats, due to their angle and SW orientation, receive more direct sunlight than the surrounding landscapes and are thus warmer and able to retain

FIGURE 4. A habitat of Needle-leaved Sedge (*Carex duriuscula*) in the Husky Lakes area of Northwest Territories (lower right), 27 June 2018. The sedge and associated plants are the same species that dominate the more extensive remnants of Tundra-steppe in Russia. The flora suggests a more eastern historical presence of this habitat in Canada than previously thought. The surrounding Shrub Tundra dominated the landscape after 4500 years ago. The slope is warmer and drier than the surrounding landscapes and was thus able to retain a rich relict flora associated with the previously drier climate. Photo: P.M. Catling.

a rich flora, once more extensive, that is associated with a previously drier climate.

Although we prefer a relict hypothesis to explain the occurrence of the two sedges and many other Beringian plants in the Husky Lakes region, there are other explanations. One of these is postglacial migration. However, this would not explain the restricted area occupied by the plants because the moist postglacial environment would have been unsuitable for plants of dry situations and it requires long-distance dispersal to small, isolated areas of occurrence. If the relictual populations are considered equivalent to islands, the small size of the island targets and the increasing distance to western or southern sources suggests that postglacial dispersal is unlikely according to the fundamentals of island biogeography where dispersal is negatively influenced by island size and distance (MacArthur and Wilson 1967).

Long distance dispersal has recently been suggested to be common in Arctic plants and possibly even relatively frequent (Alsos *et al.* 2015). However, there is a distinct eastern and western flora in the Canadian Arctic. Isolated disjunctions from the west to the east (and *vice versa*) are unusual. Major disjunctions from the south to the north are also unusual. However, there may have been extensive late glacial or postglacial dispersal over long distances within some major phytogeographic regions as suggested by Shönswetter *et al.* (2008). Although some Beringian species may have colonized areas west of the Mackenzie Delta from the west and/or south in postglacial times, it becomes difficult to explain why so many species of varying ecology and provenance have approximately the same eastern limit west of the Mackenzie Delta (see below) unless there was a landscape boundary, such as continental ice, that existed until a period of rapid climate change.

Another possible explanation is very recent introduction, which could explain why previous botanical surveys in the very extensive area east of the Mackenzie Delta (Mackay 1958, 1963; Cody 1965; Corns 1974), and plant collections made in the area as part of grazing studies by G. Scotter in 1965 and 1966 (CWS-Edmonton, DAO) and J. Lambert in 1968 and 1969 (CCO, DAO) noted by Porsild and Cody (1980) did not record these plants. The area was a wilderness with only a winter road connecting Inuvik and Tuktoyaktuk until the Tuk Highway opened in 2018. Consequently, there was insufficient human traffic to explain the disjunctions as recent dispersal by humans. The very large size of the area, isolated and rare occurrence of disjuncts, and the short duration and incomplete coverage of previous botanical surveys can readily explain how these disjunct species were overlooked.

There is also a possibility of introduction with Reindeer (*Rangifer tarandus*). The Husky Lakes are part of the Reindeer Grazing Preserve, so *C. duriuscula* may have been introduced with the Reindeer. The Reindeer originated in Kotzbue Sound, Alaska, but before that they had been imported from Siberia between 1891 and 1902 (Scotter 1972; Treude 1975). The herd of 3400 animals was driven along the coast starting in 1929, arriving on the east bank of the Mackenzie in 1935. *Carex duriuscula* has not been found along this west and north coast of Alaska or north coast of Yukon (Hultén 1968; Cody 2000; Arctos 2020; GBIF 2020). It seems unlikely that its seeds would be carried along the coast to NWT during this five year journey of a continuously moving herd in which only 10% of the original animals survived (Treude 1975).

Relicts of a past vegetation

Because Canada was covered by the Laurentide and Cordilleran Ice sheets until ~12 000 years ago, it was only the unglaciated landscape of the northwest, i.e., eastern Beringia, where the Pleistocene megafauna, including herbivores such as Eastern Moose (*Alces alces* L. subsp. *americana*), Alaskan Moose (*Alces alces* L. subsp. *gigas*), Steppe Bison (*Bison priscus* Bojanus), Helmeted Muskox (*Bootherium bombifrons* Harlan), Giant Moose (*Cervalces latifrons* Johnson), Cabilline Horse (*Equus* sp. 1), Hermione Horse (*Equus* sp. 2), Woolly Mammoth (*Mammuthus primagenius* (Blumenbach)), Muskox (*Ovibos moschatus* Zimmermann), Dall Sheep (*Ovis dalli* Nelson), Caribou (*Rangifer tarandus* L.), and Saiga Antelope (*Saiga tatarica* L.), roamed the somewhat controversial Tundra-steppe (Matthews 1979; Cwynar and Ritchie 1980; Blinnikov *et al.* 2011; Stuart 2015). The Arctic Steppe Biome, also known as the Mammoth-steppe and the largest biome that ever existed on earth, may have extended east to the Mackenzie Delta (Matthews 1979; Guthrie 1990; Elias *et al.* 2000).

Within NWT the unglaciated landscape also included a downward extension into the Mackenzie Mountains. An area of Pleistocene Tundra-steppe may have existed east from the Mackenzie Delta, the frequently-cited eastern boundary, to the Caribou Hills, the Husky Lakes, the Tuktoyaktuk Peninsula, the Anderson River, and north to Banks and Victoria Islands, based on mapping of unglaciated landscapes (Dyke *et al.* 2002, 2003; Dyke 2004). This is further supported by Pleistocene faunal remains, including horses (*Equus* spp.), Steppe Bison, Woolly Mammoths, and Saiga Antelope, most mapped and discussed by Harrington (2007) and Zazula *et al.* (2009). Saiga Antelope are valuable paleoenvironmental indicators of dry, steppe-like, grasslands (Harrington and Cinq-Mars 1995; Harrington 1998).

They occurred on the Baillie Islands, which are 270 km northeast of the Husky Lakes disjuncts, 15 000 years ago (Harrington and Cinq-Mars 1995) and prior to vegetation change in the region, which began 9500 years ago. At this time the dominant regional vegetation apparently changed from graminoid and herb-dominated Tundra-steppe to spruce forest or parkland and this was replaced by Dwarf Shrub Tundra after 4500 years ago, this persisting to the present (Ritchie 1977, 1984).

The two disjunct sedges are of particular interest as possible indicators of the Pleistocene Tundra-steppe east of the Mackenzie Delta for three reasons:

(1) As plants of dry ground capable of existing as dominants, adapted to grazing pressure and preferred food of some surviving large mammalian grazers (e.g., Hoefs 1979; Vetter 2000; Bazha *et al.* 2009; Reinecke *et al.* 2017; Chitry *et al.* 2019), the two sedges have characteristics that are expected in plant species associated with Pleistocene megafauna. Herbs may have played a more important role in megafaunal diet and the Tundra-steppe may have been a patchwork of dry, mesic, and wet habitats including extensive dry grasslands (Willerslev *et al.* 2014). However, there can be little doubt that the megafauna was adapted to the dry grasslands based on tooth structure (e.g., Guthrie 1990) and other anatomy, and it may have been adapted particularly to these two sedges.

(2) The two species draw attention to the existing phytogeographic evidence for a relict flora based on restricted distributions. The continental portion of the eastern extension of unglaciated landscape described above is treated as Phytogeographical Province 3 by Porsild and Cody (1980: 1–3) partly on the basis of "a few Amphi-Beringian species". In fact, there are more than a few restricted Beringian species that may be regarded as potential Pleistocene relicts in this area. We estimate 80 Beringian species (depending on how strictly they are defined) based on the maps in Porsild and Cody (1980). These represent 17.7% of the local flora of ~450 species (Cody 1965, P.M.C. and B.K. pers. obs.). They include plants of (1) wetlands such as Spruce Muskeg Sedge (*Carex bigelowii* Torrey ex Schweinitz subsp. *lugens* (T. Holm) T.V. Egorova) and Arctic-flower (*Wilhelmsia physodes* (Fischer *ex* Seringe) McNeill); (2) moist saline shores such as Marsh Felwort (*Lomatogonium rotatum* (L.) Fries var. *rotatum*) and Northern Primrose (*Primula borealis* Duby); (3) Shrub Tundra such as Narrow-leaved Sawwort (*Saussurea angustifolia* (L.) de Candolle) and Steven's Meadowsweet (*Spiraea stevenii* (C.K. Schneider) Rydberg), and (4) species of dry ground. It is the last group that has often been emphasized in discussion of the Arctic-steppe biome relicts because of the presumed dry conditions leading to a previously more widespread plant community of drier ground dominated by herbs and grasses. There are 45 restricted Beringian species of drier ground mapped for this area by Porsild and Cody (1980; Tables 1, 2 and 3). This is an impressive list of potential relicts. The two disjunctions are not only additions increasing the list to 47 species but are particularly good examples of potential relicts. This group is an important reminder of the value of local floristic information as one of many local proxies that need to be used to elucidate the character of the Pleistocene Arctic (Blinnikov *et al.* 2011).

(3) *Carex duriuscula* is a valuable species upon which to build the concept of existing relict Tundra-steppe in NWT because it expands the context of the idea to include some of the better-known examples. In his extensive discussion of the relict steppe vegetation in Asian (western) Beringia, Yurtsev (1982: 162, 163, 168, 169, 171) also mentions dominant species and he alludes to *C. duriuscula* more than to any other. He illustrated a steppe dominated by *C. duriuscula* in the Indigirka River valley (Yurtsev 1982: Fig. 3, 152). He considered "the vegetation of Wrangel Island to be the closest living analog to the sort of vegetation that clothed northern Beringia during Pleistocene time" (Yurtsev 1982: 157). An extensive area dominated by *C. duriuscula* is described as an indicator and dominant of rich steppe habitats, with 50–60 associated species on Wrangel Island. *Carex duriuscula* and Prairie Sagebrush (*Artemisia frigida* Willdenow) were considered as "true steppe plants" by Yurtsev (1982: 174). The Siberian examples of putative Tundra-steppe relicts are extensive and they include all slope aspects of the landscape. The Indigirka Steppe is 30 km long and up to 4 km wide and Wrangel Island, with an area of 7511 km^2, off the north coast of Siberia, was the last stand of the Mammoth, in this case the unusually small Wrangel Island Dwarf Mammoth (*Mammuthus primigenius* subsp. *wrangeliensis* Garutt, Averianov & Vartanyan), which died out only 4000 years ago (Vartanyan *et al.* 1995).

Carex filifolia has been discussed by Vetter (2000) as part of relict grasslands in southwestern Yukon. In this area it is a co-dominant species with *A. frigida*.

Among the close associates of *C. duriuscula* and *C. filifolia* in the Husky Lakes are Prairie Sagebrush, Purple Reedgrass (*Calamagrostis purpurascens* R. Brown), Blunt Sedge (*Carex obtusata* Liljeblad), Weak Arctic Sedge (*Carex supina* Willdenow *ex* Wahlenberg var. *spaniocarpa* (Steudel) Hultén), and Prairie Pasqueflower (*Pulsatilla nuttalliana* (de Candolle) Berchtold *ex* J. Presl (*P. multifida*)). Yurtsev (1982) mentions these as dominant species in the Russian Tundra-steppe. These are more than just rare potential relicts scattered over the land-

TABLE 1. Dry land species largely restricted in Canada to Beringia and its eastern limit (Phytogeographical Province 3) as mapped by Porsild and Cody (1980) and other sources (see Methods). Many of these also occur eastward to Amundsen Gulf and the southwestern Arctic Islands. Scientific names are in alphabetical order by genus and species.

Scientific name	Common name
Androsace chamaejasme Wulfén ex Host subsp. *lehmanniana* (Sprengel) Hultén (*A. chamaejasme* var. *arctica*)	Lehmann's Fairy-candelabra
Arnica griscomii Fernald subsp. *frigida* (C.A. Meyer ex Iljin) S.J. Wolf (*Arnica louisiana* subsp. *frigida*)	Griscom's Arnica
Artemisia borealis Pallas subsp. *richardsoniana* (Besser) Korobkov (*Artemisia richardsoniana*)	Richardson's Wormwood
Artemisia tilesii Ledebour	Tilesius Wormwood
Astragalus australis var. *glabriusculus* (Hooker) Isely (*Astragalus richardsonii*)	Aboriginal Milk-vetch
Astragalus bodinii E. Sheldon	Bodin's Milk-Vetch
Bupleurum americanum J.M. Coulter & Rose	American Thoroughwax
Carex petricosa Dewey var. *petricosa*	Rock-dwelling Sedge
Cnidium cnidiifolium (Turczaninow) Schischkin	Jakutsk Snow Parsely
Dryas punctata Juzepczuk	Sticky Mountain Avens
Elymus macrourus (Turczaninow) Tzvelev (*Agropyron sericeum*)	Silky Wildrye
Eremogone capillaris (Poiret) Fenzl var. *capillaris* (*Arenaria capillaris* var. *nardifolia*)	Thread-leaved Sandwort
Erigeron porsildii G.L. Nesom & D.F. Murray	Porsild's Fleabane
Erigeron yukonensis Rydberg	Yukon Fleabane
Eurybia sibirica (Linnaeus) G.L. Nesom (*Aster sibiricus*)	Siberian Aster
Gentianopsis detonsa (Rottbøll) Ma subsp. *detonsa* (*Gentianopsis richardsonii*)	Sheared Gentian
Koenigia alaskana (Small) T.M. Schuster & Reveal var. *glabrescens* (Hultén) T.M. Schuster & Reveal (*Polygonum alaskanum*)	Alaska Wild Rhubarb
Lupinus arcticus S. Watson	Arctic Lupine
Micranthes reflexa (Hooker) Small (*Saxifraga reflexa*)	Yukon Saxifrage
Oxytropis borealis var. *viscida* (Nuttall) S.L. Welsh (*Oxytropis glutinosa*)	Sticky Locoweed
Oxytropis campestris var. *varians* (Rydberg) Barneby (*Oxytropis hyperborea*)	Variable Locoweed
Packera hyperborealis (Greenman) Á. Löve & D. Löve (*Senecio hyperborealis*)	Boreal Groundsel
Phlox richardsonii Hooker (group)	Richardson's Phlox
Poa ammophila A.E. Porsild	Sand Bluegrass
Polemonium acutiflorum Willdenow ex Roemer & Schultes	Tall Jacob's-ladder
Polemonium boreale Adams	Northern Jacob's-ladder
Polemonium pulcherrimum Hooker	Showy Jacob's-ladder
Potentilla hookeriana Lehmann (*Potentilla nivea* var. *hookeriana*)	Hooker's Cinquefoil
Salix phlebophylla Andersson	Skeleton-leaved Willow
Silene involucrata subsp. *tenella* (Tolmachew) Bocquet (*Melandrium taimyrense*)	Taylor's Arctic Catchfly
Silene repens Patrin (*S. repens* ssp. *purpurata*)	Pink Catchfly
Symphyotrichum pygmaeum (Lindley) Brouillet & S. Selliah (*Aster pygmaeus*)	Pygmy Aster
Taraxacum alaskanum Rydberg	Alaska Dandelion
Tephroseris frigida (Richardson) Holub (*Senecio atropurpureus*)	Purple-haired Groundsel

scape of Phytogeographical Province 3 east of the delta. Coherent isolated communities exist that are in many ways similar to those in Russia identified by a Russian authority.

Although Yurtsev's work is a favourite and classical reference for relict Tundra-steppe, there have been more recent studies that have also indicated *C. duriuscula* as a dominant species of such relicts (Schweger 1997; Reinecke *et al.* 2017; Chitry *et al.* 2019). Other recent work has suggested that only partial analogues will be found because Tundra-steppe was likely a herbivore-driven biome (Zimov *et al.* 1995), and most of the keystone herbivores are now extinct. Regardless of how complete our concept of Tundra-steppe vegetation is, the disjunct sedges may be an informative part of it.

Voucher specimens

Carex duriuscula C.A. Meyer, Needle-leaved Sedge —CANADA, NORTHWEST TERRITORIES: Husky Lakes:

TABLE 2. Beringian and prairie species of dry ground in Phytogeographical Province 3. Some populations that occurred south of the continental ice sheet during the glacial period may have simply moved north into the present prairie region. The restricted Beringian populations may have persisted from the Pleistocene. Based on mapping by Porsild and Cody (1980) and other sources (see Methods). Scientific names are in alphabetical order by genus and species.

Scientific name	Common name
Agoseris glauca (Pursh) Rafinesque var. *dasycephala* (Torrey & A. Gray) Jepson (*Agoseris glauca scorzoneraefolia*)	Alpine Agoseris
Anticlea elegans (Pursh) *Rydberg* (*Zigadenus elegans*)	Mountain Death Camas
Artemisia frigida Willdenow	Prairie Sagebrush
Bromus pumpellianus Scribner	Pumpelly's Brome
Carex obtusata Liljeblad	Blunt Sedge
Festuca altaica Trinius	Northern Rough Fescue
Pulsatilla nuttalliana (de Candolle) Berchtold ex J. Presl (*Pulsatilla ludoviciana*, *Anemone patens*)	Prairie Pasqueflower

TABLE 3. Beringian and montane (mostly southwestern Alberta) species of dry ground in Phytogeographical Province 3. Those populations that occurred south of the cordilleran ice sheet may have moved into the mountains and foothills afterward. Those in Beringia may represent long time persistence in this region. Based on mapping by Porsild and Cody (1980) and other sources (see Methods). Scientific names are in alphabetical order by genus and species.

Scientific name	Common name
Plantago canescens Adams	Hairy Plantain
Salix barrattiana Hooker	Barratt's Willow
Salix farriae C.R. Ball	Farr's Willow
Senecio lugens Richardson	Small Black-tip Ragwort

southwest-facing steep (45°) slope, 68.8704°N, 133.5331°W, 28 June 2018, *P.M. Catling & B. Kostiuk 2018338* (DAO); southwest-facing 40° slope, 69.1010°N, 133.0868°W, 11 July 2019, *P.M. Catling & B. Kostiuk 2019400* (CAN 10102106).

Carex filifolia Nuttall var. *filifolia*, Thread-leaved Sedge—CANADA, NORTHWEST TERRITORIES: Husky Lakes: southwest-facing hilltop, 69.1833°N, 133.0158°W, *P.M. Catling & B. Kostiuk 2019410* (CAN 10102107, DAO).

Author Contributions

Both authors contributed to all parts of the study.

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Note

Potential case of pseudo-hermaphroditism in Elk (*Cervus canadensis*) in Alberta, Canada

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Abstract
Cases of true and pseudo-hermaphroditism, in which animals possess both ovaries and testes or have a single chromosomal and gonadal sex but secondary features of the other sex, have been documented in several cervids, including *Odocoileus* (deer) and *Capreolus* (roe deer) species. Another form of intersexuality that has been well documented in Domestic Cattle (*Bos taurus*) and induced in Red Deer (*Cervus elaphus*) is freemartinism, where blood is shared between heterosexual twins leading to XX/XY chimeras. We report the first case of pseudo-hermaphroditism in wild Elk (*Cervus canadensis*), observed in the central east slopes of the Rocky Mountains of Alberta, Canada, from September through December 2019. The Elk had no antlers, exhibited female external genitalia, and displayed male secondary sexual characteristics, including colouring and breeding behaviour. To determine whether this is a case of true hermaphroditism, pseudo-hermaphroditism, or freemartinism would require blood analysis and inspection of internal sex organs by necropsy.

Key words: Hermaphrodite; pseudo-hermaphroditism; Elk; freemartinism; *Cervus canadensis*; Canada

For most cervid species, determination of sex in the field is based on antler presence or external genitalia. However, there are instances when variability in these features does not adequately represent the sex of the animal. For example, antlered females are well documented in the genus *Odocoileus* (deer) and *Capreolus* (roe deer; Rorig 1899, 1907 as cited in Wislocki 1954; Wislocki 1954, 1956; Donaldson and Doutt 1965; Wishart 1985; Mysterud and Østbye 1999; Flis 2012), but less so in Red Deer (*Cervus elaphus*; Rorig 1899, 1907 as cited in Wislocki 1954) and Elk (*Cervus canadensis*; Buss and Solf 1959). Antlered females can be fertile, particularly if antlers stay in velvet, but females with polished antlers are more likely to be incapable of pregnancy (Donaldson and Doutt 1965).

In contrast to antlered females with typical reproductive organs, various degrees of hermaphroditism have been documented in cervids. These anomalies arise during one of three stages in mammalian sex development: (1) sex chromosomes at fertilization, (2) gonadal differentiation into testes or ovaries depending on the chromosomal sex and the *SRY* genetic factor that stimulates testes formation, and (3) differentiation into sex-specific phenotypes according to gonadal sex (Parma *et al.* 2016). The various outcomes of the abnormal development include true hermaphroditism, pseudo-hermaphroditism, and freemartinism, and these have been reported in cervid species since the early 1900s.

True hermaphroditism is rare and results in male and female gonads in the same individual (Parma *et al*. 2016). Pajares *et al*. (2009) reported a case in an Iberian Roe Deer (*Capreolus capreolus*) with XX chromosomes, antlers, female external genitalia, and both ovaries and testes. Pseudo-hermaphrodite describes an individual with gonads of one sex but the secondary sexual characteristics of the other sex, which can range from external genitalia to behavioural characteristics (Parma *et al*. 2016). Male pseudo-hermaphroditism has been documented in White-tailed Deer (*Odocoileus virginianus*). For example, an antlered deer exhibited female external genitalia (i.e., a vulva) but internal male reproductive organs, i.e., undescended testes (Wislocki 1956; Scanlon *et al.* 1975; Kent *et al.*1986). Distinguishing between instances of true and pseudo-hermaphroditism requires determination of chromosomal sex and a full dissection of an intact reproductive tract to confirm the presence of male and/or female gonads. In contrast, freemartinism occurs when there is vascularization of the placentae of heterosexual twins and blood is shared between twins, leading to XX/XY chimerism and often masculinization and sterility of the female twin's reproductive tract (Padula 2005). Freemartinism has been most commonly reported in Domestic Cattle (*Bos taurus*), but has also been documented in cervid species, including Red Deer that were treated with progesterone to induce twinning (Stewart-Scott *et al*. 1990).

Elk is a large, sexually dimorphic deer species with a wide distribution across North America (Toweill and Thomas 2002). Males exhibit an annual antler growing and shedding cycle that facilitates competition for females during the fall rut (mating season; Geist 2002). Here we report the potential first occurrence of pseudo-hermaphroditism in a free-ranging Elk in Alberta, Canada.

The Elk in question was observed in a partly migratory Elk herd that winters on the Ya Ha Tinda Mountain Rough-fescue (*Festuca campestris* Rydberg) grassland adjacent to Banff National Park in Alberta, Canada (51.7427°N, 115.5477°W). This Elk herd has been studied since the late 1980s (Morgantini and Hudson 1988) with intensive ongoing studies since 2000 (Hebblewhite *et al*. 2006, 2018). Based on aerial surveys, the wintering Elk population peaked in the early 1990s at ~2200 individuals and declined to 350–450 in 2019, where it has stabilized. The population decline is thought to be related to high predation rates, particularly by Gray Wolves (*Canis lupus*), which increased in the 1990s (Hebblewhite *et al*. 2018). In summer, Elk migrate west into high-elevation Banff National Park, east onto low-elevation industrial timberlands, or remain as "residents" of the Ya Ha Tinda year-round. Male Elk collect in bachelor herds mainly around the Ya Ha Tinda in winter and migrate to the same summer ranges as the females, although with more variation in timing and location.

As part of the intensive Elk studies starting in the early 2000s, regular observations using binoculars or a high-powered (20–45×) spotting scope from typical distances of 50–1000 m are made on Elk inhabiting the Ya Ha Tinda to document herd composition, group sizes, and calf survival. On 5 September 2019, we first observed an Elk that appeared to look and behave like a male but had female external genitalia. After initially noticing the Elk in a herd of 300 female Elk, the observer monitored it three times a week between 5 September and 15 December 2019 for a total of ~20 h from a distance of 300–900 m using a spotting scope to record behaviour. Photos were taken with a Coolpix P510 digital camera (Nikon Corporation, Shinagawa, Tokyo, Japan) from horseback at a distance of 20–50 m to examine the external colouring, genitalia, and potential pedicles. The Elk showed typical male facial structure and colouring, but lacked antlers (Figure 1). However, part of a pedicle appeared to be present amid indentations in the hair on the head (Figure 2). The individual had female external genitalia and was observed urinating from a vulva-like structure; neither a scrotum nor penis was visible (Figure 3).

The Elk was originally believed to be a male lacking antlers because it was exhibiting typical male mating behaviour during the rutting season, including chasing females, sniffing their posteriors, flicking the tongue in and out rapidly while following females (Figure 4), and bugling (Figure 5). The Elk's bugling contained a typical gradual increase in sound frequency followed by an extended tonal frequency and a rapid decrease in frequency, but with a shorter duration than a typical male bugle and more frequency modulations during the increase in frequency (Feighny *et al*. 2006). The rate of bugling was less frequent than that of a male, at about one bugle in 20–60 minutes. The observed individual exhibited other behaviour typical of males during the rut: high rates of movement throughout the herd in search of females and increased vigilance during foraging bouts, presumably for rival males. However, the Elk was never observed mounting a female nor fighting with rival males. We did observe the individual lowering its head as if to bluff-charge females, but it never exhibited this aggressive behaviour toward yearling spike males or adult males. In particular, male Elk did not interact with this Elk unless it aggressively chased a female near a male, in which case the male would chase the Elk in question, which then displayed submissive behaviour and moved away from the female. The Elk remained with the main female Elk herd through the end of December when most males left after the rut to form bachelor groups separate from the main herd. We observed male behaviour in the pseudo-hermaphrodite Elk during the rut that declined in late November and early December after the second estrous cycle of the females (Hudson *et al.* 2002).

There are several explanations for the origin of this "intersex" individual. First, it did not resemble an antlered female because no antlers were present and because it also displayed other male secondary sexual behaviours. Although the origin could be freemartinism, natural freemartinism has not been

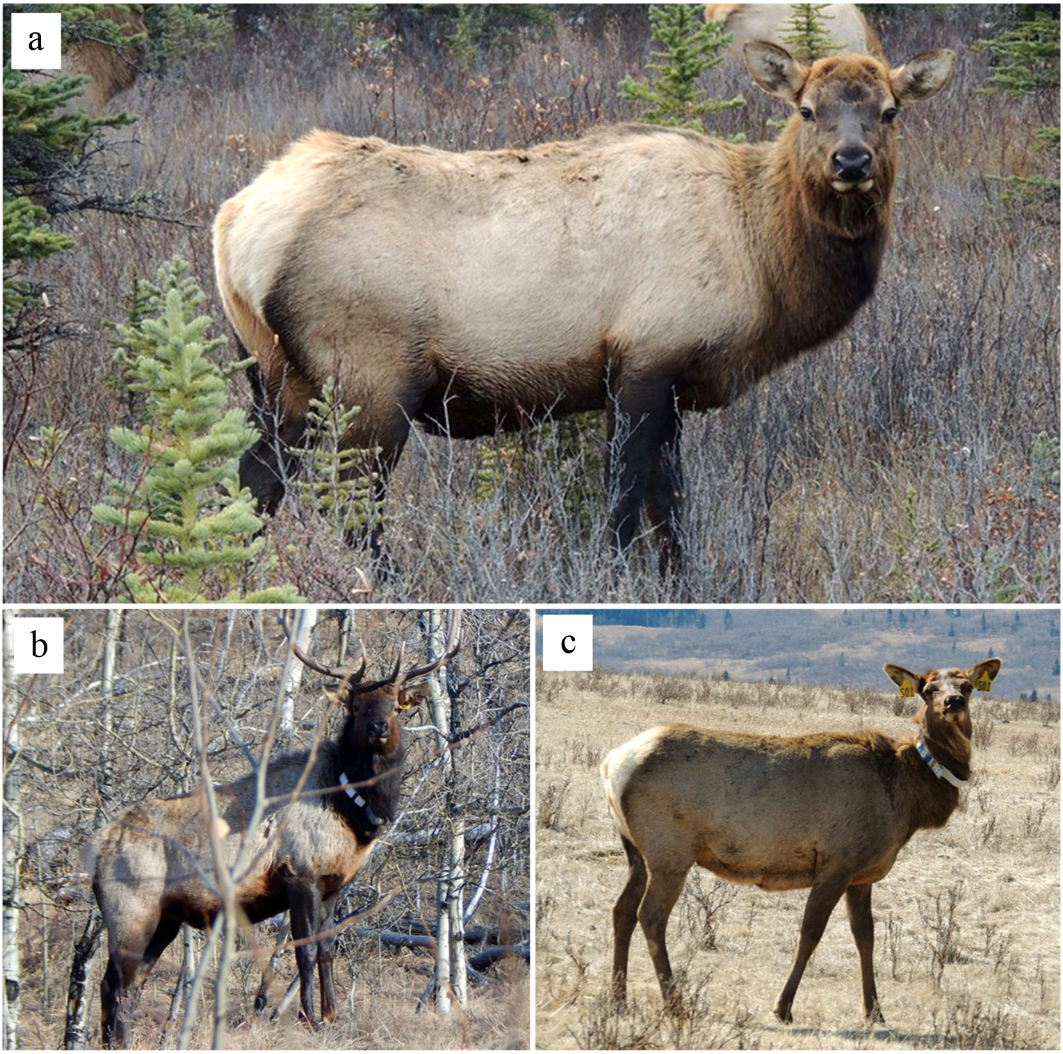

FIGURE 1. a. Potential hermaphroditic Elk (*Cervus canadensis*) with female external genitalia but male secondary sexual characteristics including pedicle-like growths on the head and lighter tan colouring with a darker ruff of the male (b) compared with the consistent darker brown colour of female Elk (c). Photos taken from 10 to 30 m at the Ya Ha Tinda, adjacent to Banff National Park, Alberta, Canada. Photos: J. Normandeau.

observed in Elk populations (Sysa and Kaluzinski 1984). However, it has been documented in closely related Red Deer that were treated with progesterone and gonadotrophin, which increased twinning. Of the eight sets of twins produced, two female XX/XY chimeras were observed that were both sterile (Stewart-Scott *et al*. 1990). In wild Elk, twinning rates are very low (<1%) making freemartinism unlikely (Hudson *et al*. 2002). In addition, freemartinism in cattle typically results in a sterile female twin with typical external genitalia without the male secondary sexual characteristics that we observed (Gregory *et al*. 1996).

Alternatively, the individual could be a pseudo-hermaphrodite through either an XX- or XY-sex reversal during development to show secondary sexual characteristics of the opposite sex. The individual may be a male pseudo-hermaphrodite with an XY-sex reversal if undescended testes are present along with a vulva, clitoris, and/or a blind vagina (that does not connect to reproductive organs) but a lack of ovaries. Elsewhere urination from a vulva-like opening associated with a retro-posed penis has been documented (Kropatsch *et al*. 2013). However, in this case, the external genitalia appeared similar to those of other

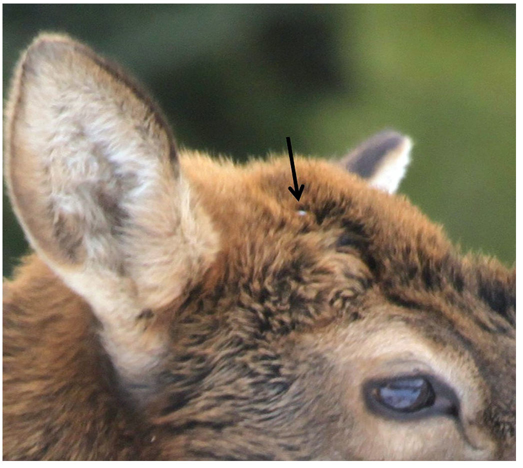

FIGURE 2. Pedicle-like formation on a potential hermaphroditic Elk (*Cervus canadensis*) exhibiting female external genitalia and male secondary sexual characteristics. Photo taken within 15 m at the Ya Ha Tinda, adjacent to Banff National Park, Alberta, Canada. Photo: J. Normandeau.

female Elk. Wislocki (1956) also documented a male pseudo-hermaphrodite White-tailed Deer with antlers, a normal-sized vagina with a blind ending, and a small, hypoplastic (underdeveloped) testicle in the abdomen, which is consistent with our observations, although we did not observe antlers. Because antler growth is regulated by hormones produced from the testes (Wislocki *et al*. 1947), hypoplastic testes could explain the lack of antler growth in a male pseudo-hermaphrodite (Wislocki 1954). We did note two symmetrical patches of depressed hair on the head of the Elk at Ya Ha Tinda where antler pedicles would form, and one image (Figure 2) shows a small greyish nub protruding over the hair, which may signal the partial formation of a pedicle. However, we also cannot rule out female pseudo-hermaphroditism or XX-sex reversal. Although we argue that this Elk likely is a case of pseudo-hermaphroditism, we cannot rule out true hermaphroditism without a necropsy, as the presence of both male and female gonads cannot be eliminated or confirmed.

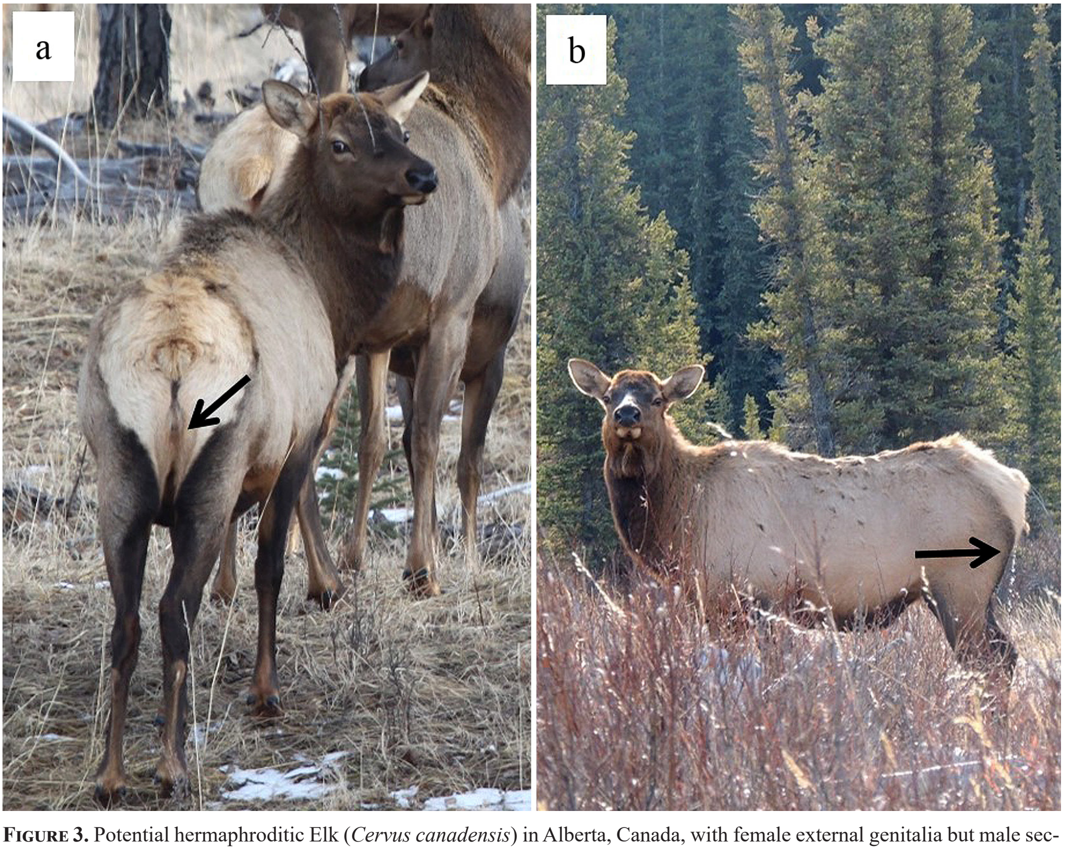

FIGURE 3. Potential hermaphroditic Elk (*Cervus canadensis*) in Alberta, Canada, with female external genitalia but male secondary sexual characteristics. The individual displays evidence of pedicles but no antler growth, no external signs of a penis or scrotum, and what appears to be female external genitalia (a). The individual was observed urinating from a vulva-like opening below the anus (b). Photos: J. Normandeau.

FIGURE 4. Potential hermaphroditic Elk (*Cervus canadensis*) with female external genitalia and male secondary sexual characteristics following a female while flicking its tongue in and out during the rut in the fall of 2019, a typical male behaviour. Photo: J. Normandeau.

FIGURE 5. Potential hermaphrodite Elk (*Cervus canadensis*) with female external genitalia and male secondary sexual characteristics attempting to bugle during the rut in the fall of 2019. The Elk does produce a bugle-like sound, but much quieter than typical male Elk bugling. Photo: J. Normandeau.

As a result, we argue that this Elk is likely a pseudo-hermaphrodite. Whether it was born into the Ya Ha Tinda herd or joined the herd is unknown. The Elk was likely over two years old at the time of observation because it was larger than a yearling male Elk. We did not observe an Elk exhibiting these characteristics before fall 2019 despite over 250 h/year of observations from January to April in 2018 and 2019. It is possible that segregation of males from the main Elk herd reduced the probability of seeing the Elk in previous winters. It is also possible that, if the Elk was a yearling with spike antlers the previous year, the female external genitalia may have been overlooked. The fact that, in 2020, the Elk remained with the main female herd and did not disperse with other males at the end of the rut is evidence it may have been part of the main herd the previous year. If this were the case, it is unclear why the individual would not have grown antlers in subsequent years. Alternatively, the Elk may have joined the herd from another population if it displayed juvenile dispersal tendencies, which have been known in Elk (Petersburg *et al*. 2000). At the same time, interchange between the Elk population in the town of Banff, which is ~80 km southwest of the Ya Ha Tinda, is as low as 1% (M.H. unpubl. data). Genetic analysis might have allowed us to determine a potential source population, but this Elk was never captured to obtain a sample.

Our ability to document an individual Elk as a potential pseudo-hermaphrodite is related to the intensity with which the Ya Ha Tinda Elk population has been studied over an 18-year period with ~25% of the herd individually marked. We were not able to capture the individual to obtain blood or a genetic sample, and without a radio collar we are unlikely to obtain the remains of the individual soon enough after death to examine internal organs because of high predator abundance. Genetic characterization of chromosomal sex and the presence of the *SRY*-gene, which stimulates testes differentiation, would be necessary to determine which type of pseudo-hermaphroditism is present. At the same time, we argue that there is sufficient evidence to claim that, to our knowledge, this is the first documentation of either true or pseudo-hermaphroditism in Elk in North America.

Author Contributions

Writing – Original Draft: J.N.; Writing – Review & Editing: J.N., E.H.M., M.H., and H.M.; Conceptualization: J.N.; Investigation: J.N.; Methodology: J.N.; Funding Acquisition: E.H.M., M.H., and H.M.

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Note

Late-autumn record of Little Brown Myotis (*Myotis lucifugus*) in north-central British Columbia

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Abstract

Little Brown Myotis (*Myotis lucifugus*) inhabits north-central British Columbia (BC), but its flight activity at the onset of hibernation is not well known. On 31 October 2019, we saw three bats flying in patterns that suggested feeding, near the north shore of the Fraser River near Prince George, BC. Observations of Little Brown Myotis flying this late in the autumn have not previously been documented this far north in interior BC. We photographed the bats, and here we describe the encounter and discuss the scientific value of our observation.

Key words: Seasonal activity; autumn; hibernation; Little Brown Bat; *Myotis lucifugus*; temperature

Few studies have documented the autumn biology of bats in northwestern Canada and no studies appear to have been conducted on the seasonal activity patterns of Little Brown Myotis (*Myotis lucifugus*) in north-central British Columbia (BC). Of the approximately 15 bat species known to occur regularly in BC (Government of British Columbia 2020), most—including *M. lucifugus*—hibernate during the winter months (defined as 1 November to 31 March by Nagorsen *et al.* 1993) and emerge sometime in the spring when they begin to return to their summer grounds (BC Community Bat Program 2018). However, much remains to be learned concerning various aspects of winter activity for North American temperate zone bats (Boyles *et al.* 2006).

In summer, Little Brown Myotis has been observed roosting in bat boxes, tree snags, rock crevices, mines, and caves, often selecting the latter three locations for hibernacula (Fenton and Barclay 1980), but it will also select and preferentially use buildings when available, particularly in northern climates (Randall 2014; Willie 2018). These bats are described as nocturnal obligate insectivores (Fenton and Barclay 1980). They have been observed throughout BC, mainly in summer, but a few records exist for use of a building (C. Lausen pers. comm. 31 May 2020), cave (Davis *et al.* 1997), and mine (Jobin 1952) at other times of the year. Caves are suspected to provide hibernacula for Little Brown Myotis; however, none have been confirmed (C. Lausen pers. comm. 31 May 2020; B. Paterson pers. comm. 10 July 2020). Late fall and early spring acoustic data strongly suggest that Little Brown and other *Myotis* spp. also use crevice habitat as hibernacula (B. Paterson pers. comm. 10 July 2020).

Information on the winter distribution and roosting habits of bats in north-central BC is anecdotal at best, with one hibernaculum documented to the southwest of our observation (Jobin 1952). Nagorsen *et al.* (1993) report that winter records exist for only seven species of bats in BC.

According to some studies, bats may intermittently emerge from hibernacula in fall and winter because of dehydration, hunger, fungal infections, or the need to relocate (Lausen and Barclay 2006; BC Ministry of Environment 2017), to exercise flight muscles (Klüg-Baerwald *et al.* 2017), to spur immune function, or to copulate (Boyles *et al.* 2006). Bat activity patterns and behaviours associated with torpor, hibernation, and emergence linked to foraging bouts are complex and poorly understood (Czenze and Willis 2015; Meyer *et al.* 2016).

On 31 October 2019, we observed three bats in flight near the 17-km marker board on the North Fraser

Resource Road on the north bank of the Fraser River adjacent to a south aspect rock face at 54.260343°N, 122.372495°W, ~60 km northeast of Prince George. The three bats, seemingly of the same species, appeared to be foraging back and forth over the river and between the rock face and the river channel. We also noticed small flying insects in the air, which the bats, based on their erratic flight paths, appeared to be pursuing. Most of the flying occurred in a 25-m radius around our car, 2–6 m above the road surface with heights of 10–12 m occasionally reached. The bats moved up and down the road where we were stopped and over the river; they did not fly farther than 300–400 m in either direction from where we were parked.

The observation occurred between 1530 and 1615 on a sunny afternoon (temperature ~4°C; little to no wind; sunset 1739). The surrounding habitat was riparian with an upland forest of mixed mature Trembling Aspen (*Populus tremuloides* Michaux), hybrid White Spruce (*Picea engelmannii* Engelmann var. *engelmannii* × *Picea glauca* (Moench) Voss.), and Douglas Fir (*Pseudotsuga menziesii* var. *glauca* (Beissner) Franco), with some large diameter (>100 cm at breast height) Black Cottonwood (*Populus balsamifera* subsp. *trichocarpa* Torrey & A. Gray) along the north shore of the Fraser River. Although the area in which we observed the bats was relatively pristine, much of the surrounding forest had been impacted by logging over the last 50 years. Average temperature for the Prince George area for October (1981–2010) is 4.5°C, with average precipitation 63.3 mm; average temperature and precipitation for November are −2.5°C and 55.3 mm, respectively (Environment and Climate Change Canada 2019).

The bats had light brown bodies, dark brown wings, and were relatively small (Figure 1). We were able to take dozens of high-resolution photographs of the bats at different angles (5D Mark 3 with a 300 f/2.8 lens and 2× extender, Canon, Ota City, Tokyo, Japan). We sent some to three bat experts: one confirmed the genus as *Myotis* sp. (B. Fenton pers. comm. 12 November 2019), and two others confirmed the species as Little Brown Myotis (C. Lausen and I.-J. Hansen pers. comm. 7 and 8 January 2020, respectively). As described by C. Lausen, "The high resolution images enabled close examination of head and tail details of the bats in flight, concluding there was no sign of a keel, the tragus was blunt, and the ear pinnae were somewhat pointed". The absence of the keel narrowed the identification to either Little Brown or Yuma Myotis (*Myotis yumanensis*), both with somewhat pointed ear pinnae and a blunt tragus, but the latter species is not known northeast of the Williams Lake–Quesnel area (BC Ministry of Environment 2008).

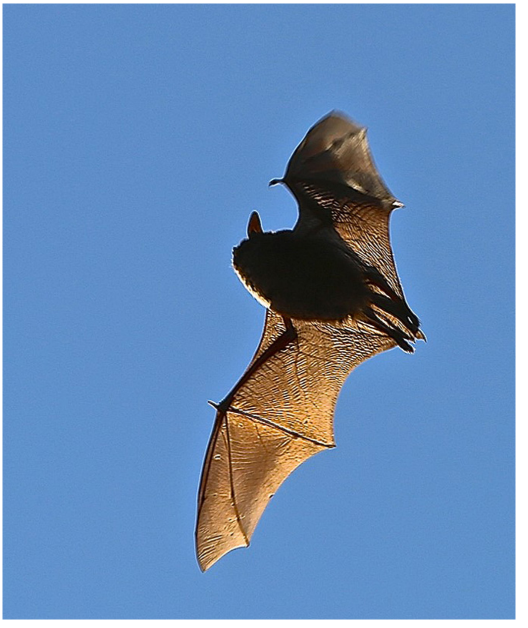

Figure 1. Little Brown Myotis (*Myotis lucifugus*) in the afternoon sun near Prince George, British Columbia, 31 October 2019. High-resolution photographs, such as this one, helped experts identify the bats. Photo: R.V. Rea.

Except for a single specimen of Little Brown Myotis that was found hibernating in a mine shaft near Williams Lake, ~300 km south of our sighting (Jobin 1952), winter occurrences of this species in BC are extremely limited (Nagorsen *et al.* 1993), especially as far north as our observation and west of the Rocky Mountains. To the best of our knowledge, this is the most northern sighting of a Little Brown Myotis this late in the autumn in north-central BC. Schowalter (1980) reported sampling Little Brown Myotis near Edmonton, Alberta (approximately same latitude as our encounter), in the late 1970s, but nearly all bats caught after the second week of September were found in a torpid condition, rather than active and foraging. Unpublished acoustic recordings of Little Brown Myotis exist from north of our encounter, at Muncho Lake (59.043°N, 125.794°W) on 23 October 2015, but the only recording of which we are aware for this species after 31 October in northern BC is coastal, at Tow Hill, Haida Gwaii, on 4 November 2014 (C. Lausen pers. comm. 31 May 2020).

Our observation has scientific value for several reasons. First, we observed bats flying during daylight hours. The BC Ministry of the Environment asks the public to report bats that are flying during the day and/or during winter months, because this may indicate early signs of infection with white-nose syndrome (BC Ministry of Environment 2017).

Second, although we did not confirm the presence of a hibernaculum, we assumed that bats flying in the late afternoon in late October would remain close to their hibernaculum (Whitaker and Rissler 1992) and that one was nearby. As such, the local area should be scrutinized for the presence of a hibernaculum.

The northernmost confirmed hibernaculum in BC (west of the Rocky Mountains) appears to be ~200 km southwest of where we made our observation (Jobin 1952). Several other overwintering hibernacula are suspected in the Williston Reservoir area (caves and rock crevices; I.-J. Hansen pers. comm. 22 September 2020) and Evanoff Provincial Park (C. Lausen pers. comm. 31 May 2020); however, none has been confirmed. Locating hibernacula, which are critical habitat (Environment and Climate Change Canada 2018), is crucial for conservation of this federally Endangered species (SARA Registry 2019). Acoustic detectors are typically set to begin recording at sunset, but researchers should consider beginning their recordings much earlier in the day in the north during the fall, winter, and spring to avoid missing opportunities to document potential hibernacula. Once hibernacula are located, they can be used to monitor bat population trends and the susceptibility of the bats to and the spread of white-nose sydrome or other, potentially emerging diseases (Misra *et al.* 2009).

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Distribution and status of Howell's Quillwort (*Isoetes howellii*, Isoetaceae) in Canada and its relation to Bolander's Quillwort (*Isoetes bolanderi*)

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Abstract

The sparsely documented lycophyte, Howell's Quillwort (*Isoetes howellii*), occurs in Canada in four distinct areas of British Columbia in a variety of microhabitats. Before 2010, two areas of occurrence were known in Canada. Two additional clusters of occurrences have been discovered in the last decade. In Canada, *I. howellii* is found in open, ephemeral wet swales, shallow ponds, and periodically flooded shorelines, channels, and back beach meadows. Habitat rarity may be the primary reason for the large gaps between areas of occurrence. The current viability of the Canadian population is dependent on maintaining the recently discovered large number of individuals in the North Thompson River Region. *Isoetes howellii* shares many similarities with fellow diploid, Bolander's Quillwort (*Isoetes bolanderi*). The possibility that it represents a low-elevation subspecies of *I. bolanderi* requires further investigation. *Isoetes howellii* is rare in British Columbia and warrants consideration as a species at risk in Canada.

Key words: Howell's Quillwort; *Isoetes howellii*; Bolander's Quillwort; *Isoetes bolanderi*; British Columbia; species at risk; Canada

Introduction

Morphologically simple, mostly aquatic quillworts (*Isoetes*, Isoetaceae) are among the oldest vascular plants on earth, originating in the Late Devonian era (375 million years ago; Larsen and Rydin 2016; Troia *et al.* 2019). Contemporary species are thought to have diversified relatively recently, in mid-Paleogene (Tertiary) times (45–60 million years ago; Wood *et al.* 2019). Approximately 200 current taxa (species, subspecies, hybrids) have been described worldwide (Troia *et al.* 2016). However, molecular investigations indicate continued and possibly rapid diversification, with many distinctive genetic traits detected among the recognized flora (Hoot *et al.* 2004; Schafran *et al.* 2018). This has led some to conclude that undetected cryptic species are numerous—at least 50 in North America alone (Schafran 2019). Although the taxonomic implications of DNA findings remain unresolved, *Isoetes* is clearly a taxonomically dynamic genus, even at the northern limits of its continental distribution. A conservative estimate is that 250+ species have been detected globally, with perhaps 100 more expected to be recognized (Brunton and Troia 2018; Troia *et al.* 2019).

Half of the dozen known Canadian *Isoetes* species are found in British Columbia (BC; Cody and Britton 1989; Taylor *et al.* 1993). Most of these grow in acidic or circum-neutral silty sand and gravel substrate on emergent shores of rivers and ponds or in the finer, peaty sand substrate of ephemeral pools and seeps in woodland glades. Two Canadian species have been described in the last 30 years (Britton and Goltz 1991; Brunton *et al.* 2019), and at least one additional undescribed taxon is suspected in western Canada (D.F.B. unpubl. data). It is also likely that some Canadian *Isoetes* occurrences represent additional taxa currently believed to occur only in the United States, Europe, or Asia.

Howell's Quillwort (*Isoetes howellii* G. Engelmann, including *Isoetes melanopoda* J. Gay & M. Durieu var. *californica* A.A. Eaton and *Isoetes underwoodii* L. Henderson; Figure 1) is a diploid (2*n* = 2x

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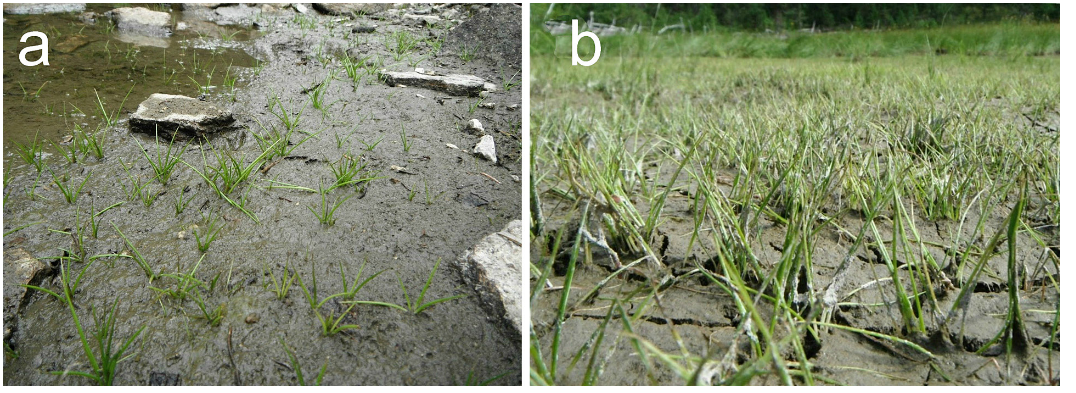

FIGURE 1. Howell's Quillwort (*Isoetes howellii*). a. Amphibious plants, initially submerged and ultimately terrestrial with seasonal pond downdraw (North Thompson River Pond 5, British Columbia [BC], 23 August 2012). b. Dense occurrence of plants in profile (North Thompson River Pond 1, BC, 24 August 2012). Photos: R.S. Krichbaum.

= 22) component of a particularly complex group of western North American quillworts that, in Canada, also includes the aquatic Bolander's Quillwort (*Isoetes bolanderi* G. Engelmann; COSEWIC 2006) and the ephemeral seepage associate, Columbia Quillwort (*Isoetes minima* A.A. Eaton [*I. howellii* var. *minima* N. Pfeiffer]; Taylor *et al.* 2003; COSEWIC 2019). *Isoetes bolanderi* and *I. minima* have been assessed as nationally Threatened and Endangered, respectively (COSEWIC 2006, 2019) with *I. bolanderi* listed as Threatened under the *Species at Risk Act* (SARA Registry 2019).

The limited geographic distribution of *I. howellii*, the apparent reduction in the number of known occurrences through taxonomic reconfiguration (e.g., the determination that some occurrences are *I. minima*; Ceska 2001), and the destruction of apparently suitable quillwort habitat (COSEWIC 2019) suggest that *I. howellii* may be a rare and declining Canadian taxon and worthy of consideration for designation as a national species at risk. However, the recent, unexpected discovery of a new and substantial cluster of occurrences, relatively far from the species' long understood distribution in Canada, complicates that assessment. It raises questions about the potential existence of other occurrences in BC, while also enhancing our understanding of the habitat requirements and limits of this species in Canada. In addition, the difficulty of separating some northern (Canadian) occurrences of *I. howellii* from the closely related *I. bolanderi* raises questions about its appropriate level of taxonomic designation.

There is almost no existing literature addressing the ecology, morphological variation, or taxonomic relationships of *I. howellii* in North America. An apparent exception might be Jon Keely's use of *I. howellii* plants for an investigation of anaerobic metabolism in aquatic plants in southern California, when he made his classic discovery of crassulacean acid metabolism (CAM) photosynthesis in *Isoetes* in the early 1980s (Keely 2014); however, those investigations were focussed almost exclusively on plant chemistry. Accordingly, an examination of the current status, habitat requirements, and distributional limitations of the species in Canada can potentially provide insights into important biological characteristics of this taxon across its range. Our study undertook such an examination and also addressed the potential taxonomic implications of ecological and morphological variability in the Canadian population. Understanding the taxonomy and evolution of basic diploid *Isoetes* is fundamental to understanding the systematics of this genus for which alloploidy is the primary engine of diversity (Hickey *et al*. 1989; Britton and Goltz 1991; Troia *et al*. 2019).

Methods

These investigations are based on field and herbarium studies of *Isoetes* occurrences and specimens from throughout the range of both *I. howellii* and *I. bolanderi* in western Canada and the western United States, as described in Taylor *et al.* (1993). Field investigations of occurrences were conducted in Canada and the United States by D.F.B. between 1992 and 2011 and by M.A.K. and R.S.K. in 2012 and 2019. Voucher specimens of *I. howellii* (80+), *I. bolanderi* (60+), and associated species from the following institutions have been examined: ASU (Arizona State University, Tempe, Arizona); CAN (Canadian Museum of Nature, Ottawa, Ontario [ON]); DAO (Agriculture and Agri-Food Canada, Ottawa, ON); DFB (D.F. Brunton herbarium, Ottawa, ON); DUKE (Duke University Herbarium, Durham, North Carolina); FSU (Florida State University, Tallahassee, Florida); Glacier National Park herbarium, Montana; IDAHO (Stillinger Herbarium, University of Idaho, Moscow, Idaho); MICH (University of Michigan, Ann Arbor, Michigan); MO (Missouri Botanical Garden, St. Louis, Missouri); NY (New York Botanical Garden, Bronx, New York); OAC (University of Guelph, Guelph, ON); OSC (Oregon State University, Corvallis, Oregon [OR]); PH (University of Pennsylvania, Philadelphia, Pennsylvania); RM (Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming ([WY]); SUNY (Oswego) herbarium, New York; UNLV (University of Nevada, Las Vegas Nevada); V (Royal British Columbia Museum, Victoria, BC); VPI (Virginia Polytechnical Institute and State University, Blacksburg, Virginia); and WTU (University of Washington, Seattle, Washington; acronyms according to Thiers 2020). These included type specimens of both *I. bolanderi* and *I. howellii*. The morphological characteristics of living *I. bolanderi* plants from WY and living *I. howellii* plants from BC were also observed in cultivation in 2019 and 2020.

Spore features (size, ornamentation, shape) are critical to the identification of Canadian *Isoetes* (Cody and Britton 1986; Taylor *et al.* 1993). The spores of 550–600 individual plants from over 140 *I. howellii* and *I. bolanderi* herbarium specimens were examined visually and/or with a scanning electron microscope (SEM). Although most megaspore ornamentation features are readily discernible under 30–40× magnification, microspores are too minute for low-power visual examination. However, as they often provide valuable supporting identification and taxonomic information, we examined the size, ornamentation, and structure of microspores from Canadian occurrences with SEM imagery.

All microscopic features of the vouchers were studied (and measured) 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. Megaspore sizes reported for individual specimens represent the average width (across the equatorial region) of at least 20 (often 40) spores. Comparable microspore measurements are based on the average of 20 (frequently 40) longitudinal measurements taken from SEM images of clusters of spores.

We reviewed an extensive library of SEM spore images of *I. howellii*, *I. bolanderi,* and related taxa prepared by D.M. Britton before 2007 (using the methods described in Brunton and Britton 2006). Additional SEM images were produced 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 SEM, ThermoFisher Scientific, Hillsboro, Oregon, USA) at 15 kV and 25 pA, with a working distance of 10 mm and a spot size of 6.

In our study, we employ the term "population" to refer to the total number of plants known in Canada. "Occurrence" is used to represent distinct groups of plants separated from any other site by more than 100 m of unoccupied habitat. The term "patch" refers to groups of plants separated by less than 100 m of unoccupied habitat.

Results and Discussion

Distribution and status in Canada

Isoetes howellii records in Canada date from shortly after its description (Engelmann 1882), as it was first collected on 29 June 1889 at Kamloops, BC (*John Macoun s.n.,* CAN 5535). Macoun identified this collection as *I. bolanderi*, a determination unchanged by subsequent investigators for over a century (Taylor 1970; Scoggan 1978). In 1991, the specimen was determined by D.M. Britton and D.F.B. to be immature *I. howellii*, based on spore morphology and site ecology. The Kamloops occurrence was apparently situated along the shore of a shallow, semi-permanent sedge-lined pond, but now appears to be extirpated (D.F.B. pers. obs. 29 June 2008). An occurrence 30 km west (downstream) at Kamloops Lake (*A. and O. Ceska 4,547*, 28 August 1980, V) indicates that *I. howellii* persisted in the local area, at a site where apparently suitable emergent silty-gravel shore habitat remains (Google Earth imagery, 29 September 2019).

Several weeks after his Kamloops collection, John Macoun collected a second BC *Isoetes* that he identified as *I. bolanderi*. That specimen (*John Macoun s.n., 17 July 1889*, by the railway bridge, Sicamous, CAN 582996) was revised by D.F.B. to *I. ×marensis* D.M. Britton and D.F. Brunton, the sterile triploid ($2n = 3x = 33$) hybrid between *I. howellii* and tetraploid ($2n = 4x = 44$) Maritime Quillwort (*Isoetes maritima* L. Underwood; Britton and Brunton 1995). Although this strongly suggests that *I. howellii* was also present, its occurrence at the site was not confirmed until 2013 (*F. Lomer 2013*, 21 August 2013, in finely gritty white sand at raised moist margin of green sward, 1.7 km due northwest of Sicamous, V241023).

The third Canadian *I. howellii* record was reported from Akamina Pass near the Alberta (AB) border in southeastern BC and is represented by a collection from a shallow, ephemeral wetland swale at 1783 m above sea level (asl) in an Engelmann Spruce (*Picea engelmannii* C. Parry), Lodgepole Pine (*Pinus contorta* D. Douglas) forest glade (*David Polster s.n., 24 August 1976*, V94753). This is in the ESSFdk1 biogeoclimatic subzone (Engelmann Spruce–Subalpine Fir dry cool Elk Variant; BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development 2018). This quillwort was also initially identified as *I. bolanderi*. Further collections from the Akamina Pass site (e.g., *D.F. Brunton and K. L. McIntosh 10,855*, 16 August 1991, DFB, MIL, OAC, VPI, WIS) resulted in the redetermination of that occurrence as *I. howellii*. Abundance was observed to be large at this site (~7500 individuals), with concentrations of plants both in the open central portion of the wetland and along the vegetated edge of an ephemeral Wheat Sedge (*Carex atherodes* K. Sprengel) marsh (Figure 2a). *Isoetes howellii* remained abundant at the site until at least 2 September 2012, with thousands of amphibious plants evident in two separate patches in distinct ephemeral wetland swales over an approximate total area of 2.5 ha (M.A.K and R.S.K. pers. obs.). This occurrence was impacted by the severe Kenow wildfire of 2017 (Parks Canada 2018). The fire was very hot and the sedge mat adjacent to the *I. howellii* site burned intensely, leaving ~5 cm of charcoal above unburned sedge peat. Some *Isoetes* plants survived, however, and normal-sized plants were found to be common at the site on 28 September 2020 (P. Achuff pers. comm. 21 October 2020).

To date, no Canadian occurrences of true *I. bolanderi* have been confirmed outside of Waterton Lakes National Park, southwestern AB (COSEWIC 2006).

The first Canadian records of *I. howellii* to be correctly identified at the time of collection were those of Adolf and Oldriska Ceska in 1980 in the Shuswap Lake–South Thompson River Region of south-central BC (e.g., Kamloops Lake, Savona, *A. and O. Ceska 4,548*, 28 August 1980, V, and View Point Motel beach, Salmon Arm, *A. and O. Ceska 4,664*, 29 August 1980, V). Some of these sites were re-examined in the early 1990s by D.F.B. (Figure 2b). Other collections were made 15 km south of Sicamous, BC at Mara Lake, which drains into Shuswap Lake (Figure 3). These collections were secured during fieldwork associated with the description of *I. ×marensis* (*I. howellii* × *I. maritima*; Britton and Brunton 1995).

The cluster of occurrences in the Shuswap Lake–South Thompson River Region are scattered across 2400 km^2, all at ~350 m asl (Figure 3). The circumscription of this cluster includes the total area considered to potentially include suitable *I. howellii* sites. *Isoetes howellii* plants in the Shuswap Lake–South Thompson River area are amphibious, growing along lakeshores in coarse sand and gravel substrate in sparsely vegetated wet swales that are often dry by late summer. The total number of individuals in all five extant occurrences is estimated to be <1000. Other *Isoetes* species, notably polyploids *I. maritima* and, less commonly, Western Quillwort (*Isoetes occidentalis* L. Henderson), grow with or near the Shuswap Lake–South Thompson River *I. howellii* plants. An apparent hybrid between *I. howellii* and *I. occidentalis* from Shuswap Lake is being investigated separately.

Before 2010, only the Shuswap Lake–South Thompson River and Akamina Pass occurrences represented the known distribution of *I. howellii* in BC and Canada (Klinkenberg 2019). In 2010, however, *I. howellii* was collected in and around the town of Castlegar in southern interior BC by Frank Lomer. He reported three small occurrences separated by ~1 km, centred on the confluence of the Columbia and Kootenay Rivers: Columbia River at Waldie Island Heron reserve, *F. Lomer 7,487*, 7 September 2010 (UBC); Columbia River north of Zuckerberg Island, *F. Lomer 7,478*, 7 September 2010 (UBC); and Kootenay River by Selkirk College, *F. Lomer 7,498*, 8 September 2010 (UBC). Each occurrence consisted of one or more patches of fewer than 50 individuals scattered over an estimated 1–300 m^2 area. The *I. howellii* plants were

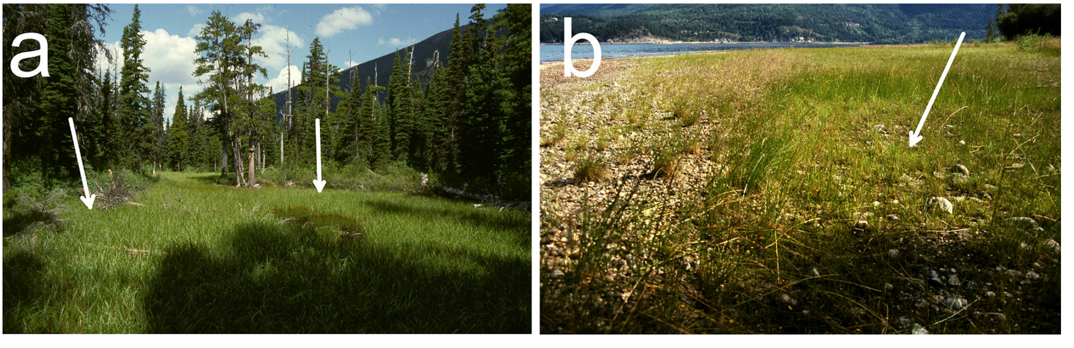

FIGURE 2. Howell's Quillwort (*Isoetes howellii*) habitat. a. Seasonally flooded sedge swale (Akamina Pass, British Columbia [BC], 16 August 1991). b. Back-beach depression (Shuswap Lake, BC, 14 August 1992). Arrows indicate concentrations of *Isoetes* plants. Photos: D.F. Brunton.

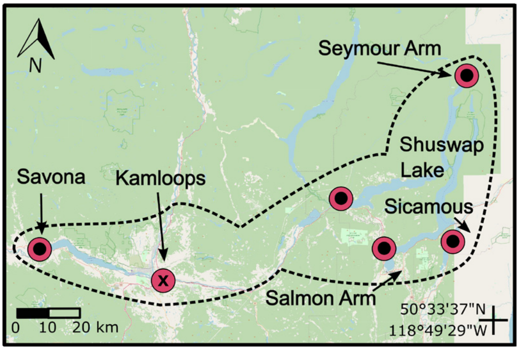

FIGURE 3. Occurrences of Howell's Quillwort (*Isoetes howellii*) at Shuswap Lake and the South Thompson River, British Columbia. Polygon outlines local area of occurrence; dots = approximate location of individual sites; × = extirpated occurrence. Map data: Open Street Map contributors via QGIS3.

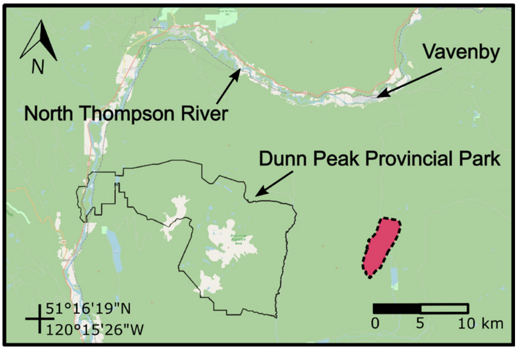

FIGURE 4. Occurrences of Howell's Quillwort (*Isoetes howellii*) in the North Thompson River Region, British Columbia (polygon outlines local area of occurrence; individual occurrences not shown for conservation/protection purposes). Map data: Open Street Map contributors via QGIS3.

growing amphibiously on exposed muddy river channels and on wet, pebbly river shoreline at 415–420 m asl. Associated vascular plant species included Water Mudwort (*Limosella aquatica* L.), Water Pygmyweed (*Crassula aquatica* (L.) Schoenlein), and Clammy Hedge-hyssop (*Gratiola neglecta* J. Torrey). This cluster of occurrences is ~190 km southeast of the Shuswap Lake–South Thompson River Region, and ~260 km west of Akamina Pass.

The most recent and significant *I. howellii* cluster in BC and Canada, which is located south of Vavenby in the North Thompson River Region, arose initially from a discovery by Curtis Björk (*Björk 25 087,* 8 September 2011, UBC). Like previous BC records, this was first thought to be *I. bolanderi*. Subsequent investigations by M.A.K. and R.S.K. in 2012 and 2019 documented four additional occurrences in the vicinity, for a total of five distinct *I. howellii* occurrences scattered across 1.4 km^2 at an elevation of 1770 m asl (*M. & R. Krichbaum 15275–15279, 23–25 August 2012*, DFB, UBC, *15301–15303*, 18 September 2019, DFB, UBC, *15304–15306*, 18 September 2019, DFB; Figure 4). This cluster of occurrences (Table 1) is ~70 km north of the next nearest known *I. howellii* in the Shuswap Lake–South Thompson River cluster at an elevation of ~350 m asl.

The five occurrences of *I. howellii* in the North Thompson River Region are located in a forested basin (~1770 m asl), the centre of which contains an intricate wetland, glade, and forest (*Picea engelmannii*/Subalpine Fir [*Abies lasiocarpa* (Hooker) Nuttall]) complex (Figure 5). This is in the ESSFwc2 biogeoclimatic zone (Engelmann Spruce–Subalpine Fir wet cold Northern Monashee Variant; BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development 2018). Large portions of the basin have been logged in the past. The *I. howellii* plants occur in silty soils in and around shallow ponds, two of which were drawn down to open wet swales and even dry glades in 2012. Four of the five occurrences are surrounded by relatively undisturbed glade and forest habitat; however, the southernmost site (Pond 2) is located next to a road track in a previously logged area. In 2012, evidence of active cattle use (dung and hoofprints) was observed at four of the five ponds; no evidence of cattle activity was observed in the area in 2019 by M.A.K. and R.S.K.

TABLE 1. Summary of occurrences of Howells' Quillwort (*Isoetes howellii*) in the North Thompson River Region, British Columbia, Canada.

Site	Occupied area, m^2	Estimated number of individuals*	Elevation, m a.s.l.
Pond 1	195	487 500	1759
Pond 2	334	835 000	1800
Pond 3	127	317 500	1759
Pond 4	309	772 500	1771
Pond 5	280	700 000	1785
Total	1245	3 112 500	

Note: a.s.l. = above sea level.
*Number of rooted, apparently spore-bearing individuals based on an estimated average density of 25 plants/100 cm^2.

At all five North Thompson River Region occurrences, *I. howellii* plants were found growing amphibiously, with the majority submersed and the remainder emergent to terrestrial, according to seasonal conditions (Figures 1 and 5). In both 2012 and 2019, *I. howellii* plants were also observed growing in dense concentrations at all five sites. In 2019, thousands of sporelings (newly emergent sporophytes) were also observed mixed with non-vascular vegetation floating

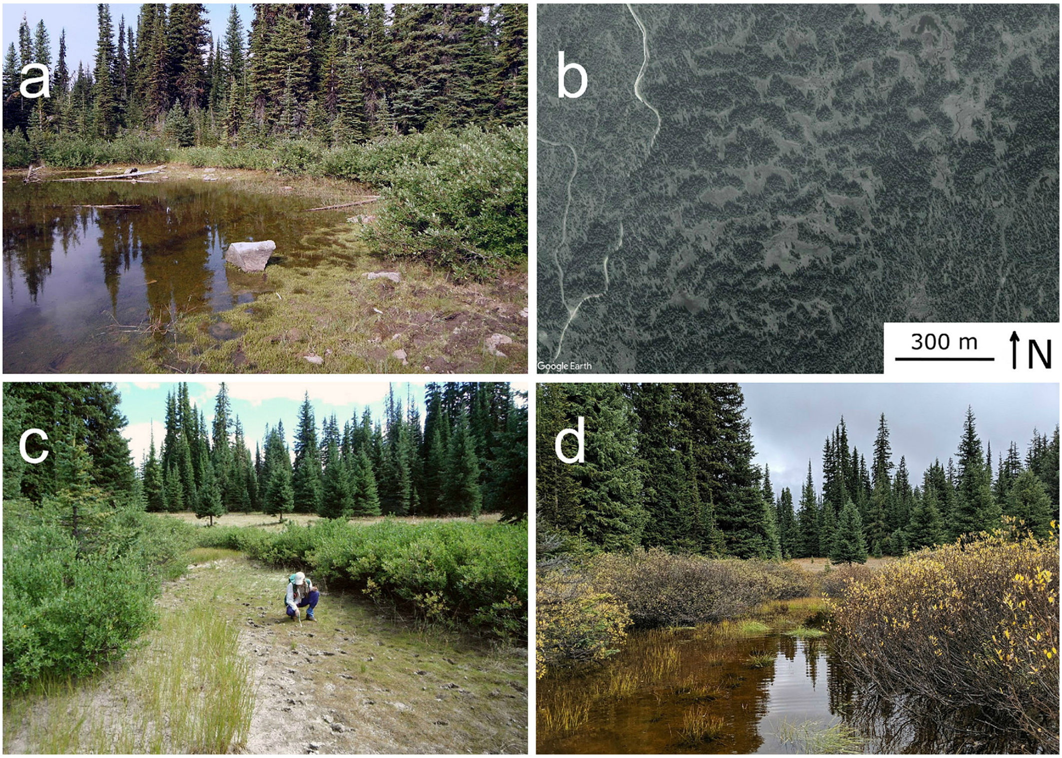

FIGURE 5. Howell's Quillwort (*Isoetes howellii*) habitat in the North Thompson River Region, British Columbia. a. Seasonally emergent shore of Pond 2 (24 August 2012). b. North Thompson River Region forest glades (28 August 2019). c. Pond 3 in desiccated condition (25 August 2012). d. Pond 3 in flooded condition (18 September 2019). Photos: a, c, d: by R.S. Krichbaum. Photo b: GoogleEarth, 28 August 2019.

in the water of some of the ponds. Associated vascular plant species included Lesser Spearwort (*Ranunculus flammula* L.), Russet Sedge (*Carex saxatilis* L.), Few-flowered False-mannagrass (*Torreyochloa pallida* var. *pauciflora* (J. Presl) J.I. Davis), and Barclay's Willow (*Salix barclayi* N.J. Andersson).

Isoetes howellii, then, occupies four distinct and mostly widely separated areas in southern BC (Figure 6). The largest number of occurrences are scattered across an extensive area of the Shuswap Lake–South Thompson River Region. However, these apparently support only several hundred plants in total. Similarly, fewer than 150 plants were reported from the cluster of Castlegar occurrences. The Akamina Pass occurrence supported thousands of plants until at least 2012; the long-term impact of the severe 2017 forest fire at the site has yet to be determined.

By far the largest number of individual plants are found in the recently discovered North Thompson River cluster of occurrences where an estimated 3 000 000+ plants occupy five distinct sites (Table 1), all located within a kilometre of each other. Clearly, the long-term security of *I. howellii* in Canada is largely dependent on the sustainability of this cluster.

Despite the recent discovery of an immense number of plants in a small cluster of occurrences north of its previously known range limit, *I. howellii* will likely continue to be recognized as a locally abundant but nationally rare species. The discovery of other occurrences in southern BC between the Okanagan Valley and the Columbia River Valley (excluding the largely limestone-based Rocky Mountain range adjacent to the AB border) is to be expected. However, these would most likely consist of small numbers of individuals at geographically small sites, such as those in the Castlegar or Shuswap Lake–South Thompson River areas.

Why there are such wide gaps in the occurrence of *I. howellii* in BC is not immediately obvious. The most likely explanation is that the habitat, structure, and substrate type of ephemeral wetlands between these areas is unsuitable within this physiographically very complex cordilleran landscape. Few data exist on the *in situ* requirements and distinctions between *I. howellii* and *I. bolanderi* in terms of substrate chemistry, habitat structure, phytosociology, etc. (Achuff *et al.* 2011).

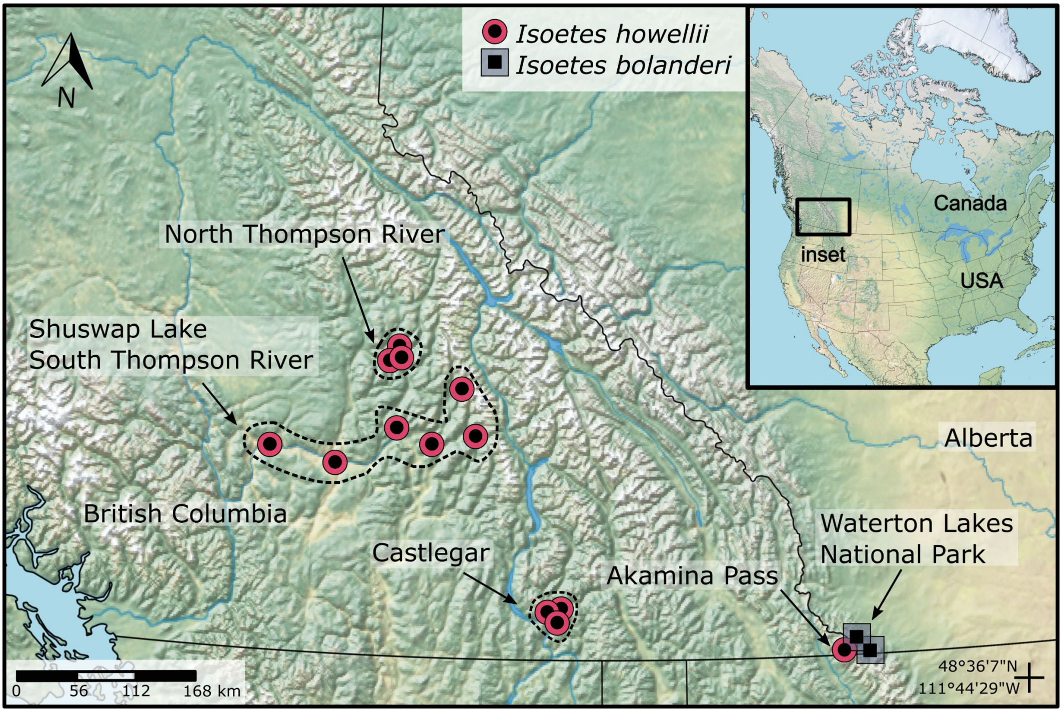

FIGURE 6. Occurrences of Howell's Quillwort (*Isoetes howellii*; dots) and Bolander's Quillwort (*Isoetes bolanderi*; squares) in Canada. Basemap from SimpleMappr (Shorthouse 2010).

The distributional data we present suggest that *I. howellii* may qualify as a species of Special Concern: "a wildlife species that may become threatened or endangered because of a combination of biological characteristics and identified threats" (COSEWIC 2020). Based on the data reported here and at our request, the BC Conservation Data Centre conducted an element subnational ranking of *I. howellii* and concluded that it would rank as provincially rare (S3; J. Penny pers. comm. 11 May 2020). Depending on the determination of contemporary and future threats in the Akamina Pass and (especially) the North Thompson River areas, however, a Threatened status could be more appropriate. That is particularly pertinent because more than 99% of the Canadian population occurs in the North Thompson River cluster, and this area is potentially at risk from a proposed large-scale open-pit mineral extraction operation (Weymark 2020).

Identification of Isoetes howellii *and* I. bolanderi

Several general, but nonetheless useful, distinctions have been documented to assist in separating *I. howellii* and *I. bolanderi*. A striking ecological distinction is noted in Taylor *et al.* (1993), who describe *I. howellii* as a plant of lower (montane) elevation ephemeral pools and wet swales and *I. bolanderi* as typically found in permanent lakes and streams at high (subalpine) elevations. Inconsistencies in this habitat segregation have been observed, however. For example, a substantial satellite occurrence of *I. bolanderi* in Waterton Lakes National Park, AB, is located at a subalpine elevation of 2050 m asl in atypically *I. howellii*-like ephemeral pools close to that species' typical fully aquatic site at Summit Lake (Achuff *et al.* 2011). In the same way, the North Thompson River *I. howellii* occurrences are situated at more typical lower elevations, but in semi-permanent ponds in a Subalpine Fir wet cold Northern Monashee ecosystem (BC Ministry of Forests, Lands, Natural Resource Operations and Rural Development 2018). In addition, plants believed to be *I. bolanderi*, but with *I. howellii*-like spore morphology, are known from high elevation (subalpine) sites in semi-permanent wetland areas in WY, e.g., Mary Lake (among) Lodgepole Pines, former wetland now at 2680 m asl, Yellowstone National Park *C.E. Hellquist, Z. Haake & K. Mott 1919-16, 22 July 2016*, SUNY–Oswego herbarium, and near Coulter Bay Maintenance Area (elevation 2065 m asl), Lake Jackson, Grand Teton National Park *Jack States s. n., August 1970*, RMH 288404. Although ecological distinctions between these two taxa seem to apply clearly to many occurrences, substantial contradictions are evident in others.

A set of morphological distinctions at both the gross and microscopic levels are employed to separate these two taxa. The morphological analysis provided here is derived from the examination of an extensive number of herbarium specimens (see Methods) as well as from our experience in the field with both species in Canada and the United States. As with virtually all other *Isoetes* globally (Pfeiffer 1922; Taylor *et al.* 1993; Chinnock 1998; Troia 2001; Brunton and Troia 2018) spore size, shape, and ornamentation are the most critical and effective features for the separation of *I. howellii* from *I. bolanderi*.

Canadian *I. bolanderi* plants have erect, stiff, and brittle leaves, readily breaking off from the corm with only slight physical impact (e.g., the action of passing or browsing ungulates). Thousands of *I. bolanderi* leaves are commonly seen floating on the surface and washed up along the shore (Figure 7a) of Summit Lake in Waterton Lakes National Park, AB (COSEWIC 2006). In contrast, *I. howellii* observed in the present study had more strongly adherent, reflected, almost flaccid leaves (Figure 7b). This distinction is also apparent in cultivated material, with the leaves of *I. bolanderi* from WY remaining stiffly upright and slightly recurved while BC (North Thompson River Region) *I. howellii* plants are weakly ascending and flaccid (D.F.B. pers. obs.). This is not a universal trait of the species, however, as a number of completely aquatic occurrences of *I. bolanderi* in WY were observed to also have slightly recurved and substantially adherent leaves more like those of *I. howellii* (D.F.B. pers. obs.).

The difference in leaf-base colour reported by Taylor *et al.* (1993), with *I. howellii* being pale brown to even lustrous black, was not conspicuous in our study. Although some *I. howellii* plants from the Akamina and Shuswap Lake, BC, occurrences had slightly darker (uniform brown) leaf bases, no black-coloured bases were observed. Similarly, the cultivated WY *I. bolanderi* and North Thompson River Region *I. howellii* plants all had white to whiteish-tan leaf bases.

Table 2 summarizes the key features we found to differentiate *I. howellii* from *I. bolanderi* most convincingly. The identification of individual specimens relies, not on a single or even a few stand-alone diagnostic feature(s), but the accumulated weight of a suite of characters pointing most convincingly to one or the other taxon. Although megaspore size and ornamentation are valued most greatly for this purpose, the relative weight of any particular identification feature has not been formally determined for these taxa (indeed, for any *Isoetes* taxon). However, typical *I. howellii* megaspores are usually larger than those of *I. bolanderi*, particularly in occurrences in the southern portion of the range; e.g., 430.7 µm (n = 30) from Ellery Lake, Mono County, California, *J.D. Montgomery and D.G. Huttleston 88-78*, 8 August 1988 (DFB). They are also more conspicuously ornamented with low, broad walls (muri; Figure 8a) or obscure mounds (Figure 8b) distributed across the spore surface (perispore) in widely varying configurations and densities. *Isoetes bolanderi* megaspore ornamentation is typically papillate to echinate-tuberculate (Figure 8c) with a dense pattern of short, narrow tubercles. When muri are present (as with some specimens of *I. bolanderi*), they are usually obscure, short (rugulate), and narrower (Figure 8d) than typically seen in *I. howellii*.

Although *I. howellii* microspores tend to have more coarsely echinate ornamentation (Figure 9a) than the more finely echinate to spinulose ornamentation of *I. bolanderi* microspores (Figure 9b), contradictions and intermediate expressions of this pattern are evident

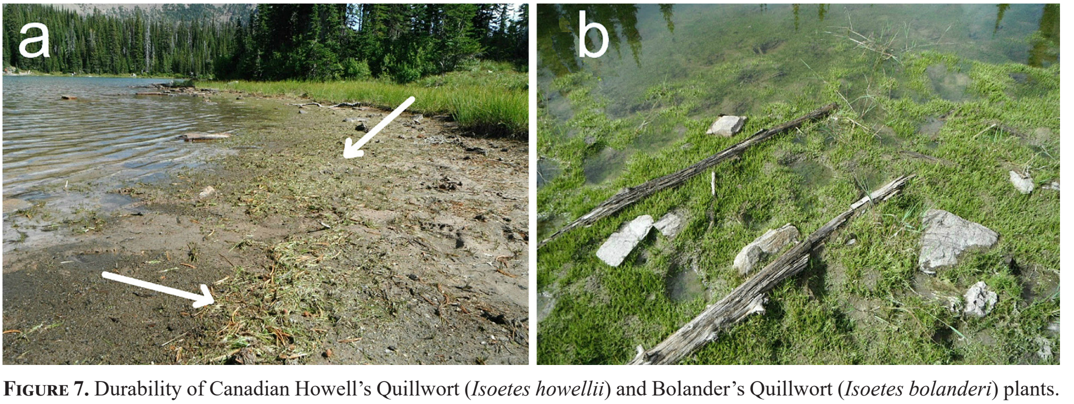

FIGURE 7. Durability of Canadian Howell's Quillwort (*Isoetes howellii*) and Bolander's Quillwort (*Isoetes bolanderi*) plants. a. Thousands of broken-off leaves of *I. bolanderi* forming drift along lakeshore (Summit Lake, Alberta, 2 September 2012). b. Intact *I. howellii* plants despite intensive cattle impact (North Thompson River area Pond 2, British Columbia, 24 August 2012). Photos: R.S. Krichbaum.

TABLE 2. Morphological and ecological distinctions between Howell's Quillwort (*Isoetes howellii*) and Bolander's Quillwort (*Isoetes bolanderi*) with particularly notable features in bold type.

	Isoetes howellii	*Isoetes bolanderi*
Habitat/habit	**Amphibious**, occurring in **lower elevation** (350–1780 m asl), typically montane **ephemeral wetlands**	**Aquatic,** occurring in **higher elevation** (1945–2200 m asl), typically subalpine **permanent lakes** and streams
Leaves	10–15 cm long (rarely to 30 cm)	5–10 cm long
	Weak (flaccid), **reflexed**	Stiff, **erect**
	± **Persistent** on corm, despite physical contact	Readily **deciduous** from corm by physical contact
	Tapering to **blunt** tip	Abruptly **sharp-pointed** tip
Velum coverage of sporangium	25–40%	15–25%
Megaspores	Mealy perispore	Smooth perispore
	Typically **rugose** or with **low, broad muri** in partial to densely **reticulate pattern,** with low, obscure **mounds**, or with short, thick**,** isolated muri and **tubercles**	Typically **densely papillate** (small, low tubercles) to **echinate-tuberculate**; also with sparsely thin-rugulate muri
	>425 µm diameter (mean 450.3 µm, *n* = 190)*	**<425 µm diameter** (mean 400.8 µm, *n* = 110)†
Microspore	Coarsely low echinate; >26 µm length (mean 27.55 µm, *n* = 160)‡	Low echinate to spinulose; <26 µm length (mean 25.72 µm, *n* = 62)§

Note: a.s.l. = above sea level.
*Six occurrences (British Columbia, California, Oregon).
†Four occurrences (Alberta, California, Wyoming).
‡Eight occurrences, (British Columbia, California, Oregon).
§Four occurrences (California, Wyoming).

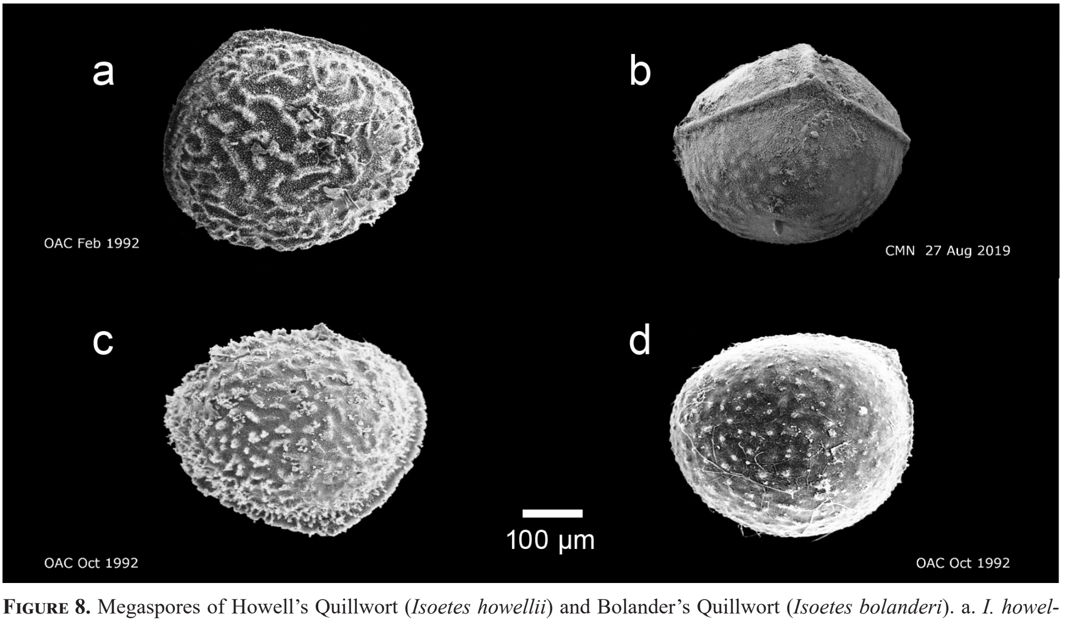

FIGURE 8. Megaspores of Howell's Quillwort (*Isoetes howellii*) and Bolander's Quillwort (*Isoetes bolanderi*). a. *I. howellii* megaspore, distal ornamentation of low muri in semi-reticulate pattern (The Dalles, Columbia River, Oregon, *J. and T. Howell s. n., 1 August 1880*, NY- Isotype). b. *I. howellii* megaspore, lateral ornamentation of low, broad mounds (North Thompson River Pond 1, British Columbia, *M. & R. Krichbaum* 15275, 24 August 2012, DFB, UBC). c. *I. bolanderi* megaspore with abundant echinate-tuberculate ornamentation (Sylvan Lake, Yellowstone National Park, Wyoming, *D.F. Brunton & K.L. McIntosh 10,841*, 13 August 1991, DFB, MU, OAC). d. *I. bolanderi* megaspore with finely papillate to obscurely rugulate muri (Meadowlark Lake, Bighorn National Forest, Wyoming, *D.F. Brunton & K.L. McIntosh 10,833*, 13 August 1991, BM, CAN, DAO, DFB, MIL, OAC, PH, TRT). Photos a, c, d: D.M. Britton. Photo b: P.C. Sokoloff and D.F. Brunton.

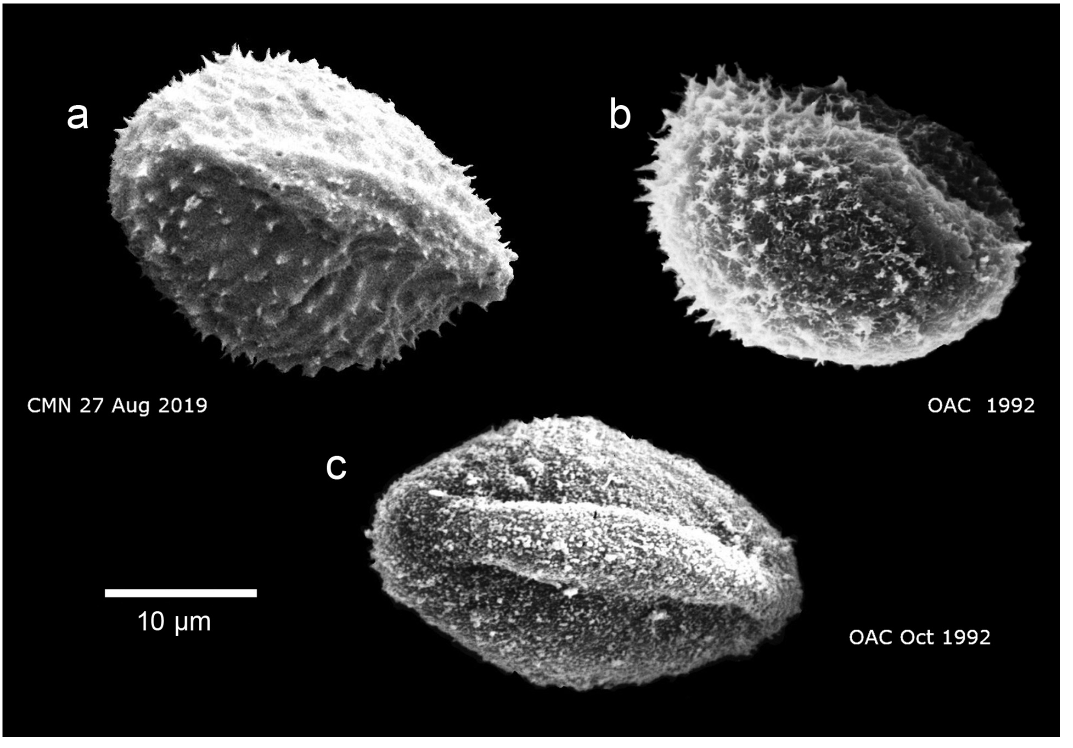

FIGURE 9. Microspores of Howell's Quillwort (*Isoetes howellii*) and Bolander's Quillwort (I*soetes bolanderi*). a. *I. howellii* microspore with echinate perispore pattern (North Thompson River Pond 1, British Columbia [BC], *M. & R. Krichbaum* 15275*, 24 August 2012*, DFB, UBC). b. *I. bolanderi* microspore with spinulose-tufted perispore pattern (Meadowlark Lake, Bighorn National Forest, Wyoming, *D.F. Brunton & K.L. McIntosh 10833*, 13 August 1991, BM, CAN, DAO, DFB, MIL, OAC, PH, TRT). c. *I. howellii* microspore with broad dorsal crest commonly expressed in *I. howellii* and *I. bolanderi* (Little Shuswap Lake, BC, *D.F. Brunton & K.L. McIntosh 11,242*, 14 August 1992, DAO, DFB, OAC). Photo a: P.C. Sokoloff and D.F. Brunton. Photos b, c: D.M. Britton.

among Canadian specimens. Microspore differences are slight between these two diploids, both being approximately the same size (Table 2) and sharing a dorsal crest (Figure 9c) that is wider than that of other western Canadian *Isoetes*.

Taxonomic status of Isoetes howellii

Although "typical" plants of *I. howellii* and *I. bolanderi* can be distinctive, ambiguous expressions of significant distinguishing features appears to be the rule rather than the exception with these two taxa in much of their substantially sympatric ranges (Figure 10). That ambiguity is exacerbated in Canada by the century of confusion over the appropriate identification of such material.

It is notable that no hybrids between *Isoetes howellii* and *I. bolanderi* have been documented even though both species are known to hybridize with other *Isoetes* species (e.g., Britton and Brunton 1995; Taylor 2002). If that absence of known hybrids reflects reality in the wild, it may also indicate that a significant genetic barrier does not exist between the two taxa.

Although being at the northern limit of range may amplify differences in the Canadian population relative to range-wide norms, the possibility that *I. howellii* and *I. bolanderi* represent infraspecific taxa within a single species is a viable possibility. The lack of any single diagnostic distinction and the apparent absence of sterile hybrids supports that interpretation. However, a taxonomic realignment of these taxa would not affect their conservation status, which could apply equally to either a species or subspecies.

It should be noted that the molecular analysis of Larsen and Rydin (2016) contradicts the physical and ecological lines of evidence for the taxonomic similarity of *I. howellii* and *I. bolanderi* that we describe. Genetic investigations of *Isoetes* taxa have been very useful in detecting and qualifying patterns of speciation and evolution in the genus (e.g., Hoot *et al.* 2004; Schafran *et al.* 2018; Wood *et al.* 2019), but in particular cases it has also resulted in unintuitive taxonomic conclusions that contradict most or all other lines of evidence (e.g., P. Schafran pers. comm. 20 February

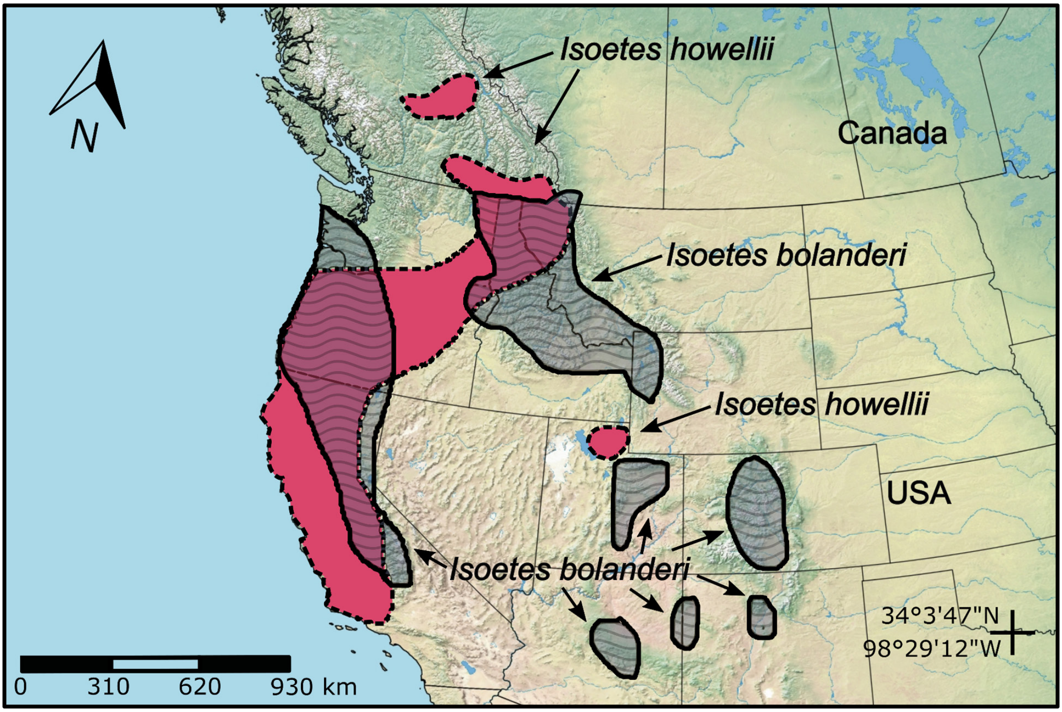

FIGURE 10. North American distribution of Howell's Quillwort (*Isoetes howellii*), indicated by red polygons with dashed outlines, and Bolander's Quillwort (*Isoetes bolanderi*), indicated by stippled polygons with solid outlines. Basemap from SimpleMappr (Shorthouse 2010).

2019, regarding St. Lawrence Quillwort [*Isoetes laurentiana* D.F. Brunton], as cited in Brunton *et al.* 2019). It was found most recently, however, that *I. howellii* and *I. bolanderi* were "difficult to distinguish molecularly" (J. Suissa pers. comm. 17 November 2020). This underscores the need for taxonomic investigations to be employing systematic DNA sequencing across the range of these sister taxa in concert with rigourous reliability testing for various seemingly significant distinguishing morphological and ecological features.

Author Contributions

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

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Note

Cougar (*Puma concolor*) predation on Northern Mountain Caribou (*Rangifer tarandus caribou*) in central British Columbia

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Abstract

Caribou (*Rangifer tarandus*) populations are sympatric with Cougars (*Puma concolor*) in only a few areas, primarily in western Canada. Records of Cougar–Caribou interactions are limited and no published accounts describe Cougar predation on the shallow-snow, terrestrial-lichen-eating Northern Mountain Caribou (*Rangifer tarandus caribou*), referred to as Designatable Unit (DU) 7 by the Committee on the Status of Endangered Wildlife in Canada. In 2018 and 2019, two incidents of confirmed Cougar predation on radio-collared Caribou were documented in the declining Itcha-Ilgachuz subpopulation in west-central British Columbia. To the best of our knowledge, this is the first published record of Cougar predation on DU7 Northern Mountain Caribou. Increased landscape disturbance and climate change may be increasing apparent competition between deer (*Odocoileus* spp.), feral Horses (*Equus ferus caballus*), and Caribou, leading to Cougar predation in areas of Caribou range where it previously has not been documented. Cougar predation may become a conservation concern, as declining Caribou herds are susceptible to any increased predation pressure.

Key words: Predator–prey dynamics; apparent competition; feral Horses; Cougar; *Puma concolor*; Northern Mountain Caribou; *Rangifer tarandus caribou*; British Columbia

Northern Mountain Caribou (*Rangifer tarandus caribou*; Designatable Unit [DU] 7; COSEWIC 2011) are a discrete and evolutionarily significant population that primarily eat terrestrial lichens in winter in shallow snow areas in British Columbia (BC), Yukon, and Northwest Territories. This DU has been assessed as Special Concern (COSEWIC 2014). Wolves are the primary predator for DU 7 Caribou (COSEWIC 2014). There is no published information on Cougar (*Puma concolor*) predation on the shallow-snow, terrestrial-lichen-eating Caribou that make up DU 7, although there are multiple records of Cougar predation on deep-snow, arboreal-lichen-eating Caribou (Kinley and Apps 2001; Wittmer *et al.* 2005a,b; Apps *et al.* 2013). Incidents of Cougar predation on Caribou north of our study area are rare, and we are aware of only one documented case. This occurred in northern BC in the Kennedy Siding subpopulation (Seip and Jones 2018), which are DU 8, Central Mountain Caribou. Cougars have not been implicated in any Boreal Caribou mortalities in BC (Culling and Cichowski 2017). Here, we report incidents of Cougar predation on Northern Mountain Caribou.

Northern Mountain Caribou includes the Itcha-Ilgachuz subpopulation (COSEWIC 2011, 2014), which occurs on the Cariboo-Chilcotin Plateau in the central interior of BC. This subpopulation declined by over 80% between 2003 and 2019 (estimated 2800 Caribou in 2003 and 385 in 2019; Shores 2019). Wolf predation is the proximate cause of mortality for this subpopulation (Shores 2019), as it is for other Caribou subpopulations in Canada (Wittmer *et al*. 2005a; Hervieux *et al*. 2013; Serrouya *et al*. 2019). The Itcha-Ilgachuz subpopulation occupies a multi-predator, multi-prey system that includes Moose (*Alces americanus*), White-tailed Deer (*Odocoileus virginianus*), Mule Deer (*Odocoileus hemionus*), Mountain Goat (*Oreamnos americanus*), feral Horse (*Equus* *ferus caballus*), Gray Wolf (*Canis lupus*), Grizzly Bear (*Ursus arctos*), Black Bear (*Ursus americanus*), and Wolverine (*Gulo gulo*), in addition to Cougar. In the Itcha-Ilgachuz Caribou range, elevations are ~850–2410 m above sea level. The low-elevation winter range for this subpopulation, at 51–53°N, is dominated by dry forests of Lodgepole Pine (*Pinus contorta* Douglas ex Loudon) and abundant wetlands with localized stands of Engelmann Spruce (*Picea engelmannii* Engelmann). Land use varies from provincial parks and wilderness areas to sites of intensive timber harvesting. Wildfire and Mountain Pine Beetle (*Dendroctonus ponderosae*) infestations have also caused significant landscape disturbance in the subpopulation's range (Goward 2000; Armleder and Waterhouse 2008).

Beginning in 2018, 80 global positioning system (GPS) radio collars (Lotek Globalstar Lifecycle, Lotek Engineering, Newmarket, Ontario, Canada, and GmBH Vertex Lite Iridium, Vectronic Aerospace, Berlin, Germany) were deployed throughout this subpopulation to infer proximate causes of death, as well as to assist population inventory. Collars were deployed primarily on females (52 of 80, 65%). All GPS collars were equipped with a mortality sensor and were pre-programmed to emit a mortality notification via email and text message when collar movement did not occur over six hours (Severud *et al.* 2015; Jung *et al.* 2018). A helicopter was used to access mortality sites within 24 h of receiving a notification. Although Cougars predominately kill ungulate prey, particularly deer (*Odocoileus* spp.; Robinson *et al.* 2002), scavenging on ungulate carcasses has been reported (Bacon *et al.* 2011). Staff responding to mortality events associated with GPS-collared Caribou were experienced in assigning cause-specific mortality; thus, a distinction could be made between predation and scavenging.

On 27 March 2018, S.C.W. and a conservation officer investigated a mortality alert received the previous day for an adult male Caribou. The carcass was partly cached under snow and covered with hair sheared from the Caribou (Figure 1a), a characteristic Cougar caching behaviour (Murphy and Ruth 2009). From observed tracks and sign, it was determined that the kill was made by a female Cougar with at least two kittens. Pre-mortem haemorrhaging was observed around the neck, and suffocation was determined to be the cause of death.

The following year, on 26 March 2019, while investigating another mortality event of a GPS-collared Caribou, we flushed a Cougar from the kill site (Figure 1b) as we approached by helicopter. Ground inspection revealed the carcass of a female Caribou cached under the root system of a fallen Lodgepole Pine and partly covered by pine needles and brush (Figure 1c). By following tracks, we located the point of initial contact and a drag trail made when the Cougar moved the Caribou carcass under a spruce tree. Hair was sheared from the Caribou carcass at this location before it was moved under the Lodgepole Pine. As in the 2018 predation event, pre-mortem haemorrhaging was evident around the neck. Both predation events occurred within 11 km of each other.

Cougar predation on this Caribou subpopulation was first reported in March 2012 (Cichowski and MacLean 2015), although details on the mortality investigation are lacking and scavenging cannot be ruled out. Our more recent observations are the first to confirm Cougar predation on DU 7 Northern Mountain Caribou; no others have been documented in the Yukon (M. Suitor pers. comm. 6 August 2020), northeastern BC (M. Bridger pers. comm. 5 August 2020), northwestern BC (A.-M. Roberts pers. comm. 5 August 2020 and C. Thiessen pers. comm. 10 August 2020), or the Northwest Territories (È. Lamontagne pers. comm. 10 August 2020).

Although multiple factors contribute to Caribou population declines, the ultimate cause is believed to be anthropogenic disturbances. The conversion of old growth forests to early seral habitats as a result of industrial development has supported an increase in Moose and deer populations and an expansion of their distribution (Serrouya *et al.* 2017). This has led to increased apparent competition with Caribou via unsustainable predation rates by predators, such as wolves and Cougars (Latham *et al.* 2011; Wittmer *et al.* 2013; Serrouya *et al.* 2017). (Apparent competition is a form of competition between species indirectly competing with another species, whereby both serve as prey of a predator.) The northern expansion of Cougars and White-tailed Deer caused by climate and landscape change has been documented in other regions of Canada (Jung and Merchant 2005; Dawe *et al.* 2014; Knopff *et al.* 2014); it is possible that a similar dynamic is occurring in the Itcha-Ilgachuz subpopulation range.

Despite the lack of estimates of Cougar density in the Itcha-Ilgachuz Caribou range, local residents have indicated increased Cougar activity in recent years (McNay and Cichowski 2015). White-tailed Deer are also relatively recent in this area, with increasing observations from local residents and the opening of a hunting season in 2003 for the management unit (MU) that encompasses the Itcha-Ilgachuz range (MU 5-12; McNay and Cichowski 2015). Furthermore, a large population of feral Horses overlaps low-elevation winter habitat of Itcha-Ilgachuz Caribou and has been increasing since 1991 (Youds *et al*. 2011). Predators, such as Cougars, may be maintained by fe-

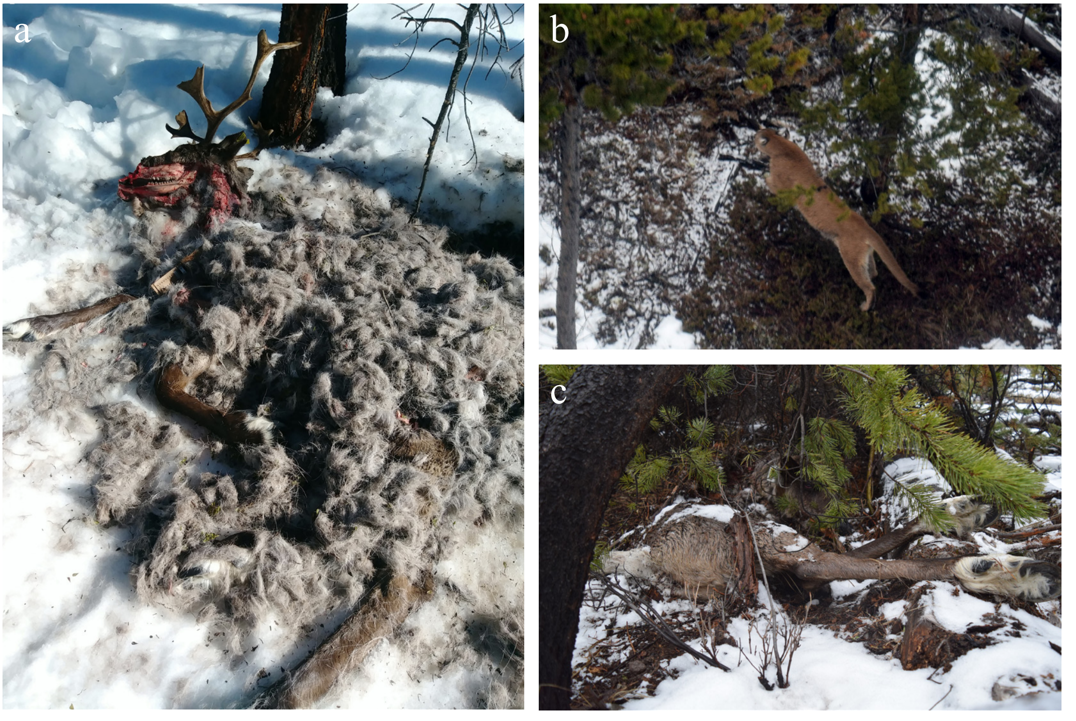

FIGURE 1. a. A radio-collared male Northern Mountain Caribou (*Rangifer tarandus caribou*) carcass investigated on 27 March 2018. b. The Cougar (*Puma concolor*) responsible for predating the female Caribou in c, flushed from the kill site by our helicopter, 27 March 2019. c. A radio-collared female Caribou cached by a Cougar and investigated on 27 March 2019. Photos: S. White.

ral Horses that provide an alternative resource subsidy (Newsome *et al.* 2015). Cougar predation on feral Horses has been documented (Turner *et al.*1992) and predation on their foals is a population-limiting factor (Greger and Romney 1999). The presence of an abundant non-native prey species has been identified as a primary factor in the decline of native species (DeCesare *et al* 2010; Wittmer *et al.* 2013) and can support other Cougar populations (e.g., Osorio *et al.* 2020). Cougars have been shown to have a negative impact on populations of secondary prey species through apparent competition (Kinley and Apps 2001; Robinson *et al.* 2002; Serrouya *et al.* 2015), and the predation impact of an individual Cougar can have a significant impact on small ungulate populations (Festa-Bianchet *et al.* 2006).

Although Moose are the primary drivers of apparent competition in Wolf-Caribou-Moose systems (Seip 1992; Serrouya *et al.* 2017), it is possible that an apparent competition dynamic between deer or Horses and Cougars is contributing to decline of Northern Mountain Caribou at the southern extent of their range. Given the steeply declining trajectory of the Itcha-Ilgachuz subpopulation, further research is warranted to understand how the abundance and distribution of feral Horses and White-tailed Deer could be exacerbating apparent competition with Caribou and potentially accelerating declines in Northern Mountain Caribou populations.

Author Contributions

Writing – Original Draft: S.C.W. and C.R.S.; Writing – Review & Editing: S.C.W., C.R.S., and L.D.; Conceptualization: S.C.W. and C.R.S.; Investigation: S.C.W. and C.R.S.; Funding Acquisition: C.R.S. and L.D.

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Tribute to R. Yorke Edwards, 1924–2011

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Introduction

On 9 January 1944, 19-year-old Yorke Edwards wrote to Dr. Rudolph M. Anderson, chief of the Biology Division at the National Museum of Canada and associate editor of *The Canadian Field-Naturalist* for almost four decades, asking questions on the focus of his nascent career in zoology. Anderson responded three weeks later, apologizing for his tardiness: "I have had to put this letter away twice without finishing, but it is a serious matter to give advice to a young man on his future career" (letter from Anderson to Yorke 31 January 1944, R.A.C. collection). The letter is full of details on small mammal identification, the building of collections, and the life of a working zoologist. Obviously recognizing the zeal and commitment in Edwards' letter, Anderson took time from a demanding job to encourage the young man's growth as a biologist. He wrote Yorke several times in the 1940s with information, literature, and guidance on publishing and was instrumental in publishing Yorke's first scientific paper, "Notes on two captive Meadow Jumping Mice (*Zapus hudsonius*)" (Edwards 1945).

Anderson's confidence in Yorke was not misplaced. The eager student grew into a man whose thoughts and energies have helped shape the minds and lives of countless naturalists across the country. For almost half a century he was a pioneer in wildlife biology, nature education (Figure 1), conservation, and museum life, stimulating people to think more deeply about the world and our place in it.

The Beginning

Roger Yorke Edwards was born in Toronto on 22 November 1924 to John Macham and Agnes Cornelia (née Yorke) Edwards. His father was a chartered accountant, his mother a secretary. Yorke was an only child, self-contained and self-motivated. Reading the nature writings of Ernest T. Seton and Thornton W. Burgess plunged him into biology; the colourful Audubon bird charts that hung on the walls of his Toronto school drove him to memorize the plumages of all the species he came across. His first ornithological notebook began in January 1937, when he was 12 years old. Yorke's passion for birds was shared by his high school friend, John Crosby, who later became one of Canada's foremost bird artists. Beginning in 1940, the two rode around Toronto on their bicycles, birding fanatically (Figure 2). To get money for a pair of binoculars in 1941, Yorke painted the next-door neighbour's house but his "first good binoculars, 7×50", came from his friend Bruce Falls five years later.

Yorke, Crosby, and other friends became enthusiastic members of the Royal Ontario Museum's (ROM) Intermediate Naturalists Club; Yorke was president in 1945. Today, some of these friends are well-known in biological and naturalist circles, including Robert Bateman (renowned wildlife artist), Bruce Falls (ecologist, University of Toronto), and Bristol Foster (former director of both the British Columbia [BC] Provincial Museum and the BC Ecological Reserves Program). In the labs and collections of the ROM, Yorke was encouraged in his bird and mammal interests by avid naturalists James Baillie and Stuart Thompson. Here were the origins of Yorke as a wildlife biologist and museum man.

Yorke wrote a lot, even in those early days. His diaries and field notes are highly organized and filled with exquisite detail, augmented by sketches and photographs; the tone is serious and earnest. He was very clear that observing and understanding nature was his life. Several manuscripts, with titles such as "A

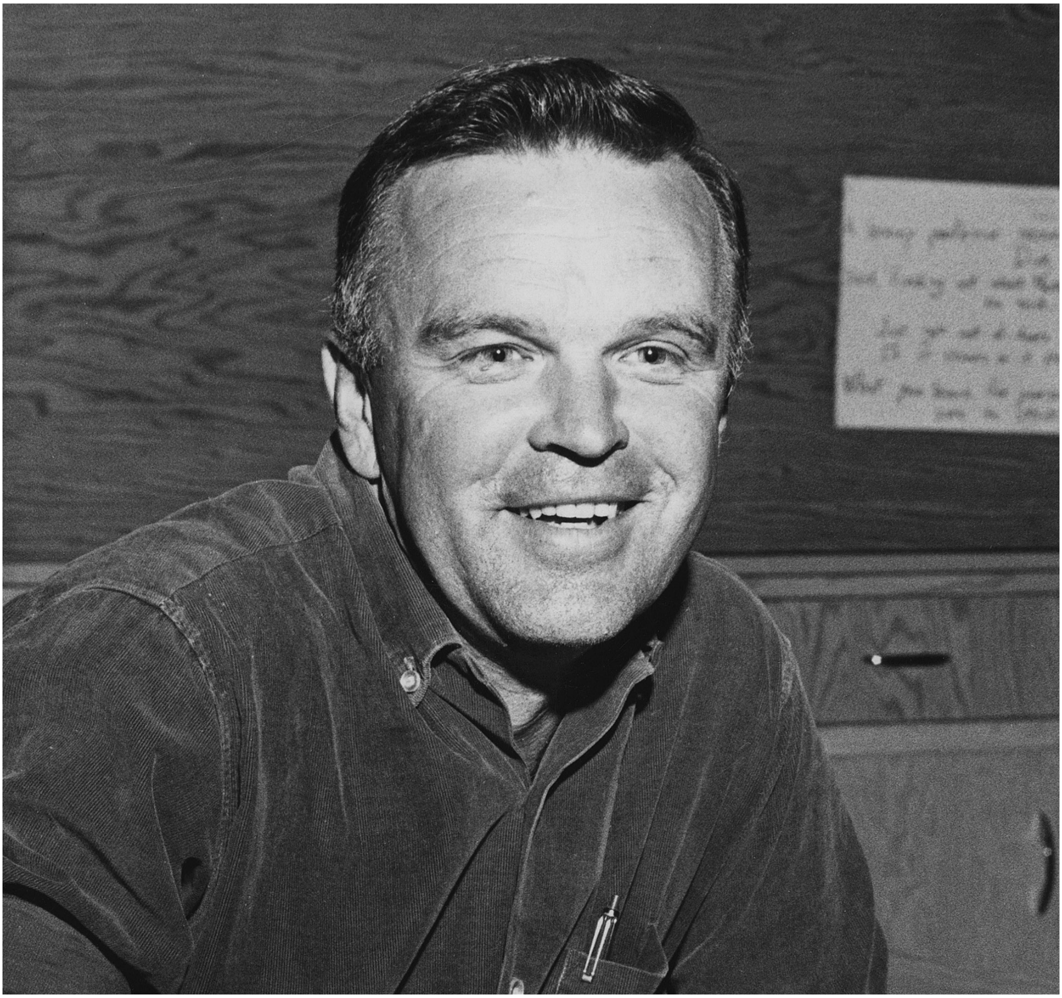

FIGURE 1. The communicator: Yorke Edwards speaking at a Canadian Audubon camp, Peachland, British Columbia, June 1965. Photo: Stephen R. Cannings.

Northland Lake", "Some Bark Lake Mammals", and "The Early Nester" (on the nesting behaviour of Great Horned Owl [*Bubo virginianus*]), and even a poem titled "Northern Lake", were apparently rejected by magazine publishers. But there were also successes. One of Yorke's first published articles, illustrated by Crosby, was a result of their intense birding activity. This lovely little piece (Edwards 1942) was entitled "Six Wood Warblers"; the editor of *Canadian Nature* and ROM staff, who reviewed it, were impressed.

Blindness in one eye kept Yorke out of military service in the last years of World War II. He spent this time improving his writing, exploring for birds and small mammals, working a couple of summers (1943–1944) on the family farm in Agincourt, and beginning university. He reminisced that

> during the war, hawks and owls about airports lured many a naturalist, complete with spy equipment like binoculars, into the arms of security guards. With luck you got home for dinner, but somehow the experience left you convinced that you really were seriously different. (Edwards 1967a: 141)

From 1944 to 1948, Yorke studied forestry at the University of Toronto and received his B.Sc. in 1948. In the summers from 1945 to 1947, he studied small mammal populations for the Ontario Department of Lands and Forests in Algonquin Provincial Park, under Doug Clarke. Yorke considered Clarke to be one of his most important mentors. "More than once," he recalled, "[Clarke] threw me into waters where the 'swimming' was pretty shaky for a while, and

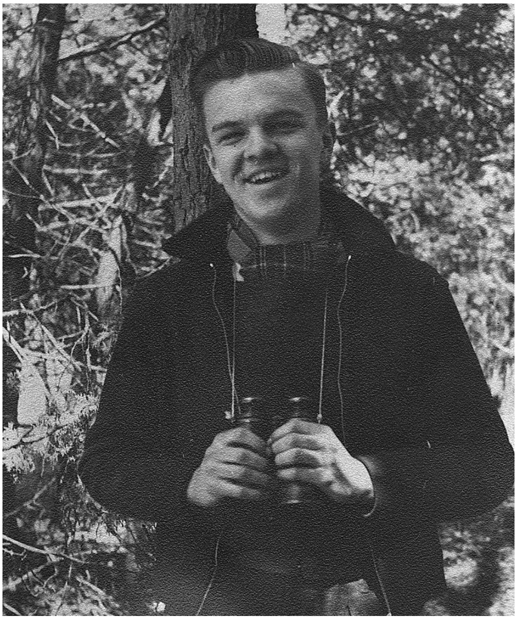

FIGURE 2. The teenage birder: Yorke in Ontario, spring 1940. Photo: courtesy of the Edwards family.

each time that I survived, I felt better about him and me" (draft letter from Edwards to Bill Barkley 25 November 1984, R.A.C. collection). David Fowle, later a professor of biology at York University and a lifelong friend, was the leader of the student team. While at university, Yorke was also a part-time preparator of vertebrate specimens at the ROM. He donated some of his own small mammal specimens—including a Hairy-tailed Mole (*Parascalops breweri*), a Star-nosed Mole (*Condylura cristata*), and an American Water Shrew (*Sorex palustris*)—to the collection.

To British Columbia

On 30 March 1946, while he was studying in Toronto, Yorke attended a lecture by Dr. Ian McTaggart Cowan, from the University of British Columbia (UBC), on wildlife research in the Rocky Mountain national parks. Yorke was enthralled, and eagerly accepted Cowan's invitation in February 1948 to study with him in UBC's Department of Zoology. Yorke arrived in BC that spring and, over the summer, worked on a BC Game Commission waterfowl nesting and banding survey in the Cariboo and Chilcotin regions. Always the keen observer, as part of that study he published a short paper on Barrow's Goldeneye (*Bucephala islandica*) nesting in old American Crow (*Corvus brachyrhynchos*) nests (Edwards 1953). Cowan recommended Yorke to Cy Oldham, head of the Parks Division of the BC Forest Service, who hired him to undertake a biological survey of Manning Provincial Park in the summer of 1949 (Edwards 1991), the year the Hope–Princeton Highway was completed. Yorke's supervisor that summer was Chess Lyons, who became a close colleague over the years (Edwards 2000). In 1950, while finishing his postgraduate studies, Yorke helped curate the UBC vertebrate museum founded by Cowan in 1943, now the Cowan Tetrapod Collection, part of the Beaty Biodiversity Museum.

Yorke completed his Master's degree in zoology in 1950 with a thesis titled "Variations in the fur productivity of northern British Columbia in relation to some environmental factors", later published in *The Journal of Wildlife Management* (Edwards and Cowan 1957). That summer he worked again in Algonquin Park and, in the autumn, began a doctoral program in the Zoology Department at the University of Toronto. However, the lure of the west proved too strong to resist and the next year, without completing his degree, Yorke returned to BC and accepted a position with the BC Forest Service in Victoria (recorded interview, W.J.M. collection). There he roomed at the home of his friends, Muriel and Charles Guiguet, the latter newly hired as Curator of Birds and Mammals at the BC Provincial Museum.

While at university in Toronto, Yorke met a young microbiologist named Joan Claudia Thicke. Back in Vancouver, Yorke and Joan married on 1 December 1951; Joan was a native of the city, born 29 years earlier, on 18 October 1922. After earning a B.A. at UBC in 1944, she worked as a microbiologist in Vancouver until 1950, when she moved to Toronto to work in the Connaught Medical Research Laboratories. Yorke noted in his diary for 1950: "Not a good winter, except met Joan Thicke". The young couple settled in Victoria.

Yorke's job in the Forest Service was to head the newly formed research section of the Parks Division, and from 1951 to 1959 he initiated numerous studies of wildlife and its management in BC parks (Figure 3). This, in his own words, consisted of "wildlife research, preservation, harvesting, habitat manipulation, censusing, hunter controls, and publishing of popular and scientific articles" (fragment of undated *curriculum vitae* of Edwards, R.A.C. collection). Much of Yorke's work was concentrated in the wilds of Wells Gray Park, where the impact of wildfire on Moose (*Alces americanus*) and Caribou (*Rangifer tarandus*) became his primary research focus. His experimental use of controlled burning greatly improved Moose habitat. Burning was a novel management tool in those days, and Yorke and his team often found themselves at odds with other Forest Service workers (Cannings 1997).

FIGURE 3. The wildlife biologist: Yorke (right) with a colleague in Tweedsmuir Provincial Park, 1957. Photo: Chess Lyons, courtesy of the Edwards family.

Some of Yorke's wildlife management papers, frequently published in collaboration with Ralph Ritcey and others, are minor classics, including works on carrying capacity (Edwards 1955), aerial census techniques (Edwards 1954a), the effects of snow on ungulate populations (Edwards 1956), and specific studies on Moose: herd migration (Edwards and Ritcey 1956), parasites and diseases (Ritcey and Edwards 1958), and mark-recapture (Ritcey and Edwards 1956). Yorke's ground-breaking research on the Caribou of Wells Gray Park is particularly relevant today, as southern British Columbia's Caribou populations seriously shrink year by year. Notable here are his investigations on fire and Caribou decline (Edwards 1954b), the use they make of lichens as winter food (Edwards *et al.* 1960), their remarkable twice-annual migrations (Edwards 1959), and the influence of landforms on their distribution (Edwards 1958).

Not all of Yorke's studies in those years were confined to ungulates. In one study, he used an American Marten (*Martes americana*) mark-recapture study to estimate their home range (Miller *et al.* 1955). In another, he evaluated the usefulness of censusing Grizzly Bears (*Ursus arctos*) using track measurements (Edwards and Green 1959). By the 1960s, Yorke was also writing about forestry and resource management (Edwards *et al.* 1967) and, on the flipside, about wilderness and conservation (Edwards 1967b,c, 1999).

Developing Interpretation in Parks and Museums

In 1957 BC provincial parks found a new home as the Provincial Parks Branch in the newly created Department of Recreation and Conservation. That year, Yorke championed a new cause—nature interpretation. How he came to this isn't certain. He'd been thinking seriously about nature interpretation at least since 1949, while working in Manning Park (Edwards 1965a). He probably witnessed Canada's first nature interpretation experiment in Algonquin Park, begun in 1944, when he worked there as a student (Merilees 2014); perhaps it was the 1957 publication of *Interpreting Our Heritage* by Freeman Tilden (Tilden 1957) that finally prompted him to act. In any case, he later wryly noted that the job found him, rather than the other way around. After convincing Cy Oldham to try park interpretation in provincial parks, Oldham turned the tables: "Edwards, you want it, so you do it. You have $300 for supplies and one summer student" (Edwards 1987: 17). Yorke chose Manning Park for the pilot project. Bob Boyd (Figure 4), the chief ranger, who Yorke knew from his 1949 stint in Manning, was supportive of the new effort, but there was little extra money. In the end Yorke settled for a mildewed wall tent and discarded tent floor, which he erected near the Pinewoods Lodge and public parking area. He hired Donald Smith, an Ontario graduate student (later professor of biology at Carleton University in Ottawa), to be the first park naturalist. Inside the tent, Yorke and Donald made exhibits of rocks and flowers, bird pictures, and American Beaver (*Castor canadensis*) workings. A wooden sign bearing the words "Nature House" hung over the door (Figure 5). Despite the fact that the province's first nature house was frequently mistaken for a washroom, the park interpretation program flourished. In the summer of 1960 over 20 000 visitors flocked to the tent nature house (Edwards 1961). A new building was constructed in 1961, and over the years the program expanded, bringing more nature houses, inter-

FIGURE 4. Bob Boyd (chief ranger) and Yorke Edwards, Manning Provincial Park Nature House, about 1960. Photo: courtesy of the Edwards family.

FIGURE 5. The makeshift tent Nature House, Manning Provincial Park, British Columbia. Photo: courtesy of BC Parks.

pretive signs, nature trails, and naturalist talks to most regions of the province.

Yorke was ably assisted over the years by several full-time staff, including Ralph Ritcey (Wells Gray Park biological studies), David Stirling (hiring and training of seasonal staff), and J.E. (Ted) Underhill. Underhill was chosen as a Manning Park naturalist in 1958 and quickly became indispensable as an inventive interpretation specialist. He wrote much of the interpretive material on many subjects for many parks, but perhaps most importantly, he was in charge of the Parks Branch Display Studio where exhibits and signs were constructed. Yorke called him "a gem". Some of the well-known artists who Yorke contracted to help produce displays and outdoor interpretive signs were Jean André (later to gain fame as the designer of many of the Royal BC Museum's permanent exhibits), Robert Bateman, and John Crosby.

By the time Yorke left the Parks Branch in 1967, there were four nature houses and programs in nine parks; more came later. Yorke described the purpose of the program succinctly: "the enhancing of public understanding, care, and recreational enjoyment of the natural environments preserved in parks" (fragment of undated *curriculum vitae* of Edwards, R.A.C. collection). Widely admired, the program set a standard for park education across the country. George Stirrett, the first chief park naturalist for the National Parks Branch (now Parks Canada; Lothian 1987), frequently consulted with Yorke on interpretation matters. When visiting Miracle Beach Provincial Park in July 1962, Stirrett told Yorke that the new nature house and nature trails there were better than anything in the United States' parks system.

As a manager and supervisor (Figure 6), Yorke was thoughtful, innovative, and tireless. He was also hands-on, working continually with park naturalists to help improve their messaging and delivery. In 1960 he was on the road for 75 days, driving from park to park, checking on the skills and morale of the summer naturalists at Manning and Miracle Beach (Figure 7) parks, seeking ideas for exhibits, drafting new park pamphlets and signage, and looking for places to start new park programs. His background in field research prepared him to view park interpretation as a prime opportunity for public education. He considered naturalists of all sorts to be scientists (Edwards 1985a) and encouraged his park naturalists to really get to know the parks they worked in, for example, by undertaking simple research projects. One of us (R.A.C.) recalls his first research on the job as a 16-year-old naturalist at Miracle Beach on Vancouver Island. With Yorke's encouragement, he undertook a mark-recapture study of the three species of garter snakes that lived in the tangle of logs on the upper beach, stud-

FIGURE 6. The administrator: Yorke Edwards in his Parks Branch office, Victoria, British Columbia, early 1960s. Photo: courtesy of BC Parks.

FIGURE 7. Nature House, Miracle Beach Provincial Park, Black Creek, British Columbia, 1960s. Photo: courtesy of the Royal BC Museum (BC Archives item 1-07042).

ying their movements and trying to understand how they co-existed.

Always the visionary, Yorke was ahead of his time in many ways. "In the late 1950s and early 1960s", notes W.J.M.,

> the Parks Branch field operations were exclusively male. It was Yorke who broke this model by hiring Betty Westerborg (now Betty Brooks) to work at Miracle Beach as a park naturalist. This caused a considerable stir within the Branch but, in time, women became the prominent component of the interpretation program and they steadily increased their representation in all other spheres of parks operations. (Merilees 2013: 1)

W.J.M. also recounts another Yorke Edwards' first:

> In the 1960s, a very spry, charismatic, youth-oriented senior citizen from Victoria by the name of Freeman King came to Yorke's attention. Regulations of that day prevented seniors from being employed in the Public Service. In Freeman's case, Yorke lobbied and received an exemption, whereby for many years thereafter, a special Order-in-Council was annually signed by the Lieutenant Governor permitting 'Skipper,' (as he was better known) to delight visitors at Goldstream Park each summer. (Merilees 2013: 1; Figure 8)

While he worked for the Parks Branch, Yorke was already involved in the museum community. He was active in the British Columbia Museums Association, founded in 1959 after the province's 1958 centennial inspired the creation of many new community museums. Yorke was elected president (1961–1963) and also edited its magazine, *Museum Roundup*, beginning in 1963. Over the years, and even while he was with the Canadian Wildlife Service (CWS) in Ottawa, this magazine served as a primary venue for his many articles on museums and education. He was made an honourary member of the association in 1967.

Yorke was no less influential in the organization of the burgeoning naturalist community in BC. In November 1962, Yorke and David Stirling wrote a proposal for the establishment of the BC Nature Council, the forerunner of BC Nature (the Federation of British Columbia Naturalists), which organizes the province's many naturalists' clubs. Yorke was a founding member of the Council (Figure 9), established in May 1963.

Occasionally Yorke was tempted to enter academia and in 1961 turned down a teaching job at UBC, perhaps because the salary offered was lower than his government one. Cowan considered Yorke one of the best biologists in Canada and, but for his lack of a Ph.D., would have hired him as a UBC zoology professor. Yorke did lecture at UBC in 1963–1964 when

FIGURE 8. Freeman "Skipper" King enthralling kids, Goldstream Provincial Park, Victoria, British Columbia, 1972. Photo: courtesy of BC Parks.

FIGURE 9. Yorke Edwards, Freeman King, and Steve Cannings at a BC Nature Council meeting, Fairview, British Columbia, May 1964. Photo: Robert A. Cannings.

he taught a course on the vertebrates of BC (excluding fishes), filling in for Jim Bendell, a friend from University of Toronto days, who was on sabbatical. Yorke would take the ferry to the mainland on Friday morning, give a morning lecture and an afternoon lab, and then return to Victoria in the evening. The ferry ride enabled him to make regular observations of the wildlife populations in Active Pass, some of which he published the following year (Edwards 1965b).

In late 1964, when construction of the new provincial museum buildings was imminent and plans for new exhibits were needed, museum director Clifford Carl turned to Yorke for help. In his diary Yorke noted: "Cliff Carl finally tells me he hopes I'll be on the staff of the new museum—as Curator of Exhibits. The situation is complicated since I now make as much as Cliff. Decisions!" The Parks Branch agreed to loan Yorke to the museum on a part-time basis. In the spring and summer of 1965, Yorke worked out a basic exhibit strategy and toured the southern Okanagan with staff to collect biological information and specimens for a diorama on BC's semi-arid grasslands. Eventually he returned to his full-time job with the Parks Branch and the museum hired a designer to continue the exhibits planning (Roy 2018).

The halcyon days of interpretation in BC Parks are now long gone. They lasted almost a decade after Yorke stepped down in 1967, but ended when budget cuts and regionalization of Parks programs in the mid-1970s eliminated the centralized organizational model of park interpretation. One telling outcome of this was the conversion of the nature house at Manning Park into a pub. In 1991, Yorke wryly wrote:

> Now the interpretation in Manning Park is different. The Nature House at Pinewoods, after many years of service revealing the unexpected details of the park, is not a nature house any more. But then, in a way it still is, for there is nothing more biological than beer, and I hear that my beautiful House, with the low eaves and the simple interior that I specified, is now a pub. As a lover of beer, I can't really complain. And alcohol is the work of nature's yeasty workers turning sugar water into grog. Nature still reigns in the House. (Edwards 1991: 47)

To Ottawa and the Canadian Wildlife Service

In the mid-1960s, David Munro, director of CWS, became convinced that the wildlife management, research, and conservation initiatives of his organization would be effective only to the degree they were widely understood and supported by Canadians. He envisioned a series of wildlife interpretation centres stretching from sea to sea, each explaining the distinctive life zone in which it was located. Munro asked Yorke to come to Ottawa and duplicate his provincial achievement on a national basis (Burnett 1999). Yorke accepted, but agreed to stay for only five years. He recalled:

> David dangled more bait than he knew. I was ready to experience again the northern hardwood region of my youth, with its scarlet tanagers and bloodroots, maple forests and winter redpolls. I also had a strong yen to know Canada better, coast to coast. (Burnett 1999: 112)

From 1967 to 1972, Yorke worked on this new national vision (Edwards 1971a). He established a philosophical foundation for CWS interpretive programs, developed interpretation methods, planned the development of a series of nature centres, and established the first one at Wye Marsh (Figures 10 and 11), a rich southern Ontario wetland. Budgets were sufficient to allow innovation, and interpretation at Wye Marsh stressed observation, with a floating boardwalk, an observation tower, and an underwater window. The CWS mandate required an even-handed exploration of the management of lands and wildlife and the impact of humans on the landscape, as well as the usual natural history interpretation (Burnett 1999). Yorke hired Bill Barkley, who had once worked as a naturalist in the BC Parks Branch, to be in charge, and contracted his old friends Ted Underhill and Jean André to produce the centre's exhibits.

After Yorke's tenure, four more centres sprang up across Canada, from Bonaventure on the Gaspé Peninsula of Quebec to Creston in the Kootenay region of BC. Work on the transcontinental vision continued until the government changed with the 1984 federal election. Slashed budgets doomed the program; the headquarters and regional units and all five wildlife centres were closed. Some centres completely disappeared, while others, such as Wye Marsh and Creston Valley, were repurposed through private/public partnerships (Burnett 1999).

Returning to Victoria and the Provincial Museum

Yorke returned to Victoria from Ottawa in September 1972 to become assistant director of the Provincial Museum, then led by Bristol Foster, an acquaintance from his early Royal Ontario Museum days. In early 1975, when Foster resigned to direct the new provincial Ecological Reserves Program, Yorke became director. His museum experience in Toronto, his background in wildlife research, his extensive involvement with exhibits and public education in both natural and human history, his work with the BC Museums Association—all prepared him for managing a major museum. Yorke was an experienced museologist who strongly believed in collections, research, and "inspirational public programming" (Roy 2018: 328). He helped develop many of the new building's early permanent exhibits. "The challenge is to turn scholarship into entertainment" is how he described his approach to the Canadian Museums Association in 1976 (Roy 2018: 328). During his tenure, a period fraught with fiscal restraint and budget cuts, the mu-

FIGURE 10. Exhibits in Wye Marsh Wildlife Centre, Midland, Ontario, 1970. Photo: courtesy of the Wye Marsh Nature Centre.

FIGURE 11. The interpreter: Yorke in conversation with Freeman Tilden (left), guru of American heritage interpretation, Wye Marsh Nature Centre, Midland, Ontario, 1970. Photo: courtesy of the Wye Marsh Nature Centre.

seum-going public attended the openings of several major exhibits including the First Peoples gallery and the natural history gallery, Living Land, Living Sea. Himself a writer, Yorke made sure the museum's publication program flourished. He also stressed the importance of travelling exhibitions; between 1976 and 1982, an average of six museum exhibits visited 15 venues annually (Roy 2018).

Although a successful administrator of major government programs and a large museum, Yorke was happiest in the field, immersed in the natural world. While working for the Parks Branch, when returning to Victoria from research in Wells Gray Park or from supervising park staff at Shuswap Lake, he would often detour south through the Okanagan Valley, arriving at White Lake near Okanagan Falls about dusk. He'd sleep in his car, or under it, listening to the calls of Common Poorwills (*Phalaenoptilus nuttallii*) in the dark and waking to the fragrance of Big Sagebrush (*Artemisia tridentata* Nuttall) and the songs of Western Meadowlarks (*Sturnella neglecta*). In 1981, just three years before his retirement, Yorke joined the Museum's Brooks Peninsula expedition to the remote northwest coast of Vancouver Island. He went not as the museum director, but as a field assistant to help museum staff collect and observe (Figure 12).

After his retirement in 1984 (Figure 13), at age 60, Yorke continued writing and working as a biological and museological consultant, and was designated a Curator Emeritus at the British Columbia Provincial Museum, soon to be renamed the Royal British Columbia Museum (RBCM) in 1987. As a research associate, Yorke usually spent one day each week in the mammal collections, mainly researching historical mammal-collecting expeditions by the provincial museum and other major North American museums. From field notes and published accounts he studied collection localities and calculated geographical coordinates for computer mapping—a significant contribution to the RBCM's handbooks on British Columbia's rodents and shrews and relatives (D.W. Nagorsen pers. comm. 25 July 2019).

Yorke suffered a serious stroke in May 1996. The cumulative effects of additional small strokes and the onset of dementia finally ended his writing career. His last major work was a chapter on British Columbia in *The Enduring Forest*, edited by his friend Ruth Kirk (Edwards 1996). His last publications date from 2003. He worked hard at the end—every one of the 12 issues of *The Victoria Naturalist* from 2001 through 2002 contains one of his articles.

Yorke died on 16 August 2011, at 86 years of age; Joan died nine days later, at 88. They had been married 60 years.

FIGURE 12. The field man: Yorke collecting aquatic samples during the Brooks Peninsula expedition, west coast of Vancouver Island, August 1981. Photo: Ruth Kirk, courtesy of the Royal BC Museum.

Family

At the time of their marriage, Joan had begun a promising career in microbiology. While working at the Connaught Laboratories in Toronto, she was the senior author on a paper documenting the culture of the poliomyelitis virus (Thicke *et al.* 1952). This organization was at the forefront of Canadian efforts to control this medical scourge. Like many women of the time, Joan gave up her career for marriage; she balanced raising a family, organizing a household and busy social life, and developing her own interests, such as teaching children to read, volunteering at the Victoria Art Gallery, and preparing flower arrangements at Government House. Joan and Yorke raised two accomplished daughters, Anne and Jane. Anne holds B.Math. and M.Math. degrees in computer science (University of Waterloo) and has had a distinguished career as a statistician and data analyst at the Chalk River Laboratories of Atomic Energy of Canada. Jane studied biochemistry (B.Sc.) at UBC and has since researched various medical conditions, such as lupus and diabetes, at the universities of Calgary and Western Ontario.

Anne and Jane remember outings with their father and his ever-present binoculars. Sundays were often birding days and Jane recalls hikes in Victoria's Francis Park (now Francis/King Regional Park) where the natural history stories of Freeman King were a highlight. Both sisters tell of road trips—the car halting abruptly, their father jumping out, binoculars in hand and striding down the road in pursuit of a bird. The family would wait patiently in the car for him to return and record the sighting in his notebook before driving off again. Anne says that while on family trips they always stopped at park visitors' centres where her father would ask her what she thought about the displays:

> We might discuss how they were constructed—for example, did the lighting make reading the text easy? Or he might explain what he would have done differently—should there be fewer words, less clutter, or more emphasis on the main message? To this day I automatically analyze any display I see in a museum or park visitor centre as I would have done with Dad. (A.C. Wills pers. comm. 8 July 2019)

Yorke's impact

Over the course of his long career, Yorke presented hundreds of talks and speeches on many subjects to many audiences, from school children to scientific societies, from museum workers and naturalists

FIGURE 13. Yorke's retirement party, Provincial Museum, Victoria, British Columbia, November 1984. Left to right: David Stirling, Charles Guiget (back), Rob Cannings, Yorke Edwards, and Joan Edwards. Photo: courtesy of the Royal BC Museum.

clubs to politicians and seniors' groups. He also wrote widely, publishing more than 400 titles across a wide range of topics, from research and science in museums (Edwards 1985b, 1993a) to more popular pieces on his first love, birds. Yorke savoured the complexities of gull identification (Edwards 1969b); hawk migration was a fascination (Edwards 1994); and birding from the windows and patio of his home overlooking Juan de Fuca Strait was a favourite pastime in later years (Edwards 1992). Naturalist newsletters and magazines, including BC Nature's *Cordillera*, which he helped to found, are full of his articles about people and the natural world, birds, mammals, plants, ecology, and multitudes of other topics. Yorke was a frequent contributor to the RBCM's newsletter, *Discovery*, with articles on subjects ranging from extinct Caribou (Edwards 1993b) to the museum's native plant garden (Edwards 1995). He wrote dozens of book reviews and forewords to books. And he wrote a few books of his own. Among them, *The Mountain Barrier* was a popular treatment of the ecology of the mountains of western Canada (Edwards 1970c). He also recognized the value of writing for children and worked hard at it (Edwards 1970b, 1971b).

But perhaps his most influential papers are those in which he waxes philosophical about parks (Edwards 1965c,d, 1989), museums (Edwards 1977, 1979a, 1994a), and interpretation (Edwards 1968, 1969a, 1970a, 1976, 1981, 1997). In his book, *The Land Speaks*, Yorke sums up decades of thinking about heritage interpretation (Edwards 1979b).

Some of Yorke's writings remained unpublished at the time of his death, or else appeared in hard-to-find newsletters and government reports. Partly to make these and other writings available to a wider audience, the Royal BC Museum has published a book of Yorke's essays (Kool and Cannings *in press*). Titled *The Object's the Thing*…, this volume looks back at the glory days of nature interpretation in British Columbia and Canada through the eyes of the man who, perhaps more than anyone, helped bring them about.

Yorke served on the executive boards of many conservation and natural history organizations: the Nature Conservancy of Canada; Royal Canadian Geographical Society; the Wildlife Society; Ottawa Field-Naturalists' Club; Canadian Museums Association; Grants Committee of the Museum Assistance Program, National Museums of Canada; Canadian Nature

Federation; *Owl* and *Chickadee* magazines; Council of Associate Museum Directors; BC Historic Sites Advisory Board; *Wildlife Review* magazine; *Nature Canada* magazine; BC Forest Museum (now the BC Forest Discovery Centre); Whale Museum, Sidney, BC; Federation of BC Naturalists Foundation; and BC Government House Foundation. As a teenager he was president of the ROM's Intermediate Naturalists; later he was president of the BC Museums Association, the Victoria Natural History Society, and the BC Forest Museum. He served as editor of the journals of the Canadian Society of Wildlife and Fishery Biologists and the BC Museums Association.

Yorke won many awards for his dedication to the understanding and preservation of Canadian nature, including the Interpretation Canada Award for Outstanding Achievement (1979) and Canada's 125th Year Medal (1992). He was recognized for distinguished service to the Canadian Council on Ecological Areas (1989, 1991). Yorke was an elected member of the Brodie Club in Toronto (1947) and a Fellow of both the Royal Canadian Geographical Society (1984) and the Canadian Museums Association (1980). He was an honourary member of the BC Museums Association (1967) and the Ottawa Field-Naturalists' Club (1980).

Just as Rudolph Anderson's advice to Yorke years earlier convinced him that biology could be his life, Yorke's counsel helped many others on their way. There are others like us who count Yorke as a significant influence on their lives and tried to live his teachings. The three of us were park naturalists in BC Parks and later became his friends. R.A.C. worked at Yorke's nature centre at Wye Marsh, inventoried the biological diversity of new BC parks, and was a curator at the RBCM. W.J.M. had a long but intermittent (1960–1996) career in the BC Parks interpretation program and has extensive experience in community service in natural and human history and conservation. T.G. has devoted much of his life to conserving and understanding Wells Gray Park; as Yorke did, Trevor loves the park. He worked as a naturalist there for many years and has since dedicated his life to research and public education in the area. In 1984 he built a home on four hectares adjacent to the park and has developed the property into an outdoor campus for naturalists. Trevor has gathered over 250 reports, papers, and books pertaining to Wells Gray and has initiated the Edwards-Ritcey Online Library Project, which will post many of these titles online for a new generation of naturalists and researchers. The library is named in honour of those two scientists whose early work on Wells Gray's wildlife created a solid foundation for future research (Goward 2014).

In 1991, Trevor, with the help of many others, and especially the involvement of the University College of the Cariboo (now Thompson Rivers University [TRU]), set up the Wells Gray Education and Research Centre. A highlight of "Yorke Edwards' Day in Wells Gray", a tribute to British Columbia's "Father of Interpretation", organized by Trevor on 5 October 2013, was the sod-turning ceremony for the Wells Gray TRU Wilderness Centre.

Our stories are hardly unique. Hundreds of university students who worked as park naturalists in Canada during those years came away infused with his ideas. Today they are biologists, university professors, writers, artists, doctors, lawyers, teachers, parents, and grandparents. Thousands of others who visited parks, wildlife centres and museums, or who read his articles or heard his talks, also came away with a bit of Yorke Edwards.

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The Canadian Field-Naturalist

Book Reviews

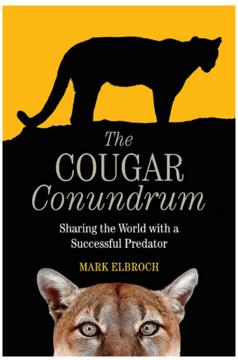
Book Review Editor's Note: *The Canadian Field-Naturalist* is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those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

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

Biology

The Cougar Conundrum: Sharing the World with a Successful Predator

By Mark Elbroch. 2020. Island Press. 272 pages, 30.00 USD, Paper.



In *Cougar Conundrum*, author and Cougar (*Puma concolor*) biologist Mark Elbroch describes how to live successfully with a predator that has restored itself to much of the west and is slowly moving east as it recolonizes parts of the Great Plains. Having studied Cougars in many areas—most recently finishing up a long-term study in Wyoming—the author is certainly the perfect person to weave in biology, politics, and commonsense when describing how to coexist with an animal who "lives among us like ghosts" (p. 217). The book was an easy read (I finished it in 1.5 weeks while working full time) and is perfect for wildlife biologists, the general public, and nature enthusiasts, especially those who want to learn how to live successfully with a large carnivore that has been given an unduly bad rap for being dangerous around people (Chapter 1). Elbroch overwhelmingly hopes we choose a peaceful coexistence (p. xxiv) with an ecologically important animal (pp. 156–161) that is relatively common where it currently lives. Despite more Cougars and people on the landscape, there are less than a handful of attacks per year (p. 32) which is much fewer than the number of cows and dogs that injure humans (p. 31). And this is ultimately the conundrum that Elbroch discusses throughout the book; i.e., should Cougars be protected, especially in a human-dominated world, as their population and range expand as they recover from persecution that mostly ended in the 1960s?

There are nine chapters after a 13-page Preface that sets the stage for the rest of the book. Elbroch makes it clear that facts are needed to help lions (p. xvi), as they are often called, in addition to Puma, Cougar, Mountain Lion, panther, mountain screamer, painter, and red tiger, just some of the more than 80 names for this animal that has the largest range of any terrestrial mammal in the Western Hemisphere (p. xiii). This book is important in the age of social media when extreme voices are often heard. I especially like how Elbroch weaved in personal accounts of individual researchers and Cougars to illustrate actual Cougar behaviour. We are taken from urban regions around Los Angeles, the outskirts of Jackson Hole and Grand Teton National Park, Wyoming, and to the swamplands of Florida where the only population of "panthers", as they are called in that region despite there being no records of a black Cougar ever having been recorded anywhere (p. 10; FYI: a black panther is either a black Leopard [*Panthera pardus*] or Jaguar [*Panthera onca*]). While all of these anecdotes were most interesting, I had heard of many of them from other sources (e.g., p. 22, the Hollywood Lion). What especially fascinated me, however, was reading Elbroch's accounts of wild Pumas in southern Chile being used as a tourism magnet (pp. 19, 201), an important economic asset in Patagonia where they are viewed like Bison or bears in Yellowstone National Park; that is, locally common and very visible (p. 21). Elbroch provides photographic proof of wild Pumas in those regions who behave much differently than an average Cougar in North America which many people will never observe even if they live in lion country. However, Elbroch does recount an event from 1999 on the National Elk Refuge, Wyoming, where a Cougar family (mother and three kittens) was watched by some 15 000 people over 42 days, demonstrating the importance of direct experience to speak to the hearts and minds of people and the potential for wildlife tourism in more places in this country (pp. 145–146).

In the first half of the book, Elbroch documents how Cougars are not dangerous animals but rather are ecologically important. He provides husbandry strategies, like corralling livestock in high risk areas, to avoid negative interactions with these cats. We learn that a miniscule 0.01% of cattle in the U.S. are killed by Cougars (p. 62) and even that is often an exaggerated and inflated value in a corrupt system that often determines kills made by "crediting" Cougars for killing cattle where the cats don't even live (p. 62). While misinformation fuels fear (p. 63), we also learn that hunting Cougars does not help livestock and that reimbursement programs are more effective than killing the cats (p. 70). This might sound counter-intuitive, but it is due to Cougar behaviour. As adolescents move into the territories of larger males that are killed by hunters, they often cause more problems and are more apt to kill livestock (pp. 70–72) and possibly even attack more people because they are less experienced (p. 150). These facts highlight the importance of biologists providing accurate information on a species even when wildlife agencies try to cover up the effects of hunters, which Elbroch documents in numerous sections of the book (e.g., pp. 42–46, 150).

In the second half of *The Cougar Conundrum*, we delve into more specific chapters that fascinated me. In Chapter 5, The Great Hunting Debate, we learn how wildlife agencies try to silence those against Cougar hunting, mainly because they have different worldviews (p. 100). And therein lies another conundrum: Elbroch makes clear that hunting Cougars is not a threat to their long-term survival (pp. 118, 204), but we should limit it to ensure ecological and social integrity (pp. 111, 119) as human hunting clearly has the greatest impact on Cougar survival (p. 102). There is evidence of overhunting that should guide managers to lower quota numbers even if not dire to their long-term existence (pp. 108–110). For instance, he describes places like Washington State that has low quotas in small management areas so as to not over-kill adult resident Cougars (see Beausoleil *et al.* 2013). A direct result of Elbroch's research has been the suggestion that delaying Cougar hunting until 1 December, when most females have mobile kittens, should reduce cub orphaning (p. 206). The discussion on hunting was relevant to my research with Coyotes (*Canis latrans*) as he described the resilience of both species (p. 104) and how a carnivore's ecological importance and social bonds are rarely, if ever, considered in their management. The importance of individuality in Cougars (p. 116) was also noted and how they feel pain, exhibit fear and affection, and have close bonds with each other (p. 117), which are not even acknowledged by wildlife managers. The author went into great depth about the bias of wildlife agencies and how they are non-inclusive. A key component to the conundrum is to increase inclusivity in decision-making (p. 167) by involving non-hunters and other demographic groups as there is an obvious bias toward conservative white males (p. 155). I also learned in the second half of the book that not all hunters are the same and that wildlife advocates should work with, rather than against, certain hunting groups, most notably houndsmen who often want to lower quotas and battle against Elk (*Cervus canadensis*) and other 'big game' hunters who want more Cougars killed. In fact, there isn't another hunter-led advocate group for any other carnivore species besides houndsmen (p. 153), in part because they can chase and "catch" (i.e., tree) Cougars then walk away without killing them (p. 155).

The most anticipated chapter for me was Lions on the Eastern Seaboard (Chapter 6). In this section, we find that Cougars are most definitely moving east, with the nearest populations in South Dakota and Nebraska, but at the rate they are colonizing new areas it would take them about 300 years to reach the eastern United States (p. 130). Elbroch discounts those who believe there are resident Cougar populations in the East outside of the couple hundred "panthers" living in south Florida (p. 134). Importantly, Elbroch describes how there never was an "eastern cougar" as all lions in North America belong to the same subspecies (p. 131). This is actually a good thing as it could pave the way to reintroducing them (p. 132) from other source populations (e.g., Florida, South Dakota, Nebraska) and accept migrating Cougars as native to the region (e.g., Way 2017).

The overarching theme of the book is improving tolerance for large carnivores (p. 140). Elbroch highlights the contributions that carnivores make (p. 139), such as the potential to save millions of dollars and hundreds of human lives if Cougars returned to the East and even somewhat reduced White-tailed Deer (*Odocoileus virginianus*) numbers (pp. 142–143). He also suggests that more research describing their ecological benefits needs to get out to the general public to improve peoples' acceptance of living with Cougars (pp. 157, 160; but see p. 184).

Elbroch concludes the book by modelling how wildlife management can be revised to be more inclusive and a better representative of democracy in managing public trust resources. He establishes quite clearly that hunters are prioritized over all other stakeholders (p. 170) and agencies even brazenly exclude the non-consumptive public from decision-making despite being the vast majority of Americans today (p. 176). Part of this issue is the fact that hunters fund a large percentage of the budget of state wildlife agencies even though they do not fund conservation more broadly (p. 177). This funding scheme is purposeful for hunting groups fear losing power (p. 178); e.g., the National Rifle Association has stymied any attempts of inclusiveness (p. 183). All of this affects the Cougar conundrum with more lions dying at the hands of entrenched stakeholders who want fewer predators on the landscape. This bias is so prevalent, in fact, that it even affects research where studies that emphasize conservation or ecological importance are denied or forced to be revised (p. 184). I find this astounding, but sadly true, in 2020 when science is supposed to be a core tenet in wildlife management. Elbroch also critiques the North American Model of Wildlife Management (NAM) for doubling down on hunting and maintaining the status quo (pp. 185–186). The author exposes Cougar hunting (and carnivore hunting in general) as violating most of the core tenets of NAM and concludes that to embrace NAM is to go backwards from being inclusive (p. 194). Rather, wildlife commissions need representation from non-consumptive users (p. 210), and proposals such as the Teaming with Wildlife legislation should be reintroduced to Congress (p. 211).

In *Cougar Conundrum*, non-hunters don't get off scot free either. As a biologist, Elbroch is sort of in between hunters and state wildlife agencies on one side and non-hunters and wildlife advocates on the other. He blames non-hunters for not participating in wildlife issues and being spectators, such as adding frown emojis to social media posts (p. 212), rather than truly participating in wildlife management. Ultimately, he concludes that all these stakeholders need to work together, for Cougars enhance our lives and are evidence of true wilderness (p. 218). We aren't as different from each other as we think:

> Not all mountain lion lovers are anti-hunting, anti-guns, liberal, vegetarian city slickers who drive Priuses, and not all hunters are conservative ranchers who kill African lions in canned hunts, drive big trucks, drink cheap beer, and shoot anything that moves. (p. 211)

We have an amazing opportunity to witness the restoration of a native carnivore to its former range which will improve our continent's ecological resilience and build bridges among people of different backgrounds (p. 217).

Overall, this is an important book that is well written, has few errors, and contains some great black and white pictures and graphs to illustrate Cougars and their ecology and behaviour. Many books written by biologists lack discussion about the ethics of killing sentient large carnivores which are ecologically important, and are social, sentient, family-oriented animals which regulate their own numbers by defending territories (Vucetich and Nelson 2014). I was pleased to read this balanced book that put the onus on state wildlife departments to be more inclusive and recognize the importance of predators like Cougars. I can't read enough about Cougars and dream of the day when they are restored to the Northeast United States where I reside! This book will hopefully take us one step closer to that goal if enough citizens and wildlife managers get their hands on it and act on its premises.

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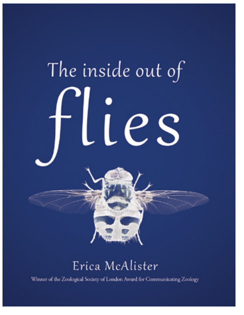
The Inside Out of Flies

By Erica McAlister. 2020. Firefly Books and London Natural History Museum. 288 pages, 24.95 CAD, Cloth.



Erica McAlister is the flies' best friend—knowledgeable, experienced, passionate about both her chosen field and turning others on to the mysteries and magic of the Diptera. A natural teacher, she spends a good deal of time and effort engaging the public through programs at the London Natural History Museum—as her webpage there reveals—for which she has been recognized through the Zoological Society of London Award for Communicating Zoology. This is her second book—her first, *The Secret Life of Flies* (2017, Firefly Books), was reviewed in these pages in 2017 (Bocking 2017). The two books are similar in many ways—the same quality of production (including sewn binding), style, page layout, use of excellent photographs and diagrams to illustrate her topics, and back matter in tiny font; even the covers are similar, the second being a negative, in the photographic sense, of the first, making them companions on the bookshelf.

They differ in substantive ways, of course. While *The Secret Life* explored the various roles flies play, from pollinators and detritivores to predators and parasites, this one takes a morphological look at the flies themselves, exploring the extensive and amazing differences among families and species from Preadulthood (Chapter 1) through all the major body parts, from head to terminalia, in Chapters 2–9. Not only do we learn a lot about each of these areas, we are often reminded how impossibly much remains to be learned. Important subthemes include the connection between research on flies and developments in human medical and other technologies. We learn, for example, of important research into the medical uses of maggots, particularly in healing of wounds (pp. 36, 45–47), but also in figuring out how nanorobots could be used in "moving drugs or repair materials to target certain specific areas" of the human body (p. 45). Research into the functioning of mosquito mouthparts is leading to "bioinspired microneedles" that are "smaller and less painful" than current syringes (pp. 124–125). And did you know that, owing to the capacity of larval midges to tolerate varying levels of oxygen, study of their head capsules results in "a midge thermometer, to help us understand past climatic events, and previous atmospheric concentrations of oxygen" (p. 33)?

McAlister eschews anything like a standard textbook approach, telling stories instead, often about the fascinating and highly variable extremes exhibited by this large and disparate group. A North American tephritid that mimics the jumping spider that is its primary predator (pp. 182–184), and another fruit fly species, 3 mm in length, whose males produce curls of sperm up almost 6 mm long, "the longest known sperm of any animal on the planet" (pp. 255–256), are but two examples among many. Her personal experiences in different parts of the world—she has studied Australia, Costa Rica, and Dominica—also enliven the book. In the process, McAlister marshalls a wide array of sources, from the historical work of early dipterists to research as recent as last year. In short, she provides an often fascinating array of information directed at interested lay folks and would-be dipterists, with many of the works mentioned being organized by chapter and listed in Further Reading. The result is a fresh appreciation of these arcane animals that all too often are seen from the working end of a fly swatter or can of repellent.

One other substantive difference needs to be mentioned, however, and that is the regrettable lack of a firm editorial hand. I can't recall reading a book as discouragingly and poorly edited as this one. Numerous errors appear, especially in the first third of the book: misspellings, disagreements of verb and subject, misuse of commas, unclear pronoun referents, incorrect word usage, muddled sentences, inconsistent use of capitals, and citation errors. Her off-the-wall sense of humour, relatively constrained in the first book, here is off the charts, becoming simply disruptive rather than funny. But that, I suppose, is a question of taste…

Shortly after finishing this book, and while still writing this review, I went outside, camera in hand, to take my usual wander around our country place. It was a chilly October day, with little happening in the insect world I so keenly photograph. But a few flies were out and about, and I found myself looking at them through new eyes, a result of reading *The Inside Out of Flies*. My criticisms above notwithstanding, there is much to learn here. This book suffers from the sophomore jinx, but hopefully a third book is in the offing. If there is, I plan to read it.

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Bocking, E. 2017. [Book Review] The Secret Life of Flies. Canadian Field-Naturalist 131:287–288. https://doi.org/10.22621/cfn.v131i3.2059

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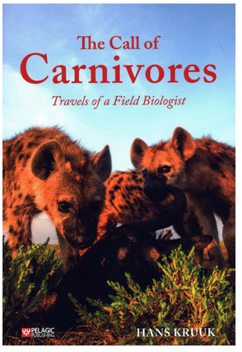
The Call of Carnivores: Travels of a Field Biologist

By Hans Kruuk. 2019. Pelagic Publishing. 200 pages, 176 colour illustrations, and 55 drawings, 34.58 CAD, Paper.



Part travel log, part research biography, this book is a love letter to wild places and the animals that reside in them—a chronicle of the author's life's work and time spent finding "excuses" (as he puts it), to visit and study fascinating species. The author is a distinguished field biologist and natural scientist who emphasizes observation first, questions second, and experiments third. One of the 'old school' behavioural ecologists, the common thread in *The Call of Carnivores* is an exploration of what makes a species social versus solitary, gregarious versus independent. Even the table of contents is immediately interesting—Gulls and their enemies (Chapter 3), Olfactory delights and olives (Chapter 18)—and promises an interesting read.

The book begins in roughly chronologic order, with a short introduction to the author's childhood, their research on Dover Sole fish as a nascent biologist, and their student assistant and graduate work on the (unfortunately now devastated) gull colony of Ravenglass, on the shores of the Irish Sea. The bulk of the book takes place on the African continent, primarily focussing on Spotted Hyenas but also speaking on the behavioural ecology of other carnivorous species, including Lions, Honey Badgers, Brown Hyenas, Striped Hyenas, Cheetahs, and prey animals. Additional brief (one to four chapter) forays into otters, vultures, badgers, dogs, and a smattering of other species round out the remaining chapters.

Refreshingly, although the main focus of the book is the large carnivores that are the subject of the author's research, this is not a book devoid of humans, not one of the score that paint a picture of a majestic landscape devoid of the people who have inhabited it for generations. Kruuk writes with obvious respect for the people of the Serengeti savannah and Kalahari deserts, and descriptions of their interactions and opinions of the large carnivores they share their lives with is accompanied by a generous dash of culture and traditions.

Interspersed with the text are hand-drawn sketches by Ineke Kruuk and Diana Brown, which are excellent additions. The photographs included, although obviously of various ages, serve to reinforce and add to the text. The *Call of the Carnivores* delivers on the early promise of its enticing table of contents, teaching the reader to view Spotted Hyenas as top predators and lions as scavengers, grappling with questions of specialization and sociality, and retaining its sense of fun throughout. Kruuk is a humble and engaging narrator, admitting lack of experience and mastery, confessing mistakes made and lessons learned.

This is a book I came to enjoy more and more as I read it, and the author's sense of humour is well reflected in the writing. At the start of Chapter 23, talking this time about staying stock still to observe a Platypus, Kruuk's description of his mental anguish at being set upon by "an army of leeches galloping towards" (p. 202) him had me smiling ear to ear. Although the relatively short chapter format may lend itself to short bouts of convenience-based reading, in my experience this is a book best read on purpose, when one can carve out deliberate time to read.

As much as it will teach you new facts and entertain you, the highlights of this work for me were the moments where the writing truly pulls you into the author's world—the diverse, breathing ecosystems of incredible wildlife. The book is worth reading if only for these moments alone. Kruuk's passion for his study species and temptation towards 'side projects' is palpable, and his tendency towards temporary distraction based in fascination is endearing and very recognizable for the naturalist inside all of us. I wholeheartedly recommend this book to anyone who has felt the call of wild places and wild species. One thing is for certain, you will never look at hedgehogs the same way again.

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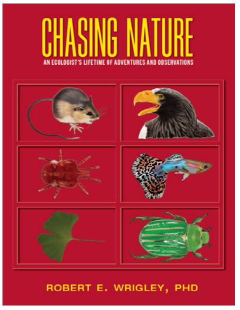
Chasing Nature: An Ecologist's Lifetime of Adventures and Observations

By Robert E. Wrigley. Illustrated by Rob Gillespie. 2020. FriesenPress. 367 pages, 67.49 CAD, Cloth, 53.99 CAD, Paper, 20.99 CAD, E-book. Signed premium copies available from the author (robertwrigley@mymts.net) for 55.00 CAD, Paper, + 17.00 CAD, shipping.



Naturalists have a penchant for writing accounts of their explorations of and enthusiasms for the natural world. Books of collected essays or full-blown autobiographies featuring their years of research are too numerous to mention. Robert Wrigley has developed his own delightful twist, adopting storytelling as a means of relating his life-time avocation and vocation of *Chasing Nature*. Thus, while his book is organized autobiographically, his *Lifetime of Adventures and Observations* is related through 230 stories that begin with his early childhood, when he first discovered his fascination for the natural world, extend through his years of education—high school followed by three degrees in biological fields and associated field work—and continue throughout his career in the museum/zoo world into his years of active retirement. The continuous, connecting thread is a healthy and inexhaustible curiosity about the natural world that goes beyond the living present to encompass the Earth's ancient past and anticipate its anxious future.

The premium copy I reviewed is printed on glossy, letter-sized, sewn-bound paper, with its cover—as you can see—comprised of 14 paintings of specimens noted in the book by artist Autumn Lough. The whimsical humour of friend and cartoonist Rob Gillespie's colourful drawings animates a number of stories; line drawings by the author and friend Todd Lawton and photographs, often by museum volunteer Darlene Stack, complete the 100 or so illustrations. The book is not indexed, but the list of illustrations and the table of contents naming each of the stories make up for this. These lists are preceded by a short foreword and dedication, followed by an introduction and acknowledgements. In his introduction, Wrigley writes about, and thus places himself in, the long history of storytelling, from prehistoric and early historic through to early modern, i.e., 19th century, times, then outlines his lifelong pursuit of "information about Nature" (p. ix). A pair of appendices that provide a List of Common and Scientific Names (pp. 341–349) used in the book and Nature Quotes Through the Ages (pp. 350–360) precede a list of Selected References (pp. 361–365). About 650 names are listed, by my rough count, a real indicator of the extent and variety of Wrigley's interests beyond his expertise in mammalogy.

The storytelling approach works, for Wrigley's "goal is for this book to stimulate others to go outside and explore Nature, whether in a backyard, park, or an exotic location, and to be receptive to life's diversity, dynamism and lessons" (p. x). This is, of course, exactly what Wrigley has been doing throughout his entire life. He takes an interest in literally everything, and his education and work experience have provided myriad opportunities to satisfy that desire to explore and share his knowledge. He had a lot of practice on the job honing his story-telling skills through creating write-ups for exhibits and press releases, writing 18 previous books and numerous articles—his very first was published in 1969 in *The Canadian Field-Naturalist*—and as Zoological Editor for *The Encyclopedia of Manitoba* (2007, Great Plains Publications).

The stories vary in length from one to five or so pages and are organized around the major events of the author's life, although the chronology within each chapter can be as flexible as the topics. The constant thread is a curiosity-driven search for insights into nature wherever he finds it. As related in Chapter 1, Youth Days (1943-61), Wrigley's memories date from his years as a child in Buenos Aries, Argentina, where he became "fascinated by the natural world as soon as I could walk" (p. 3). The family moved to Quebec when he was about six, and he spent the kind of boyhood there that is increasingly unavailable—roving the out of doors. He had the good fortune of having very tolerant parents and an excellent high school biology teacher, and so his unrestricted curiosity took him to nine years of University Days (1961–1970) that involved adventures in Cape Cod, Maine, and field work experience in the Canadian North, collecting degrees—and many mammals—along the way at McGill University and the University of Illinois, Urbana-Champagne.

Chapters 3–5 cover, respectively, his years as a first director of the Manitoba Museum of Natural History, 1970–1988; director of the new Oak Hammock Marsh Interpretive Centre, 1989–1995; and curator of Winnipeg's Assiniboine Park Zoo, 1996–2012. Along with the many natural history accounts of a stunning variety of animals and plants, we get behind-the-scenes tours of museum and zoo operations from an insider who enjoyed his work a great deal. Throughout, Wrigley was, and still is, an avid collector and contributor to various provincial and national collections, both those in which he worked and others around the world. Museums and zoos are often the best, if not the only, places that the public can see firsthand a broad diversity of species and learn about their habitats, life histories, and the tremendous threats under which human activities have placed them. We may have mixed feelings about animals in captivity for the infotainment of the masses, but at times these are the only viable populations left, or the only way to enhance genetic diversity in decreasing stocks in the wild. Wrigley's adventures and resulting stories continue apace throughout Chapter 6, Retired Days (2013–2020), as now he can follow his own lead, exploring and reminiscing as the spirit moves him, and fully indulging a renewed interest in entomology.

Conservation and the fate of life on earth become increasingly strong themes throughout the book, finally given free rein in Chapter 7, Last Thoughts. *Chasing Nature* has taken us from the innocence of happy childhood explorations through the pleasures and challenges of adult activities, but now the tone shifts to Wrigley's increasing concerns about climate change, habitat destruction, escalating loss of biodiversity, human over-population, and crises of health that affect us all. A book which has demonstrated the richness of the life of one man engaged in the pursuit of nature now becomes a solemn overview of life on earth from its most remote beginnings to its ultimate end in a very distant future. There is a reason his book is dedicated to LUCA, "all current and extinct species' Last Universal Common Ancestor" (p. vii)! His concluding question is also a challenge: "Are our instincts and intelligence too primitive to act collectively to save our species and our home?" (p. 338).

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NEW TITLES

Prepared by Barry Cottam

Please note: Only books marked † or * have been received from publishers. All other titles are listed as books of potential interest to subscribers. Please send notice of new books—or copies for review—to the Book Review Editor.

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BIOLOGY

Myxomycetes: Biology, Systematics, Biogeography, and Ecology. Edited by Carlos Alvarado and Steven Stephenson. 2017. Academic Press. 474 pages, 99.95 USD, Paper or E-book, 99.94 USD, both Paper and E-book.

†The Natural History of the Crustacea, Volume VI: Reproductive Biology. Edited by Rickey Cothran and Martin Thiel. 2020. Oxford University Press. 584 pages, 175.00 CAD, Cloth. Also available as an E-book.

†The Natural History of the Crustacea, Volume VII: Developmental Biology and Larval Ecology. Edited by Klaus Anger, Steffen Harzsch, and Martin Thiel. 2020. Oxford University Press. 464 pages, 175.00 CAD, Cloth. Also available as an E-book.

†The Natural History of the Crustacea, Volume VIII: Evolution and Biogeography of the Crustacea. Edited by Martin Thiel and Gary Poore. 2020. Oxford University Press. 520 pages, 175.00 CAD, Cloth. Also available as an E-book.

†Vertebrate Biology: Systematics, Taxonomy, Natural History, and Conservation. Third Edition. By Donald W. Linzey. 2020. Johns Hopkins University Press. 744 pages, 32 colour illustrations, 240 black and white photos, and 370 black and white illustrations, 125.00 USD, Cloth or E-book.

BOTANY

50 Plantes envahissantes: protéger la nature et l'agriculture. Par Claude Lavoie. 2020. Les Publications du Québec. 416 pages, 29,95 CAD, Papier. Aussi disponible en format PDF.

Colour Atlas of Woody Plants and Trees. By Bryan G. Bowes. 2020. CRC Press. 168 pages and 226 colour illustrations, 200.00 CAD, Cloth, 69.95 CAD, Paper, 62.96 CAD, E-book.

Grasses, Sedges, Rushes: An Identification Guide. By Lauren Brown and Ted Elliman. Foreword by Jerry Jenkins. 2020. Yale University Press. 256 pages, 22.00 USD, Flexibound Paper.

Mushrooms of Western Canada. By Helene Schalkwijk-Barendsen. 2020. Partners Publishing / Lone Pine. 416 pages, 28.95 CAD, Paper.

Plants of the Western Forest. By Derek Johnson, Linda Kershaw, Andy MacKinnon, and Jim Pojar. 2020. Partners Publishing / Lone Pine. 392 pages, 29.95 CAD, Paper.

Plants, People, and Culture: The Science of Ethnobotany. Second Edition. By Michael J. Balick and Paul Alan Cox. 2020. Garland Science. 228 pages and 223 colour illustrations, 127.95 CAD, Cloth, 50.95 CAD, Paper, 45.86 CAD, E-book.

Seaweed, An Enchanting Miscellany. By Miek Zwamborn. Translated by Michele Hutchison. 2020. Greystone Books. 192 pages, 26.95 CAD, Cloth.

Spring Wildflowers of the Northeast: A Natural History. By Carol Gracie. Foreword by Eric Lamont. 2020. Princeton University Press. 296 pages and 500 colour photos, 29.95 USD, Cloth. Also available as an E-book.

Summer Wildflowers of the Northeast: A Natural History. By Carol Gracie. Foreword by Robert Naczi. 2020. Princeton University Press. 384 pages and 700+ colour photos, 29.95 USD, Cloth. Also available as an E-book.

Woodland Flowers. British Wildlife Collection. By Keith Kirby. 2020. Bloomsbury Wildlife. 400 pages and 250 colour photos, 45.00 USD, Cloth. Also available as an E-book.

CLIMATE CHANGE

Angry Weather: Heat Waves, Floods, Storms, and the New Science of Climate Change. By Friederike Otto. Translated by Sarah Pybus. 2020. Greystone Books. 256 pages, 32.95 CAD, Cloth. Also available as an E-book.

As the World Burns: The New Generation of Activists and the Landmark Legal Fight Against Climate Change. By Lee van der Loo. 2020. Workman Publishing. 284 pages, 27.95 USD, Cloth, 21.95 USD, E-book.

Hope Matters: Why Changing the Way We Think Is Critical to Solving the Environmental Crisis. By Elin Kelse. 2020. Greystone Books. 224 pages, 22.95 CAD, Paper. Also available as an E-book.

The Rise of Climate Science: A Memoir. By Gerald R. North. 2020. Texas A & M University Press. 336 pages, 35.00 USD, Cloth.

CONSERVATION

Bringing Back the Beaver: The Story of One Man's Quest to Rewild Britain's Waterways. By Derek Gow. Foreword by Isabella Tree. 2020. Chelsea Green Publishing. 208 pages, 25.00 USD, Cloth. Also available as an E-book.

Cats and Conservationists: The Debate Over Who Owns the Outdoors. Dara M. Wald and Anna L. Peterson. 2020. Purdue University Press. 158 pages, 19.99 USD, Paper.

Conservation Biology: Foundations, Concepts, Applications. Third Edition. By Fred Van Dyke and Rachel L. Lamb. 2020. Springer Nature. 613 pages, 233 colour illustrations, and 127 black and white illustrations, 109.00 CAD, Cloth, 84.99 CAD, E-book.

Environmental Management of Marine Ecosystems. Applied Ecology and Environmental Management Series. Edited by Md. Nazrul Islam and Sven Erik Jørgensen. 2020. CRC Press. 362 pages, 54.95 USD, Paper. Cloth and E-book versions published in 2018.

The Greenway Imperative: Connecting Communities and Landscapes for a Sustainable Future. By Charles A. Flink. 2020. University Press of Florida. 344 pages, 28.95 USD, Cloth.

Handbook of Ecological Indicators for Assessment of Ecosystem Health. Second Edition. Edited by Sven Erik Jørgensen, Fu-Liu Xu, and Robert Costanza. 2019. CRC Press. 498 pages, 240.00 USD, Cloth, 89.95 USD, Paper, 80.96 USD, E-book.

ENTOMOLOGY

Army Ants: Nature's Ultimate Social Hunters. By Daniel J.C. Kronauer. 2020. Harvard University Press. 384 pages, 65.00 USD, Cloth.

†**The Art of the Bee: Shaping the Environment from Landscapes to Societies**. By Robert E. Page, Jr. 2020. Oxford University Press. 256 pages, 34.95 CAD, Cloth. Also available as an E-book.

Butterfly Biology Systems: Connections and Interactions in Life History and Behaviour. By Roger L.H. Dennis. 2020. CABI. 472 pages, 210.00 USD, Cloth.

The Butterfly Effect: Insects and the Making of the Modern World. By Edward D. Melillo. 2020. Doubleday US. 272 pages, 45.99 USD, Cloth.

The Disappearance of Butterflies. By Josef H. Reichholf. Translated by Gwen Clayton. 2020. Polity. 260 pages, 42.00 CAD, Cloth, 20.99 CAD, E-book.

Dragonflies at a Biogeographical Crossroads: The Odonata of Oklahoma and Complexities Beyond its Borders. By Brenda D. Smith and Michael A. Patten. 2020. CRC Press. 738 pages, 569 colour illustrations, and 55 black and white illustrations, 39.95 USD, Cloth.

The Moths of America North of Mexico, Fascicle 22.1A: Drepanoidea, Doidae – Noctuoidea, Notodontidae (Part): Pygaerinae, Notodontinae, Cerurinae, Phalerinae, Periergosinae, Dudusinae, Hemiceratinae. By James S. Miller, David L. Wagner, Paul A. Opler, and J. Donald Lafontaine. 2019. The Wedge Entomological Research Foundation. 348 pages, 62 plates, and 76 distribution maps, 95.00 USD, Cloth.

Pollination: The Enduring Relationship between Plant and Pollinator. By Timothy Walker. 2020. Princeton University Press. 224 pages, 29.95 USD, Cloth. Also available as an E-book.

HERPETOLOGY

Amphibians of Oregon, Washington and British Columbia. Third Edition. By Charlotte C. Corkran and Chris Thoms. 2020. Partners Publishing / Lone Pine. 176 pages, 22.95 CAD, Paper.

Lizards of the World: Natural History and Taxon Accounts. By Gordon H. Rodda. 2020. Johns Hopkins University Press. 832 pages, 150.00 USD, Cloth or E-book.

ICHTHYOLOGY

Annual Fishes: Life History Strategy, Diversity, and Evolution. Edited by Nibia Berois, Graciela García, and Rafael O. de Sá. 2020. CRC Press. 327 pages, 54.95 CAD, Paper. Cloth and E-book editions published in 2015.

Emperors of the Deep: Sharks—the Ocean's Most Mysterious, Most Misunderstood, and Most Important Guardians. By William McKeever. 2019. Harper-One. 320 pages, 25.99 USD, Cloth, 16.99 USD, Paper, 11.99 USD, E-book.

Impacts of Oil Spill Disasters on Marine Habitats and Fisheries in North America. By J. Brian Alford, Mark S. Peterson, and Christopher C. Green. 2020.

CRC Press. 327 pages, 54.95 CAD, Paper. Cloth and E-book editions published in 2014.

ORNITHOLOGY

The Biology of Moult in Birds. By Lukas Jenni and Raffael Winkler. 2020. Helm. 320 pages and 151 illustrations, 76.50 USD, Cloth, PDF E-book, or EPUB/MOBI E-book.

Birds of Alberta. New Edition. By Chris Fisher and John Acorn. 2020. Partners Publishing / Lone Pine. 384 pages, 28.95 CAD, Paper.

Book of Birds: Introduction to Ornithology. Gideon Lincecum Nature and Environment Series. By John Faaborg. Illustrated by Claire Faaborg. 2020. Texas A&M University Press. 472 pages, 65.00 USD, Cloth.

The Common Kestrel. By Richard Sale. 2020. Snowfinch Publishing. 392 pages, 49.99 GBP, Cloth.

†**Essential Ornithology. Second Edition**. By Graham Scott. 2020. Oxford University Press. 224 pages, 45.95 CAD, Cloth. Also available as an E-book.

Flights of Passage: An Illustrated Natural History of Bird Migration. By Mike Unwin and David Tipling. 2020. Yale University Press. 288 pages and 220 colour illustrations, 40.00 USD, Cloth.

The Gull Next Door: A Portrait of a Misunderstood Bird. By Marianne Taylor. Foreword by David Lindo. 2020. Princeton University Press. 192 pages, 24.95 USD, Cloth. Also available as an E-book.

Great Gray Owl: A Visual Natural History. By Paul Bannick. 2020. Mountaineers Books. 128 pages, 18.95 USD, Paper.

How to Read a Bird: A Smart Guide to What Birds Do and Why. By Wenfei Tong. Foreword by Ben C. Sheldon. 2020. The History Press. 224 pages and 150 colour photos and colour illustrations, 20.00 GBP, Cloth.

The Kestrel: Ecology, Behaviour and Conservation of an Open-Land Predator. By David Costantini and Giacomo Dell'Omo. 2020. Cambridge University Press. 222 pages, 74.95 CAD, Cloth. Also available as an E-book.

The Narrow Edge: A Tiny Bird, an Ancient Crab, and an Epic Journey. By Deborah Cramer. 2016. Yale University Press. 304 pages, 18.00 USD, Paper.

Peterson Reference Guide to Bird Behavior. Peterson Reference Guides Series. By John C. Kricher. 2020. Houghton Mifflin Harcourt. 360 pages, 35.00 USD, Cloth, 19.99 USD, E-book.

Snowy Owl: A Visual Natural History. By Paul Bannick. 2020. Mountaineers Books. 128 pages, 18.95 USD, Paper.

Steller's Sea Eagle. By Vladimir Borisovich Masterov, Michael S. Romanov, and Richard Sale. 2018. Snowfinch Publishing. 384 pages, 65.00 USD, Cloth.

When Birds Are Near: Dispatches from Contemporary Writers. Edited by Susan Fox Rogers. 2020. Comstock Publishing Associates. 304 pages, 22.95 USD, Paper.

ZOOLOGY

Experimental Hydrodynamics of Fast-Floating Aquatic Animals. By Babenko Viktor Vitaliiovych. 2020. Academic Press. 270 pages, 85.00 USD, Paper or E-book, 100.00 USD, both Paper and E-book.

How Zoologists Organize Things: The Art of Classification. By D. Bainbridge. 2020. Pemberley Books. Frances Lincoln Adult. 256 pages, 26.00 USD, Cloth. Also available as an E-book.

The Invertebrate World of Australia's Subtropical Rainforests. By Geoff Williams. 2020. CSIRO Publishing. 392 pages, 195.00 AUD, Cloth.

Mammals of the Southeastern United States. By Troy L. Best and John L. Hunt. 2020. University of Alabama Press. 496 pages, 331 colour photographs, and 137 maps, 64.95 USD, Cloth or E-book.

Otters of the World. By Paul Yoxon. 2019. Whittles Publishing. 160 pages, 24.95 USD, Paper. Also available as an E-book.

***The Reign of Wolf 21: The Saga of Yellowstone's Legendary Druid Pack**. By Rick McIntyre. Foreword by Marc Bekoff. 2020. Greystone Books. 272 pages, 34.95 USD, Cloth.

Wildlife of Nebraska: A Natural History. By Paul A. Johnsgard. 2020. University of Nebraska Press. 528 pages, 34.95 USD, Paper or E-book.

***Wolf Island: Discovering the Secrets of a Mythic Animal**. By L. David Mech with Greg Breining. Foreword by Rolf O. Peterson. 2020. University of Minnesota Press. 200 pages, 24.95 USD, Cloth. Also available as an E-book.

***Yellowstone Wolves: Science and Discovery in the World's First National Park**. Edited by Douglas W. Smith, Daniel Stahler, and Daniel R. MacNulty. Foreword by Jane Goodall. 2020. University of Chicago Press. 344 pages, 62 color plates, 29 halftones, and 24 line drawings, 35.00 USD, Cloth or E-book.

OTHER

About Method: Experimenters, Snake Venom, and the History of Writing Scientifically. By Jutta Schickore. 2020. University of Chicago Press. 320 pages, 40.00 USD, Paper. Cloth and E-book editions published in 2017.

Aesthetic Science: Representing Nature in the Royal Society of London, 1650–1720. By Alexander Wragge-Morley. 2020. University of Chicago Press. 272 pages, 120.00 USD, Cloth, 40.00 USD, Paper. Also available as an E-book.

As the Twig Is Bent: A Memoir. By Wallace Byron Grange. Edited by Joseph L. Breitenstein and Richard Thiel. 2020. University of Wisconsin Press. 344 pages, 29.95 USD, Cloth.

***Capturing Motion: My Life in High-Speed Nature Photography**. By Stephen Dalton. 2020. Firefly Books. 192 pages and 80 color photographs, 35.00 CAD, Cloth.

Encyclopedia of the World's Biomes, 5 Volumes. Editors in Chief: Michael I. Goldstein and Dominick A. DellaSala. 2020. Elsevier. 3500 pages, 2400.00 USD, Cloth or E-book.

†Foundations for Advancing Animal Ecology. By Michael L. Morrison, Leonard A. Brennan, Bruce G. Marcot, William M. Block, and Kevin S. McKelvey. 2020. Johns Hopkins University Press. 208 pages, 69.95 USD, Cloth. Also available as an E-book.

The Ice at the End of the World: An Epic Journey into Greenland's Buried Past and Our Perilous Future. By Jon Gertner. 2020. Penguin Random House. 410 pages, 18.99 USD, Paper. Cloth and E-book editions published in 2019.

In Praise of Paths: Walking Through Time and Nature. By Torbjørn Ekelund. Translated by Becky L. Crook. 2020. Greystone Books. 240 pages, 29.95 CAD, Cloth.

Into Wild Mongolia. By George B. Schaller. 2020. Yale University Press. 224 pages, 28.00 USD, Cloth.

Iwígara: American Indian Ethnobotanical Traditions and Science. By Enrique Salmón. 2020. Workman Publishing. 248 pages, 34.95 USD, Cloth, 25.95 USD, E-book.

A Life on Our Planet: My Witness Statement and Vision for the Future. By Sir David Attenborough and Jonnie Hughes. Illustrated by Lizzie Harper. 2020. Witness Books (Ebury Press). 272 pages, 20.00 GBP, Cloth or E-book.

Methods to Study Litter Decomposition: A Practical Guide. Second Edition. Edited by Felix Bärlocher, Mark O. Gessner, and Manuel A.S. Graça. 2020. Springer International Publishing. 629 pages, 155.99 EUR, Cloth, 117.69 EUR, E-book.

The Nature of Fear: Survival Lessons from the Wild. By Daniel T. Blumstein. 2020. Harvard University Press. 256 pages, 25.95 USD, Cloth.

Nature's Mirror: How Taxidermists Shaped America's Natural History Museums and Saved Endangered Species. By Mary Anne Andrei. 2020. UCP. 264 pages, 35.00 USD, Cloth or E-book.

Nature Strange and Beautiful: How Living Beings Evolved and Made the Earth a Home. By Egbert Giles Leigh, Jr. and Christian Ziegler. 2019. Yale University Press. 304 pages, 65 colour illustrations, and 70 black and white illustrations, 28.00 USD, Cloth.

Seeking the American Tropics: South Florida's Early Naturalists. By James A. Kushlan. 2020. University Press of Florida. 248 pages, 26.95 USD, Cloth.

Stopping by Woods: Robert Frost as New England Naturalist. By Owen D.V. Sholes. 2018. McFarland and Company Inc. 190 pages, 39.95 USD, Paper.

Tales from the Ant World. By Edward O. Wilson. 2020. Liveright. 240 pages, 26.95 USD, Cloth.

Tropical Forests in Prehistory, History and Modernity. By Patrick Roberts. 2019. Oxford University Press. 350 pages, 119.95 USD, Cloth.

Vesper Flights. By Helen Macdonald. 2020. Hamish Hamilton. 272 pages, 29.95 CAD, Cloth, 14.99 CAD, E-book.

Wildlife as Property Owners: A New Conception of Animal Rights. By Karen Bradshaw. 2020. University of Chicago Press. 152 pages, 95.00 USD, Cloth, 27.50 USD, Paper. Also available as an E-book.

***The Wildlife Techniques Manual. Volume 1: Research. Volume 2: Management. Eighth Edition**. Edited by Nova J. Silvy. 2020. Johns Hopkins University Press. 1400 pages, 174.95 USD, Cloth. Also available as an E-book.

William Stimpson and the Golden Age of American Natural History. By Ronald Scott Vasile. 2018. Cornell University Press. 300 pages, 29.00 USD, Paper, 13.99 USD, E-book.

The Canadian Field-Naturalist

News and Comment

Compiled by Amanda E. Martin

Upcoming Meetings and Workshops

Canadian Herpetological Society Conference (Part 2)

The 2020 Canadian Herpetological Society Conference (Part 2) to be held as an online meeting 6 December 2020. Registration for this event is free but limited to Society members. More information is available at http://canadianherpetology.ca/conf/index.html.

11th Colloque Annuel du CSBQ/11th Annual QCBS Symposium

The 11th Colloque Annuel du CSBQ/11th Annual QCBS Symposium to be held by the Centre de la Science de la Biodiversité du Québec (CSBQ)/Quebec Center for Biodiversity Science (QCBS) as an online meeting 14–16 December 2020. More information is available at https://qcbs.ca/symposium.

The Society for Integrative & Comparative Biology Annual Meeting

The Society for Integrative & Comparative Biology Annual Meeting to be held as an online meeting 3 January–28 February 2021. Registration is currently open. More information is available at http://burkclients.com/sicb/meetings/2021/site/general_info.html.

Evidence Synthesis & Meta-analysis in R Conference

The Evidence Synthesis & Meta-analysis in R Conference to be held as an online meeting 21–22 January 2021. More information is available at https://www.eshackathon.org/events/2021-01-ESMAR.html.

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Tributes

Book Reviews

News and Comment

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