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COVER: Painting by Aleta Karstad, a 2021 Honorary OFNC Member inductee, of the nesting Red-throated Loon (*Gavia stellata*), Drizzle Lake, Haida Gwaii, British Columbia, one of the subjects of Douglas and Reimchen's article on vocalization in the species, pages 165–180. As an added bonus, see the online supplement (https://www.canadianfieldnaturalist.ca/index.php/cfn/article/view/2899/2729) for a few pages of Aleta's natural history journal about the encounter and initial sketches.

The Canadian Field-Naturalist

Note

The first documented migration of a potter wasp, *Ancistrocerus adiabatus* (Hymenoptera: Vespidae: Eumeninae)

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Abstract

Eumenine wasps are not known to be migratory and have never been proposed as migrants, let alone documented as such. We document a large-scale migration of a common eumenine, *Ancistrocerus adiabatus*, during which 44 000–68 000 wasps moved through a known migration corridor in southwestern Ontario, Canada, in less than an hour. Evidence for migration of another eumenine, *Pachodynerus erynnis*, six species of flower flies (Diptera, Syrphidae), and two dragonflies (Odonata) is also provided. We hope that this note encourages naturalists to focus their attention on insects at known migration concentration sites to learn more about this grossly understudied aspect of animal behaviour.

Key words: Insect migration; Vespidae; Odonata; Syrphidae

During 12–16 September 2020, J.H.S. was observing flora and fauna in the Point Pelee area of southwestern Ontario, Canada. On 12 September, he noted an abundance of *Ancistrocerus* wasps (Hymenoptera: Vespidae: Eumeninae). Every goldenrod inflorescence contained dozens of these insects, mainly stationary, none moving farther than between flower heads on adjacent plants.

The weather was mostly clear with easterly winds switching to southerly in the afternoon with a high of 24°C (J.H.S. pers. obs.) and continued, through the morning of 13 September, mostly clear with southerly winds switching to easterly through the day. The weather changed abruptly in the late afternoon when the wind switched to northwest. Bird migration increased and, at 1748, J.H.S. moved to a lakeshore location at the junction of Zion Road and Bluff Line (42.1127°N, 82.4083°W). This site on the north shore of Lake Erie is known to concentrate bird migrants moving southwest along the lakeshore on northwest winds.

On arriving, J.H.S. immediately noticed *Ancistrocerus* wasps moving from east to west in large numbers, typical of the direction of movement of visibly migrating birds. The wasps were moving in a narrow band along the lakeshore, almost entirely between the agricultural fields and the lake over an 80-m wide swath of grasses, goldenrods, and other meadow plants. Their movement and flow were assessed over 69 min. For the first 50 min of observation, they moved steadily over the 80-m lakeshore buffer area. Migration started to slow at 1840, but some wasps were still moving when J.H.S. departed at 1857. Three one-minute-long counts were conducted with the following results: 170 in one min at 1815; 110 in one min at 1823; and 121 in one min at 1831. Wasps were only visible within 10 m of the observer and, given that numbers appeared to be consistent across the 80-m buffer, an estimated 880–1360 wasps were passing per min. Based on consistent passage observed for 50 min, that equals 44 000–68 000 wasps. Five specimens were collected as vouchers (stored in the Canadian National Collection of Insects, Arachnids and Nematodes: CNC1738754–CNC1738758) and one specimen was photographed at Point Pelee on 15 September (Figure 1). M.B. identified all of these specimens as females of a species of potter wasp, *Ancistrocerus adiabatus* (de Saussure, 1852); see Buck *et al.* (2008) for a key to species.

FIGURE 1. Female *Ancistrocerus adiabatus* at Point Pelee National Park, 15 September 2020 (record also on iNaturalist at https://www.inaturalist.org/observations/59734868). Photo: J.H. Skevington.

The next day, J.H.S. observed orders of magnitude fewer wasps on flowers. Presumably most had moved to points further south during the cold front on 13 September. Monarch butterfly (*Danaus plexippus* (Linnaeus, 1758) – Lepidoptera, Nymphalidae) migration at Point Pelee is similar, with numbers building on days with southerly winds followed by a mass movement south with north winds (J.H.S. pers. obs.). Wasp numbers appeared to build daily from 14 to 16 September when J.H.S. departed (south winds daily), presumably massing again until the next northerly flow.

Ancistrocerus adiabatus breeds in holes bored in twigs, stems, and wood; empty insect galls and sawfly cocoons; old mud-dauber nests; and rubber tubing. They make nest cell partitions and closing plugs from mud and provision their young with moth caterpillars from several families (Buck *et al.* 2008). As far as we know, eumenines overwinter as prepupae; thus, migration in this subfamily of wasps is unexpected. *Ancistrocerus adiabatus* is multivoltine (M.B. pers. obs.), occurring throughout the growing season in overlapping generations, so it is possible that migrant adults can reproduce again if they move south.

Migration in this species, other *Ancistrocerus* species, or in fact other eumenines has never been documented, but it has been hinted at. For example, some eumenines have been recorded as possible vagrants in late autumn, suggesting that they may be migratory. For example, *Pachodynerus erynnis* (Lepeletier, 1841) was recorded at Point Pelee on 11 October 2020 (https://www.inaturalist.org/observations/62367247). The only other Canadian record is a male from Rondeau Provincial Park, South Point, 42°15′N, 81°52′W, on 7 September 2003 (collected by M.B., deposited in the University of Guelph Insect Collection, recorded by Buck *et al.* [2008]). Other previously published extralimital records for this species are cited in Buck *et al.* (2008). More recent observations have been reported on BugGuide, namely a male on 25 September 2019 from Cape May Point State Park, New Jersey (https://bugguide.net/node/view/1733674) and on iNaturalist, a female on 23 September 2019 on Staten Island, New York (https://www.inaturalist.org/observations/33291119). This species normally occurs from North Carolina to Texas and we hypothesize that these vagrants were displaced migrants..

The notable difference between these examples and our observation is that the former apparently migrated far north at the end of the season, whereas *A. adiabatus* at Point Pelee was apparently moving in the opposite direction. Furthermore, the latter was observed in large numbers. By contrast, the *P. erynnis* male at Rondeau Provincial Park was a singleton

(M.B. pers. obs.; no abundance information available for the other observations).

These trends are difficult to interpret. It remains to be clarified whether migrations are regular events or caused by exceptional circumstances. Regular seasonal migrations have only been reported for social vespids in the genera *Polistes* Latreille, 1802 and *Mischocyttarus* Saussure, 1853 (both Polistinae) in Central America (Hunt *et al.* 1999). Because of the different nesting biology of social wasps and their different stage of dormancy (adult versus prepupa) their behaviours are likely driven by different adaptive pressures.

Other apparent insect migrants (all moving east to west), noted at Zion Road on 13 September, included: Common Drone Fly (*Eristalis tenax* (Linnaeus, 1758) – Diptera, Syrphidae); Eastern Band-winged Hoverfly (*Ocyptamus fascipennis* (Wiedemann, 1830) – Diptera, Syrphidae); Monarch; Black Saddlebags (*Tramea lacerata* (Hagen, 1861) – Odonata, Libellulidae); and Green Darner (*Anax junius* (Drury, 1773) – Odonata, Aeshnidae). Shannon (1926) noted that insect migration was virtually an untouched field of study. Remarkably, this has changed little since that time. Shannon noted that *E. tenax* was migrating at several sites along the eastern seaboard, but did not note any other syrphids.

Few observations, such as these, have been made in North America despite considerable attention in Europe (e.g., Max Planck Society 2019; Wotton *et al.* 2019). Menz *et al.* (2019) documented a large passage of over 100 000 syrphids along the west coast of California in April 2017, but no specimens were collected to support more specific identification of these insects. On 22 September 2013, Skevington (2020) collected numbers of Oblique Stripetail (*Allograpta obliqua* (Say, 1823)), Aphideaters (*Eupeodes* Osten Sacken, 1877 spp.), Yellow-legged Flower Fly (*Syrphus rectus* Osten-Sacken, 1875), and Common Flower Fly (*Syprhus ribesii* (Linnaeus, 1758)) at Hawk Cliff near Port Stanley, southwestern Ontario (CNC8460–CNC8503) and speculated that these were migrants. Similarly, it is speculated here that *E. tenax* and *O. fascipennis* were migrating, but more fieldwork is required to confirm this.

Point Pelee and other known bird migration hotspots offer an excellent opportunity for entomologists interested in migration. Few species of insects have been documented migrating, but most naturalists are familiar with buildups of certain species in migration corridors, suggesting that the phenomenon is far more common than documented in the literature on insects. Hopefully, the advent of online databases, such as iNaturalist, other improved identification aids, better cameras, closer-focussing binoculars, and the increased number of people exploring nature will ensure that we learn more about insect migration in the next few years than we have in the last 100. The lack of research on this subject in North America can be partly attributed to the difficulty of studying and tracking small animals over large distances, but the surge of interest in Europe suggests that we are simply behind. We encourage naturalists to focus their attention on insects at known migration concentration sites, such as Point Pelee National Park, Long Point, Rondeau Provincial Park, and locations along the eastern and western seaboards from late August to November. Citizen science offers great potential to better estimate the scale of insect migration as well as the species involved through mark–recapture, thorough documentation, and dedicated long-term observation.

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Note

Coyote (*Canis latrans*) predation of colonial rodents facilitated by Golden Eagles (*Aquila chrysaetos*)

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Abstract

Interactions between Coyote (*Canis latrans*) and Golden Eagle (*Aquila chrysaetos*) are complex and likely not yet fully documented or understood. I observed a Coyote prey on a Black-tailed Prairie Dog (*Cynomys ludovicianus*) at the edge of a large colony in Grasslands National Park, Saskatchewan. The prairie dogs were vigilant toward three Golden Eagles circling above, and the Coyote apparently used this to its advantage. As such, the eagles appeared to facilitate the ability of the Coyote to rush in virtually undetected and prey on a prairie dog that was distracted by the avian predators. This observation is of scientific interest because it is another example of the varied interactions between Coyotes and Golden Eagles, which is competitive and includes kleptoparasitism.

Key words: Golden Eagle; *Aquila chrysaetos*; Coyote; *Canis latrans*; Black-tailed Prairie Dog; *Cynomys ludovicianus*; Grasslands National Park; interspecific competition; predation

Behavioural interactions among carnivorous vertebrates occupying similar trophic levels are not well known and have been highlighted as an area requiring further investigation (e.g., Linnell and Strand 2000; Saggiomo *et al*. 2017). On the Great Plains, Coyote (*Canis latrans*) and American Badger (*Taxidea taxus*) share similar prey and sometimes form hunting associations that appear mutualistic (Kiliaan *et al*. 1991; Minta *et al*. 1992). Several observations describe a Coyote waiting beside a badger that is excavating rodent burrows, presumably for a chance to capture animals as they rush out of their burrows, past the badger (reviewed in Kiliaan *et al*. 1991). As such, Coyotes may parasitize badgers, with the association benefiting Coyotes but not badgers (Minta *et al*. 1992). Moreover, occasionally these associations are competitive, rather than mutualistic, with both species reported to kill one another (Rathbun *et al.* 1980). However, badgers may benefit from Coyotes that locate and chase burrowing rodents underground, trapping them for the badger. Although Coyote–badger hunting associations appear mainly mutualistic, with both species reducing energetic costs of hunting when together (Minta *et al*. 1992), interactions between them are rich and complex.

Coyotes and Golden Eagle (*Aquila chrysaetos*) also share similar food items, including ungulates (Flook and Thomas 1962; Bruns 1970; Bowen 1980), lagomorphs (Ford and Alcorn 1964; Engel and Vaughan 1966; Jung *et al*. 2009), and colonial rodents such as ground squirrels (Bekoff 1977; Elliot and Flinders 1991; Best 1995; Hoogland 1996). Interactions between Coyotes and Golden Eagles, however, appear to be competitive rather than mutualistic. For instance, Coyotes may follow Golden Eagles to steal prey they find, flush, or kill (Engel and Vaughan 1966). Yet, it is difficult to discern from available field observations which species is dominant. Although Golden Eagles have kleptoparasitized (i.e., stolen food that was caught, collected, or stored by another) food from Coyotes (Jung *et al.* 2009), Coyotes have similarly stolen prey from Bald Eagle (*Haliaeetus leucocephalus*; Parris *et al*. 1980). In one observation, Coyotes drove Golden Eagles off an ungulate carcass so they could feed on it (Bowen 1980). Conversely, Coyotes have been driven from carcasses by both Golden Eagles (Flook and Thomas 1962) and Bald Eagles (Wells and Bekoff 1978). In several extreme instances, Golden Eagles have been reported attacking or killing Coyotes (Miner 1954; Ford and Alcorn 1964; Woelfl and Woelfl 1995; Mason 2000), although I could find no reports of Coyotes killing Golden Eagles. Clearly, the extent of competitive interactions between Coyotes and Golden Eagles is complex and likely not yet fully documented or understood. Here, I add to the limited literature on competitive interactions between these species by reporting an observation of Coyote predation of a Black-tailed Prairie Dog (*Cynomys ludovicianus*) that appeared to be facilitated by Golden Eagles.

On 9 September 2018, from atop a knoll along a ridge, I used binoculars to observe the Monument Colony of Black-tailed Prairie Dogs and Richardson Ground Squirrels (*Urocitellus richardsonii*) in the Frenchman River Valley of Grasslands National Park, Saskatchewan. At about 0920 local time, I observed three Golden Eagles (one mature, two immature) soar together above the prairie dog colony about 400 m west of my location. The prairie dogs became quite vocal and vigilant as the eagles circled ~250 m above ground level. About 60–90 s after the Golden Eagles began circling above the colony, I heard a particularly loud, sharp "yip" from immediately north of my hilltop position, and I turned to see a Coyote shaking a prairie dog on the slope of the adjacent knoll. After shaking it for a few seconds, the Coyote bounded over the hill with the prairie dog and was out of view. I did not see the eagles attempt to prey on a prairie dog, but they continued to fly above the colony for another few minutes before they flew out of sight.

I did not see the Coyote before it grabbed the prairie dog, but presume it came over the knoll and down the slope to the area where burrows were located, as I had an unobstructed view of much of the area and did not see it coming. There are three hypotheses regarding how the Coyote came to attack the prairie dog so quickly after the Golden Eagles started circling the colony. First, similar to the observation by Engel and Vaughan (1966), the Coyote may have been following the eagles, seeking a chance to prey on an individual flushed or otherwise startled by them. Ravens (*Corvus corax*) similarly follow Gray Wolves (*Canis lupus*) to find food (Stahler *et al.* 2002; Kaczensky *et al.* 2005). However, I reject this hypothesis because the Coyote undoubtedly came from the north and the eagles were flying from the south, suggesting that the Coyote was not following the eagles. Second, the Coyote was coincidentally in the vicinity of the colony and was cued to the sudden, loud alarm calling by prairie dogs and ground squirrels and rushed to the site to try to capture one. Third, the Coyote may have been resting below a shrub on the other side of the hill, near the colony, waiting for prairie dogs and ground squirrels to be startled by another predator so that it could opportunistically try to capture one. Both the second and third hypotheses seem plausible, but it is not possible to discern which was the case. Regardless, both hypotheses point to the Coyote opportunistically preying on a prairie dog when the eagles had distracted it, thus, profiting from their apparent hunting efforts.

The third hypothesis is particularly intriguing because it implies that the Coyote may have been waiting for an opportunity to ambush a prairie dog or ground squirrel. Ambushing prey is not a well-observed tactic of Coyotes, which normally kill their prey by flushing and chasing them (i.e., "coursing") or using a "stalk-and-pounce" approach (Bekoff 1977). Black-tailed Prairie Dog colonies are predictable on the landscape and attract potential predators (Lomolino and Smith 2004). A Coyote resting out of sight near a colony may use a "sit-and-wait" strategy to opportunistically prey on prairie dogs when their attention is focussed on another predator.

It is also interesting that the prairie dog was captured adjacent to a burrow that was at the extreme edge of the colony and mid-slope on a knoll (Figure 1). Black-tailed Prairie Dogs are likely a keystone species on the North American Great Plains, chiefly because they are ecosystem engineers that modify local site conditions to benefit other species, while also being important in the food webs of grassland biomes (Ceballos *et al.* 1999; Kotliar *et al.* 1999). They represent predictable patches of potential prey on the landscape, and predators are attracted to their colonies (Hoogland 1996; Lomolino and Smith 2004). Indeed, a colonial lifestyle by fossorial rodents living in open habitats is likely an adaptation that allows for heightened vigilance by colony members and a concomitant reduction in individual predation risk (Hoogland 1981). However, this observation provides an example of the risk that some colonial rodents take by locating their burrow in apparently sub-optimal habitat at the edge of a colony.

In conclusion, I describe an incident of a Coyote taking advantage of Golden Eagles distracting prairie dogs, so that it could capture prey that the eagles were apparently hunting. This interaction between these predators likely occurs more frequently than indicated in the literature, given that they often hunt the same prey species. The success of the Coyote's hunting efforts was apparently facilitated by the eagles. As such, my observation provides another aspect to the rich, complex, and largely unknown interactions between Coyotes and Golden Eagles.

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FIGURE 1. Mid-slope burrow, where a Black-tailed Prairie Dog (*Cynomys ludovicianus*) was predated by a Coyote (*Canis latrans*) in Grasslands National Park, Saskatchewan. Photo: T.S. Jung.

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Seasonal occurrence of waterbirds in Minas Passage, Bay of Fundy, Nova Scotia, Canada, 2010 to 2012

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Abstract

We determined patterns of seasonal abundance and diversity of seabirds and coastal waterfowl in Minas Passage, Bay of Fundy, Nova Scotia, Canada using quantitative, shore-based point surveys from mid-March to late August and mid-October to December 2010 to 2012. This area experiences the world's highest tides and greatest tidal currents. We showed that species and seasonal cycles of waterbirds in Minas Passage reflect patterns typical of the inner Bay of Fundy and the northeast Atlantic coast of North America. The study highlights the importance of Minas Passage as an important local migration pathway for waterbirds including Black Scoter (*Melanitta americana*) and Red-throated Loon (*Gavia stellata*) passing through the Bay of Fundy. Large numbers of sea ducks (Black Scoter, Surf Scoter [*Melanitta perspicillata*], White-winged Scoter (*Melanitta fusca*), and Long-tailed Duck [*Clangula hyemalis*]), and Red-throated Loon were observed at the site in spring and fall, corresponding to known peak movements elsewhere in the Bay of Fundy. Fewest species and smallest abundances of waterbirds overall occurred in summer and early winter, while most species and largest abundances occurred in April-May and early November. Of the 46 species observed, resident breeders such as Herring Gull (*Larus argentatus*), Great Black-backed Gull (*Larus marinus*), Common Eider (*Somateria mollissima*), Black Guillemot (*Cepphus grylle*), and Double-crested Cormorant (*Phalacrocorax auritus*), were most abundant in spring to early summer during breeding and migrants including Red-throated Loon, Black Scoter, Ring-billed Gull (*Larus delawarensis*), Surf Scoter, and Northern Gannet (*Morus bassanus*) occurred in moderate numbers during migration periods.

Key words: Waterbirds; shorebirds; seabirds; abundance; seasonal cycles; Bay of Fundy; Minas Passage; Nova Scotia

Introduction

Waterbirds—seabirds, waterfowl, waders, and shorebirds—are important higher-trophic-level organisms in the Bay of Fundy, Nova Scotia, Canada, the site of the world's highest tides (Hicklin and Smith 1984a; EPRI 2005; Karsten *et al.* 2008; Mills and Laviolette 2011). Longstanding interest in tidal energy development in the Bay of Fundy focussed attention on potential effects on the environment, in particular in the southeastern arm of the inner Bay of Fundy where Minas Passage, a narrow strait, connects Minas Channel and Minas Basin, a semi-enclosed tidal bay (Figure 1). Minas Passage is occupied throughout the year by various seabird, waterfowl, wader, and shorebird species.

Recently, the ecological significance of Minas Passage and Minas Basin has been recognized by their inclusion in the proposed new Ecologically and Biologically Significant Area (EBSA)—the Evangeline-Blomidon-Minas Basin EBSA—under the Canadian *Oceans Act* (Buzeta 2014; DFO 2018). This designation recognizes, in part, the importance of the area for shorebirds and coastal raptors such as Peregrine Falcon (*Falco peregrinus anatum*). Avifauna in Minas Basin and adjacent areas of the inner Bay of Fundy was comparatively poorly studied until the 1970s when the inner Bay of Fundy mudflats were recognized as important stopovers for transoceanic shorebird migrations (McNeil and Burton 1977), and interest in tidal power development led to increased scientific attention (Daborn 1977; Hughson 1977; Morrison 1977; Hicklin and Smith 1984a,b; Hicklin 1987). More recently, studies have increased the overall knowledge of waterbirds in both the inner bay and in the Bay of Fundy as a whole (e.g., Lock *et al.* 1994; Dietz and Chiasson 2000; Bond *et al.* 2007; Mills and Laviolette 2011; Cotter *et al.* 2012; Allard *et al.* 2014; Cameron 2014; MacKinnon and Kennedy 2014; Wong *et al.* 2018). Many of these studies focussed on particular species (e.g., shorebirds; Hicklin 1987) or

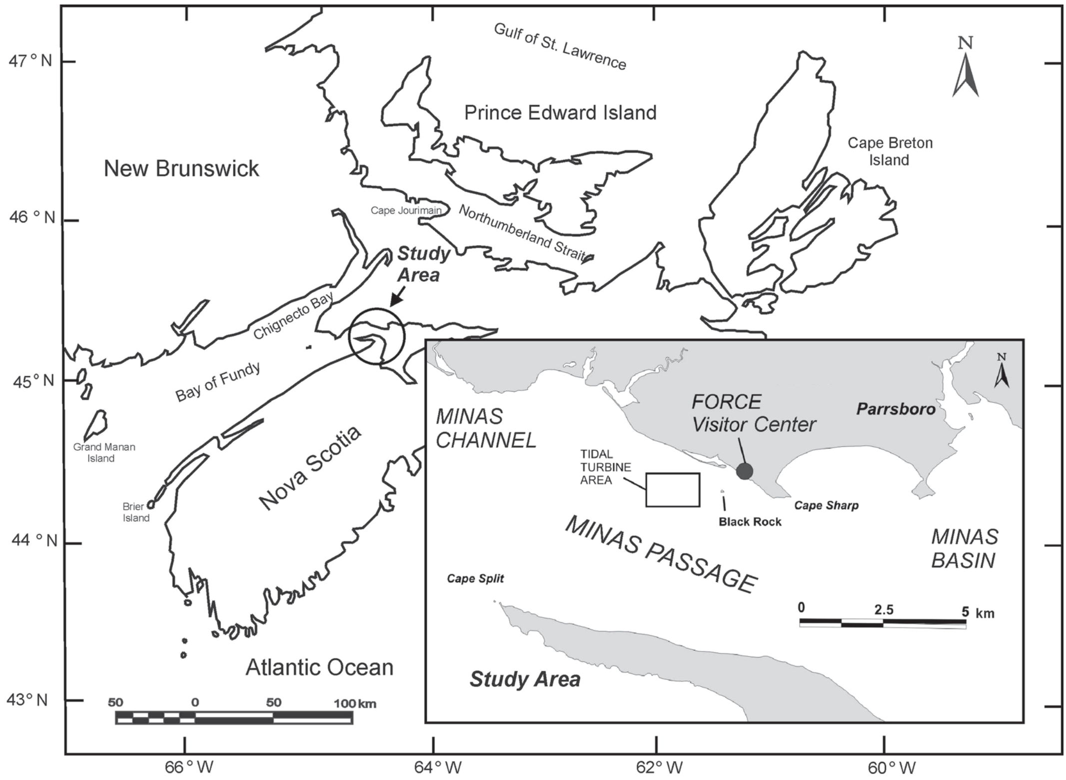

FIGURE 1. Study area for shore-based surveys for waterbirds in Minas Passage, 2010 to 2012.

seasonal migrations (e.g., Cameron 2014).

We report on baseline studies required for regulatory approvals of tidal energy development at Nova Scotia's first tidal energy demonstration site (Fundy Ocean Research Center for Energy, FORCE). These included quantitative observations of abundance, diversity, and behaviour of waterbirds in spring, summer, and fall to early winter, i.e., throughout most of the year, a perspective which is not typically available. These observations could then be used for assessing and managing risks of tidal energy development. The FORCE site is located at Black Rock near Cape Sharp in Minas Passage near Parrsboro, Nova Scotia (Figure 1), where the strongest tidal currents occur (EPRI 2005; Karsten *et al.* 2008). Such studies are also useful for establishing long-term trends in abundance, distribution, and migratory patterns of waterbirds, and for determining impacts of environmental changes such as global warming and impacts of other human activities and natural events (Votier *et al.* 2005; Sydeman *et al.* 2012; Paleczny *et al.* 2015).

Methods

From 2010 to 2012, FORCE undertook a series of 19, 6 h/day shore-based, spring-to-late summer, and late-fall to early-winter surveys at the Minas Passage site. Six to seven surveys were conducted each year, focussed on particular periods (late spring to early summer and late fall in 2010, early spring and early winter in 2011, and summer in 2012) deliberately omitting winter and late summer to reduce effort when abundance and diversity was expected to be low. Observations were conducted from approximately noon to 1800 on days with a high tide around noon and coinciding with the transition from high to low ebb tide. This schedule resulted in 12, 30 min observation periods each day except for 1 May and 22 November 2010 that had 11 periods. Fixing the survey timing in relation to tidal and daylight cycles (i.e., beginning at high tide near noon) ensured consistent conditions of tide and time of day to reduce some of the variability due to environmental factors.

Observations were made either from the beach berm (4 m above mean high water, used in 2010 only), or the FORCE Visitor Center (45.3702°N, 64.4037°W, 22 m above mean high water) which gives an unobstructed view for about 5 km across Minas Passage (Figure 1) and a panoramic view including Cape Split (Figures 1 and 2). Black Rock, a basalt island ~85×25 m at high tide, is a prominent physical feature ~650

FIGURE 2. View of study area in Minas Passage from observation location (FORCE Visitor Center), showing Black Rock and Cape Split. Photo: Patrick Stewart.

m from shore and is a nesting, resting, and aggregation site for some species. A broad, steeply-sloping gravel beach flat occupies the intertidal zone extending seaward for ~100 m from an alongshore barrier beach berm.

Surveys were coordinated by P.L.S. with principal observer F.L.L. and field assistants P.L.S. in 2010 or Matthew MacLean in 2011 and 2012. The observer used a tripod-mounted, 22× spotting scope and 10×42 binoculars, and had previous experience with, and could confidently identify, all the birds encountered. For the first five minutes of each 30 min period, the observer scanned the entire study area. For the rest of the period, birds entering or moving through the area were noted, providing an estimate of the number observed in each 30 min period. All birds in the designated survey area, flying or on the water, including those on Black Rock were included.

The average count of each species per 30 min period based on 11 to 12 periods on a given day was used to summarize bird occurrence during each survey. Average counts do not distinguish among species normally seen as individuals, versus those typically occurring in groups, or the frequency of occurrence during the day; many of the birds were seen in only a single 30 min period during the day. Survey timing was arranged to ensure suitable viewing weather conditions (wind, rain, fog, glare, etc.) as recommended in standard survey protocols (e.g., Gjerdrum *et al.* 2012).

Reports on the seabird monitoring studies in Minas Passage are presented on the FORCE website (https://fundyforce.ca/). Kruskal-Wallace non-parametric analysis of variance (Systat 5.0; Systat Software Inc. 1990) was used to compare the number of species occurring among seasons.

Results

Dominant species and seasonality

Forty-six species of seabirds, waterfowl, and shorebirds occurred at the study site (Table 1). Herring Gull (*Larus argentatus*), Great Black-backed Gull (*Larus marinus*), and Common Eider (*Somateria mollissima*) were observed in all surveys, while Black Guillemot (*Cepphus grylle*), Common Loon (*Gavia immer*), and Red-throated Loon (*Gavia stellata*) were each seen in 16 surveys (84.2%) and Double-crested Cormorant (*Phalacrocorax auritus*) and Great Cormorant (*Phalacrocorax carbo*) in 14 surveys (Table 1).

TABLE 1. Counts of waterbirds (average per 30 min) and (SD), May 2010 to August 2012, Minas Passage, Nova Scotia, Canada. Blank cells represent zero counts. Species are arranged alphabetically by common name in taxonomic order from Clements *et al.* (2019).

Species	Survey date																		
	1-May-2010	13-May-2010	27-May-2010	12-Jun-2010	23-Oct-2010	13-Nov-2010	22-Nov-2010	16-Mar-2011	31-Mar-2011	15-Apr-2011	30-Apr-2011	2-Dec-2011	13-Dec-2011	21-Jun-2012	4-Jul-2012	18-Jul-2012	2-Aug-2012	15-Aug-2012	29-Aug-2012
Ducks, geese, swans, and mergansers (Anseriformes)																			
Diving ducks and bay ducks (Anatidae, Athyinae)																			
Black Scoter (*Melanitta americana*)					0.92 (2.87)	0.08 (0.29)		0.58 (1.38)	1.17 (2.12)	12.75 (20.37)	6.75 (9.44)		0.25 (0.45)						
Common Eider (*Somateria mollissima*)	3.45 (4.78)	1.83 (1.47)	2.50 (2.61)	12.75 (4.49)	2.83 (4.20)	5.58 (7.06)	0.27 (0.90)	1.42 (2.64)	0.75 (1.54)	4.75 (4.31)	2.83 (4.04)	0.33 (0.78)	0.67 (0.49)	13.42 (7.14)	8.08 (5.18)	0.58 (1.00)	2.08 (3.29)	0.58 (0.90)	0.17 (0.58)
Common Goldeneye (*Bucephala clangula*)								0.25 (0.86)											
Harlequin Duck (*Histrionicus histrionicus*)				0.17 (0.39)	0.58 (1.73)														
King Eider (*Somateria spectabilis*)											0.08 (0.29)								
Long-tailed Duck (*Clangula hyemalis*)					0.42 (0.79)	0.17 (0.58)	0.09 (0.30)			7.75 (12.45)	0.08 (0.29)	0.25 (0.87)	0.25 (0.87)						
Scoter unidentified									0.17 (0.58)		0.08 (0.29)								
Surf Scoter (*Melanitta perspicillata*)	0.27 (0.90)				0.42 (1.44)	0.33 (1.15)		0.25 (0.87)	0.25 (0.87)	4.76 (10.48)	7.58 (14.41)		0.75 (1.54)						
White-winged Scoter (*Melanitta fusca*)		0.33 (1.15)			0.25 (0.62)	0.25 (0.62)	0.45 (1.51)	0.67 (0.49)	0.67 (0.65)	0.33 (1.15)	0.42 (1.44)	0.83 (0.39)	0.58 (0.67)						
Dabbling ducks (Anatidae, Anatinae)																			
American Black Duck (*Anas rubripes*)		0.17 (0.58)			1.50 (4.34)	0.58 (1.38)	0.09 (0.30)	1.08 (2.19)	2.92 (3.82)	0.50 (1.17)	0.08 (0.29)	0.17 (0.58)	0.25 (0.87)						
Mallard (*Anas platyrhynchos*)					0.17 (0.58)														
Northern Shoveler (*Anas clypeata*)										0.08 (0.29)									
Geese (Anatidae, Anserinae)																			
Canada Goose (*Branta canadensis*)					0.08 (0.29)			6.25 (11.89)	1.25 (4.33)										

Table 1. *Continued.*

Species	Survey date																		
	1-May-2010	13-May-2010	27-May-2010	12-Jun-2010	23-Oct-2010	13-Nov-2010	22-Nov-2010	16-Mar-2011	31-Mar-2011	15-Apr-2011	30-Apr-2011	2-Dec-2011	13-Dec-2011	21-Jun-2012	4-Jul-2012	18-Jul-2012	2-Aug-2012	15-Aug-2012	29-Aug-2012
Mergansers (Anatidae, Merginae)																			
Common Merganser (*Mergus merganser*)					0.33 (1.15)	0.42 (1.00)							0.67 (1.56)						
Red-breasted Merganser (*Mergus serrator*)	0.09 (0.30)				0.08 (0.29)	1.17 (1.59)	0.09 (0.30)	0.25 (0.45)	0.17 (0.39)	0.25 (0.87)	0.50 (1.17)	0.08 (0.29)	0.33 (0.78)						0.17 (0.58)
Grebes (Podicipediformes)																			
Horned Grebe (*Podiceps auratus*)						0.25 (0.62)	0.09 (0.30)					0.08 (0.29)							
Red-necked Grebe (*Podiceps grisegena*)					0.25 (0.87)	0.08 (0.29)													
Sandpipers, plovers, gulls, auks, and allies (Charadriiformes)																			
Sandpipers and allies (Scolopacidae)																			
Greater Yellowlegs (*Tringa melanoleuca*)																			0.08 (0.29)
Red Phalarope (*Phalaropus fulicarius*)																			0.08 (0.29)
Red-necked Phalarope (*Phalaropus lobatus*)																			2.08 (7.22)
Ruddy Turnstone (*Arenaria interpres*)																	0.08 (0.29)		
Sanderling (*Calidris alba*)																	1.25 (3.19)		
Semipalmated Sandpiper (*Calidris pusilla*)																0.08 (0.29)	0.08 (0.29)		
Spotted Sandpiper (*Actitis macularius*)																	0.17 (0.58)		
Auks, murres, and puffins (Alcidae)																			
Alcid unidentified										0.08 (0.29)									
Atlantic Puffin (*Fratercula arctica*)						0.92 (1.37)	0.09 (0.30)												

TABLE 1. *Continued.*

Species	Survey date																		
	1-May-2010	13-May-2010	27-May-2010	12-Jun-2010	23-Oct-2010	13-Nov-2010	22-Nov-2010	16-Mar-2011	31-Mar-2011	15-Apr-2011	30-Apr-2011	2-Dec-2011	13-Dec-2011	21-Jun-2012	4-Jul-2012	18-Jul-2012	2-Aug-2012	15-Aug-2012	29-Aug-2012
Black Guillemot (*Cepphus grylle*)	3.18 (2.71)	1.08 (2.02)	3.75 (2.18)	2.83 (2.25)	0.08 (0.29)	0.83 (1.27)	0.27 (0.47)	0.25 (0.45)	0.50 (1.24)	2.33 (1.87)	1.83 (1.80)	0.25 (0.62)	0.08 (0.29)	3.42 (3.34)	6.58 (3.00)	2.50 (3.40)	1.92 (3.06)	0.58 (0.79)	
Common Murre (*Uria aalge*)						0.17 (0.58)	0.18 (0.60)				0.58 (1.50)								
Razorbill (*Alca torda*)	0.55 (1.81)					1.92 (3.75)	3.55 (7.05)				0.75 (1.76)	0.08 (0.29)							
Thick-billed Murre (*Uria lomvia*)							0.09 (0.30)				0.08 (0.29)								
Gulls, terns, and skimmers (Laridae)																			
Black-legged Kittiwake (*Rissa tridactyla*)					0.08 (0.29)	3.67 (10.20)	1.00 (2.32)	0.17 (0.39)				0.25 (0.62)	0.17 (0.39)						
Black Tern (*Chlidonias niger*)															0.08 (0.29)				
European Common Gull (*Larus canus*)						0.08 (0.29)													
Great Black-backed Gull (*Larus marinus*)	24.27 (3.17)	22.5 (4.56)	23.42 (5.55)	22.25 (4.90)	3.50 (8.02)	0.17 (0.39)	0.18 (0.40)	17.58 (5.87)	19.83 (8.32)	16.67 (6.85)	20.50 (6.33)	0.83 (2.04)	0.08 (0.29)	18.33 (6.46)	8.42 (3.20)	3.92 (2.31)	0.50 (0.90)	0.33 (0.89)	0.08 (0.29)
Herring Gull (*Larus argentatus*)	10.0 (4.17)	11.17 (6.75)	19.58 (7.01)	22.67 (8.52)	2.00 (1.21)	5.17 (6.56)	6.00 (6.00)	2.00 (1.76)	3.75 (4.02)	2.17 (1.27)	6.25 (2.77)	2.33 (3.05)	0.67 (1.07)	32.17 (13.13)	7.50 (2.15)	7.25 (3.28)	4.42 (3.40)	5.00 (4.49)	5.17 (5.44)
Iceland Gull (*Larus glaucoides*)		0.08 (0.29)	0.08 (0.29)										0.08 (0.29)						
Laughing Gull (*Leucophaeus atricilla*)				0.08 (0.29)															
Lesser Black-backed Gull (*Larus fuscus*)		0.08 (0.29)	0.08 (0.29)		0.08 (0.29)				0.08 (0.29)										
Ring-billed Gull (*Larus delawarensis*)					1.58 (1.50)	2.08 (3.15)	1.09 (1.70)		0.92 (2.02)	0.08 (0.29)		0.42 (0.67)	0.33 (0.89)	0.58 (1.73)			0.75 (1.05)	7.67 (10.97)	1.17 (1.75)
Loons (Gaviiformes)																			
Common Loon (*Gavia immer*)	0.45 (0.68)		1.08 (1.68)	0.25 (0.62)	0.42 (0.67)	0.58 (0.90)	0.09 (0.30)		0.17 (0.39)		0.42 (0.67)	0.25 (0.45)	0.42 (0.51)	0.25 (0.62)	0.25 (0.62)	0.25 (0.45)	1.58 (2.81)	0.58 (0.90)	0.08 (0.28)
Pacific Loon (*Gavia pacifica*)	0.27 (0.47)		0.08 (0.29)	0.08 (0.29)		0.17 (0.58)			0.08 (0.29)				0.08 (0.29)		0.17 (0.58)		0.58 (1.00)		

TABLE 1. *Continued.*

Species	Survey date																		
	1-May-2010	13-May-2010	27-May-2010	12-Jun-2010	23-Oct-2010	13-Nov-2010	22-Nov-2010	16-Mar-2011	31-Mar-2011	15-Apr-2011	30-Apr-2011	2-Dec-2011	13-Dec-2011	21-Jun-2012	4-Jul-2012	18-Jul-2012	2-Aug-2012	15-Aug-2012	29-Aug-2012
Red-throated Loon (*Gavia stellata*)	2.27 (3.66)	0.25 (0.87)	2.83 (1.64)	0.17 (0.39)	0.58 (1.16)	31.67 (39.66)	6.82 (6.53)		0.42 (0.67)	3.42 (6.39)	7.42 (6.61)	2.33 (2.31)	0.83 (2.59)	0.33 (0.65)	3.33 (6.20)		0.17 (0.39)		0.08 (0.29)
Petrels, shearwaters, albatrosses, and diving petrels (Procellariformes)																			
Shearwaters and petrels (Procellariidae)																			
Cory's Shearwater (*Calonectris diomedea*)																			0.08 (0.28)
Great Shearwater (*Ardenna gravis*)														0.25 (0.87)			0.08 (0.29)		0.75 (1.54)
Sooty Shearwater (*Ardenna grisea*)																			0.83 (2.89)
Frigatebirds, boobies, and cormorants (Suliformes)																			
Boobies and Gannets (Sulidae)																			
Northern Gannet (*Morus bassanus*)		2.17 (3.64)	0.83 (1.80)	3.08 (3.75)		0.17 (0.38)				0.50 (0.90)	1.75 (2.67)			0.08 (0.29)	0.08 (0.29)	2.42 (8.06)	0.42 (0.90)	0.17 (0.39)	
Cormorants and shags (Phalacrocoracidae)																			
Double-crested Cormorant (*Phalacrocorax auratus*)	1.45 (1.92)	0.33 (0.49)	1.92 (2.27)	4.50 (2.15)	0.33 (0.49)	0.58 (0.90)				0.42 (1.44)	24.17 (3.38)			0.83 (1.27)	1.92 (1.38)	0.58 (0.51)	1.58 (2.91)	1.00 (0.74)	0.33 (1.15)
Great Cormorant (*Phalacrocorax carbo*)	1.00 (0.63)	0.08 (0.29)	0.58 (0.51)	1.08 (0.67)	0.08 (0.29)	0.17 (0.39)			0.17 (0.58)	1.17 (2.33)	0.75 (1.21)	0.08 (0.29)		0.08 (0.29)	0.08 (0.29)	0.42 (0.51)			0.67 (1.15)
Number of periods	11	12	12	12	12	12	11	12	12	12	12	12	12	12	12	12	12	12	12
Combined counts / 30 min	47.3 (9.7)	40.1 (11.3)	56.8 (11.8)	69.8 (16.0)	16.6 (12.3)	57.3 (43.6)	20.5 (10.8)	30.8 (13.8)	33.3 (15.5)	57.8 (34.9)	82.9 (23.0)	8.6 (4.0)	6.5 (4.4)	69.8 (16.0)	37.3 (9.4)	18.0 (12.1)	15.7 (10.3)	16.2 (13.2)	11.8 (12.2)
Number of species	12	12	12	9	23	25	17	12	16	16	19	15	17	9	11	8	14	8	14

Highest combined counts (average per 30 min) of all birds at the site occurred in April to mid-June and mid-November 2010 reflecting regional migration patterns, while the lowest numbers were seen in early winter (December 2011) and late summer (mid-July to late August 2012; Table 1, Figure 3). As a group, resident species (those that breed in and around the Bay of Fundy) accounted for most sightings year-round (Figure 3). However, during spring and fall, migrants (that occur seasonally but do not typically breed), particularly sea ducks (scoters and Long-tailed Duck [*Clangula hyemalis*]) and Red-throated Loon passed through (Table 1, Figures 4 and 5). As well, in late summer to fall, Ring-billed Gull (*Larus delawarensis*) moved into the area in moderate numbers (Table 1, Figure 6). Peak numbers of Black Scoter (*Melanitta americana*) and Surf Scoter (*Melanitta perspicillata*) and smaller numbers of White-winged Scoter (*Melanitta fusca*) were recorded in two mid-to-late April 2011 surveys, and a smaller late-fall, early-winter peak was also observed (Table 1, Figure 4). Great Black-backed Gull and Herring Gull were usually most numerous, but Double-crested Cormorant, Red-throated Loon, and Black Scoter were as or more abundant during migration. Peak counts of Herring Gull and Great Black-backed Gull were observed from early May to mid-to-late June 2010 (Table 1, Figure 6), with Great Black-backed Gull dominating in early spring and Herring Gull at other times of year (Table 1, Figure 6).

Common Eider and American Black Duck (*Anas rubripes*), which both breed in the Bay of Fundy, were seen in late winter to early spring (mid-December and mid-to-late March 2011), occasionally with migrating White-winged Scoter, Surf Scoter, Black Scoter, and Red-breasted Merganser (*Mergus serrator*; Table 1, Figures 4 and 7). Counts of both cormorant species peaked in April to mid-June 2010 and were low in late summer and early fall (Table 1, Figure 8). Migrant sea ducks predominated in mid-to-late April 2011, mainly Black Scoter, Surf Scoter, and Long-tailed Duck, but including Common Eider, White-winged Scoter, and Red-throated Loon (Table 1, Figures 4 and 5), and Double-crested Cormorant made up a third of counts (29%) in late April 2011 (Table 1, Figure 8). Combined counts (average per 30 min) remained relatively high in late spring to mid-June, mostly due to Herring Gull and Great Black-backed Gull (Table 1, Figure 6), with other resident species including Common Eider, Black Guillemot, Double-crested Cormorant, and Great Cormorant contributing (Table 1, Figures 4, 8, and 9). Black Guillemot was common and seasonally abundant, occurring in 18 surveys (94.7%) from mid-March to December, with largest counts from May to late July, reflecting nesting observed on Black Rock and post-breeding aggregation (Table 1, Figure 9). Common Eider occurred in most surveys (18 surveys, 94.7%; Table 1), with peak abundance in early summer coincident with breeding and post-breeding occupation and a smaller peak in fall presumed to include both resident and migrant birds (Table 1, Figure 4). Red-throated Loon was an occasionally abundant and frequent visitor (16 of 19 surveys, 84.2%; Table 1). High numbers passed through the site during spring migration (mid-April to early May) and in late fall (mid-to-late November; Table 1, Figure 5).

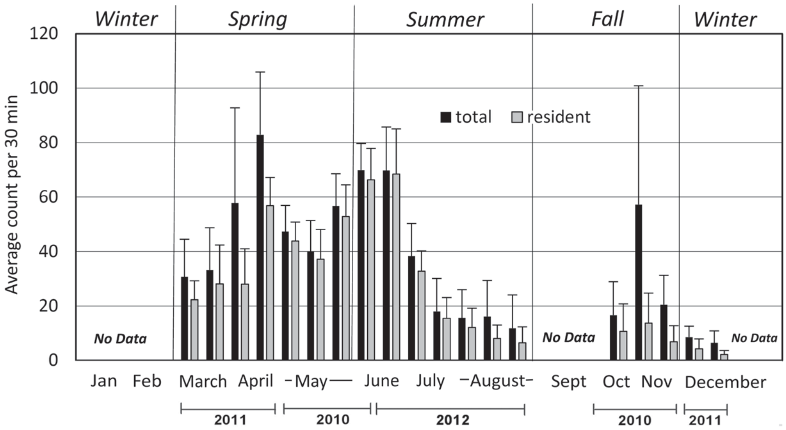

FIGURE 3. Annual cycle of abundance of waterbirds determined from surveys conducted in Minas Passage, Nova Scotia, presented as average counts (+ SD) per 30 min. Year in which each survey was conducted is presented at the bottom of the figure. Supporting abundance data are presented in Table 1. Resident species = Great Black-backed Gull (*Larus marinus)*, Herring Gull (*Larus argentatus*), Double-crested Cormorant (*Phalacrocorax auritus*), Great Cormorant (*Phalacrocorax carbo*), Black Guillemot (*Cepphus grylle*), Common Eider (*Somateria mollissima*), Common Loon (*Gavia immer*), and American Black Duck (*Anas rubripes*).

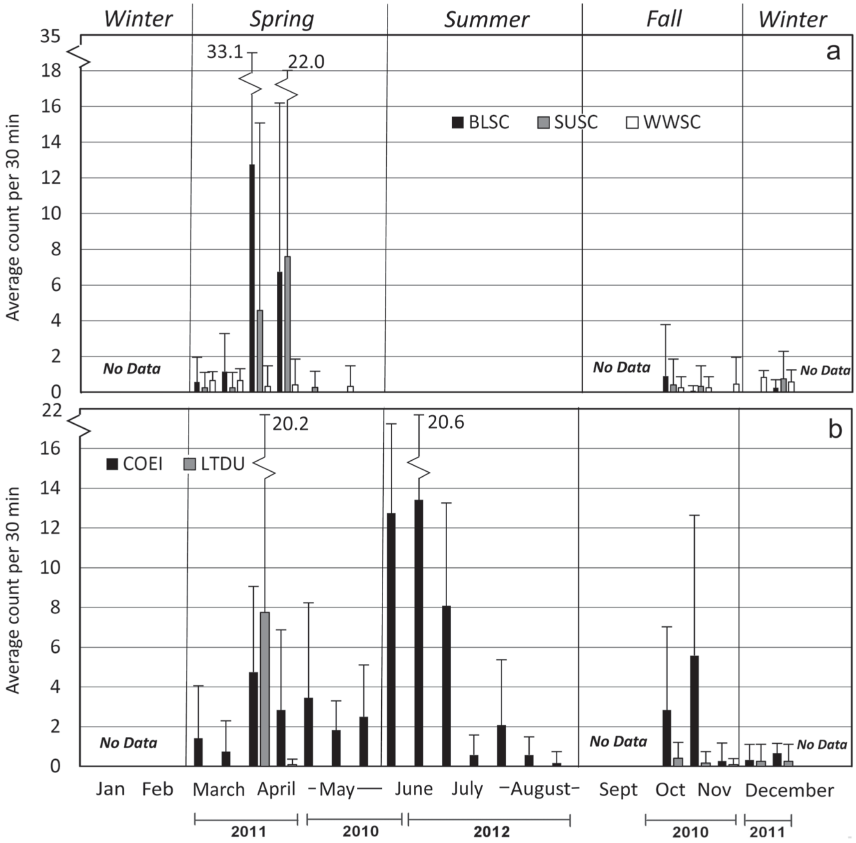

FIGURE 4. Annual cycle of abundance of predominant sea ducks determined from surveys conducted in Minas Passage, Nova Scotia, presented as average counts (+ SD) per 30 min. Year in which each survey was conducted is presented at the bottom of the figure. Supporting abundance data are presented in Table 1. Illustrated are: a. Black Scoter (*Melanitta americana*, BLSC), Surf Scoter (*Melanitta perspicillata*, SUSC), and White-winged Scoter (*Melanitta fusca*, WWSC); and b. Common Eider (*Somateria mollissima*, COEI) and Long-tailed Duck (*Clangula hyemalis*, LTDU).

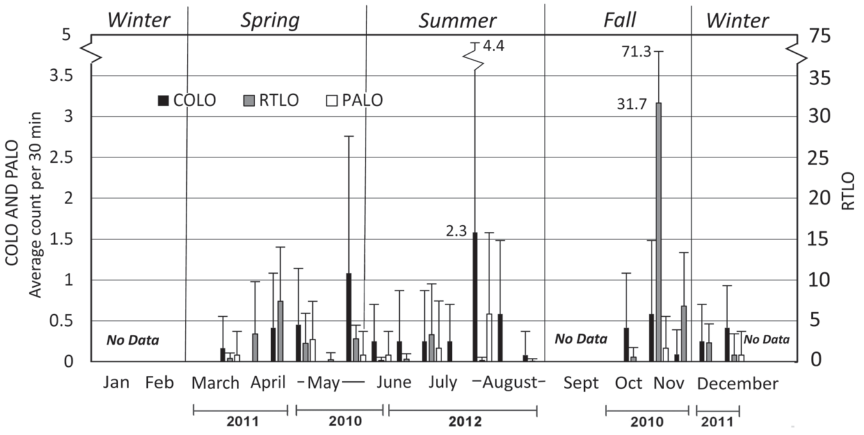

FIGURE 5. Annual cycle of abundance of loons determined from surveys conducted in Minas Passage, Nova Scotia, presented as average counts (+ SD) per 30 min. Year in which each survey was conducted is presented at the bottom of the figure. Supporting abundance data are presented in Table 1. Illustrated are Common Loon (*Gavia immer*, COLO), Red-throated Loon (*Gavia stellata*, RTLO), and Pacific Loon (*Gavia pacifica*, PALO).

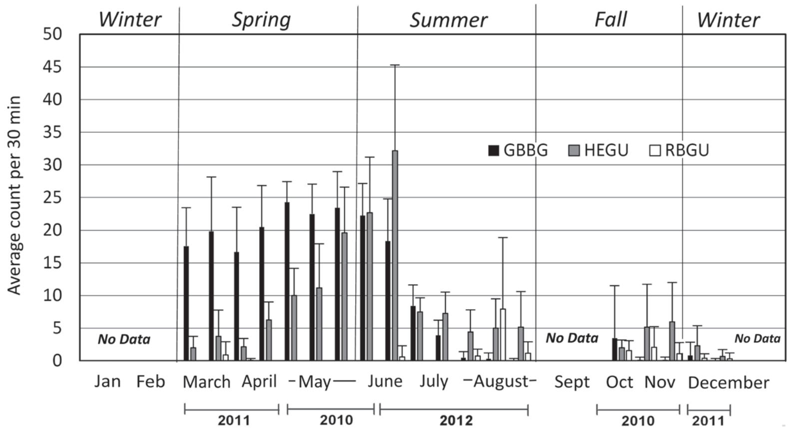

FIGURE 6. Annual cycle of abundance of predominant gulls determined from surveys conducted in Minas Passage, Nova Scotia, presented as average counts (+ SD) per 30 min. Year in which each survey was conducted is presented at the bottom of the figure. Supporting abundance data are presented in Table 1. Illustrated are Great Black-backed Gull (*Larus marinus*, GBBG), Herring Gull (*Larus argentatus*, HEGU), and Ring-billed Gull (*Larus delawarensis*, RBGU).

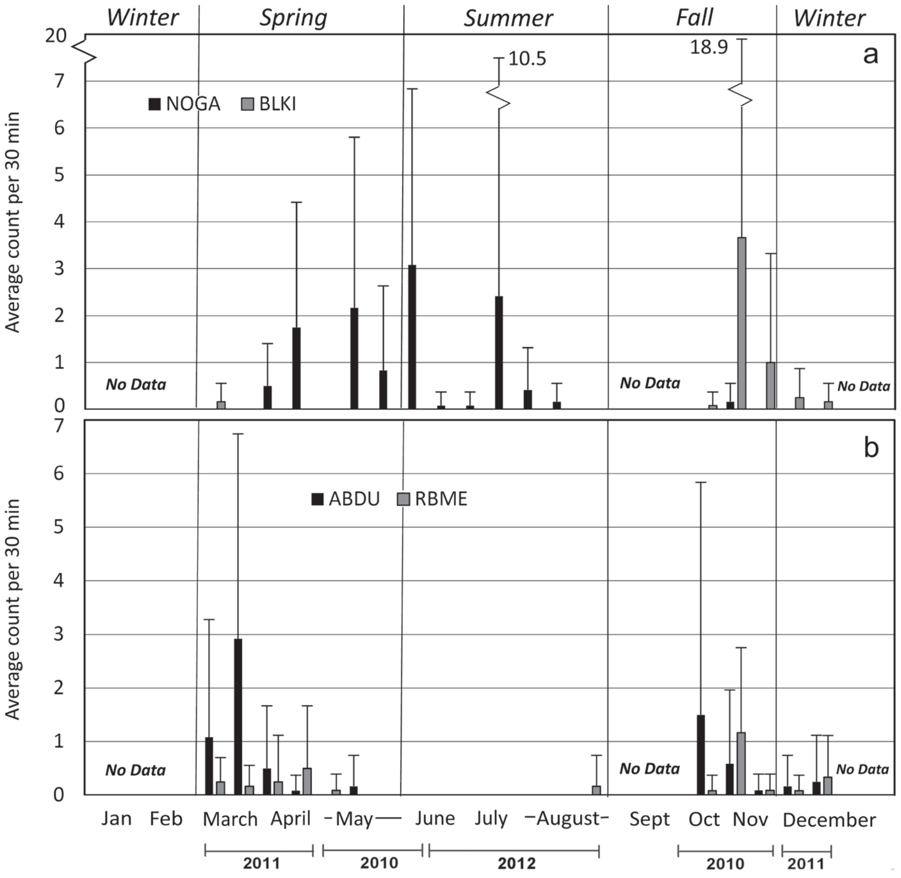

FIGURE 7. Annual cycle of abundance of: a. Northern Gannet (*Morus bassanus*, NOGA) and Black-legged Kittiwake (*Rissa tridactyla*, BLKI); and b. American Black Duck (*Anas rubripes*, ABDU) and Red-breasted Merganser (*Mergus serrator*, RBME) in Minas Passage, Nova Scotia, presented as average counts (+ SD) per 30 min. Year in which each survey was conducted is presented at the bottom of the figure. Supporting abundance data are presented in Table 1.

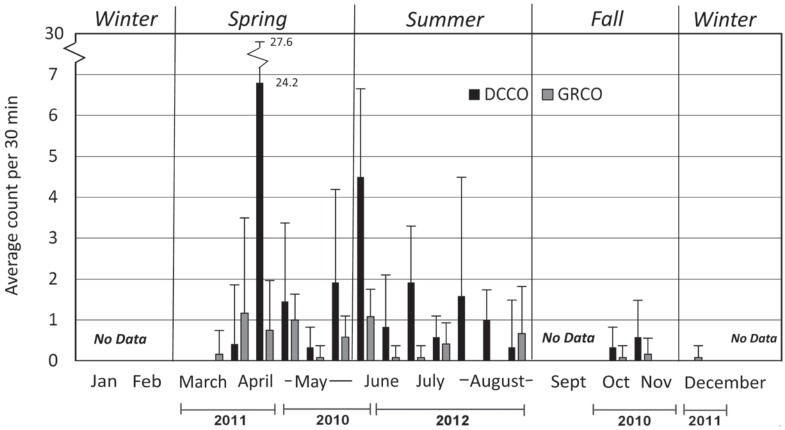

Figure 8. Annual cycle of abundance of cormorants determined from surveys in Minas Passage, Nova Scotia, presented as average counts (+ SD) per 30 min. Year in which each survey was conducted is presented at the bottom of the figure. Supporting abundance data are presented in Table 1. Illustrated are Double-crested Cormorant (*Phalacrocorax auritus*, DCCO) and Great Cormorant (*Phalacrocorax carbo*, GRCO).

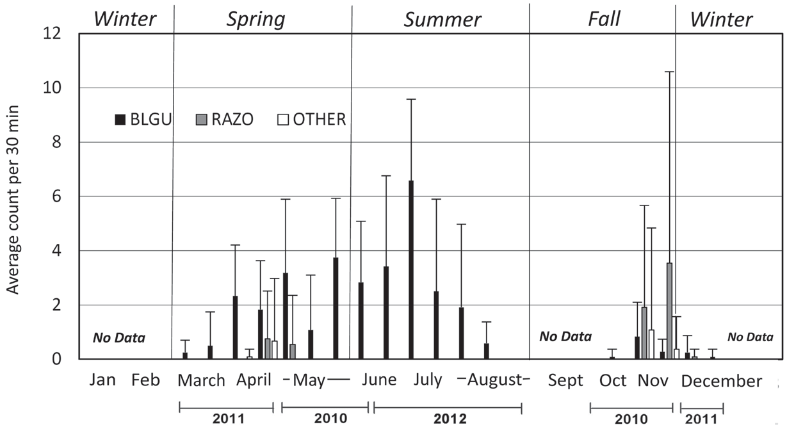

Figure 9. Annual cycle of abundance of alcids determined from surveys in Minas Passage, Nova Scotia, presented as average counts (+ SD) per 30 min. Year in which each survey was conducted is presented at the bottom of the figure. Supporting abundance data are presented in Table 1. Illustrated are Black Guillemot (*Cepphus grylle*, BLGU), Razorbill (*Alca torda*, RAZO), and OTHER (Common Murre [*Uria aalge*], Thick-billed Murre [*Uria lomvia*], and Atlantic Puffin [*Fratercula arctica*]).

Common Loon occurred in low numbers on most surveys (16 of 19, 84.2%), and Pacific Loon (*Gavia pacifica*) was seen in eight surveys (42%; Table 1, Figure 5). Northern Gannet (*Morus bassanus*) occurred occasionally (11 surveys, 57.9%), chiefly from late April to mid-July (Table 1, Figure 7).

Combined counts (average per 30 min) were low from mid-June to late August (Figure 3), mainly due to the same resident species as in early summer, but both Black Guillemot and Great Black-backed Gull showed reduced numbers in mid-to-late August 2012 (Table 1, Figures 6 and 9), and Ring-billed Gull moved into the area in mid-August (Figure 6). Several species of shorebirds in August 2012 also contributed to combined counts at that time (Table 1). North-south migrants appeared in late-fall to early-winter surveys in 2010 with a peak in late November, mainly Red-throated Loon but including Red-breasted Merganser, Common Merganser (*Mergus merganser*), and Common Eider (Table 1, Figures 4, 5, and 7). Red-breasted Merganser occurred commonly in low numbers (11 surveys, 57.9% of surveys), and was most abundant in early-spring and late-fall to early-winter surveys in 2011 and 2010, respectively (Table 1, Figure 7). Common Merganser occurred only occasionally in late fall to early winter (five surveys; Table 1). Low, early-December numbers included Common Eider and Red-throated Loon (Table 1, Figures 4 and 5).

Miscellaneous seabirds, shorebirds and waterfowl

Various other species occurred in smaller numbers or were infrequently recorded at the site. Alcids are an important group occurring in the Bay of Fundy, and apart from Common Guillemot, which was the predominant alcid species at the site, Common Murre (*Uria aalge*), Razorbill (*Alca torda*), Thick-billed Murre (*Uria lomvia*), and Atlantic Puffin (*Fratercula arctica*) occurred occasionally, mainly in spring (late April and early May) and late fall to early winter (Table 1). Razorbill occurred both in spring 2010–2011 and mid-to-late November 2010 (Table 1, Figure 9), while Atlantic Puffin were seen only in mid-to-late November 2010 (Table 1).

Among less common and abundant gulls, Black-legged Kittiwake (*Rissa tridactyla*) was seen at the site from late October to early March (Table 1), mostly as singles but two flocks of nine and 35 individuals were observed on 13 November 2010. Iceland Gull (*Larus glaucoides*), Lesser Black-backed Gull (*Larus fuscus*; seen on four surveys at different times of year), Laughing Gull (*Leucophaeus atricilla*), and European Common Gull or Mew Gull (*Larus canus*; Table 1) also visited the site. A single Black Tern (*Chlidonias niger*) was seen on 4 July 2012 (Table 1).

Three oceanic shearwaters (Cory's Shearwater [*Calonectris diomedea*], Great Shearwater [*Ardenna gravis*], and Sooty Shearwater [*Ardenna grisea*]) were seen at the site in August 2012. These included a single Great Shearwater on 2 August 2012, and all three species on 29 August 2012, which included a single Cory's Shearwater, several singles and a group of four Great Shearwater, and a group of 10 Sooty Shearwater, all seen in one 30 min mid-afternoon observation period (Table 1).

Shorebirds were seen at the site only during surveys in August 2012, including a flock of Ruddy Turnstone (*Arenaria interpres*; 2 August) and a flock of Red-necked Phalarope (*Phalaropus lobatus*; August 29), and individual sightings of Red Phalarope (*Phalaropus fulicarius*), Sanderling (*Calidris alba*), Semipalmated Sandpiper (*Calidris pusilla*), Spotted Sandpiper (*Actitis macularius*), and Greater Yellowlegs (*Tringa melanoleuca*; Table 1).

Waterfowl species occurring occasionally included Northern Shoveler (*Anas clypeata*) and Canada Goose (*Branta canadensis*) in early spring, Common Goldeneye (*Bucephala clangula*; early spring), Mallard (*Anas platyrhynchos*; fall), Horned Grebe (*Podiceps auritus*), and Red-necked Grebe (*Podiceps grisegena*) in late fall to early winter (Table 1). Individual Harlequin Duck (*Histrionicus histrionicus*) were recorded in mid-June and late October 2010 (Table 1). A single King Eider (*Somateria spectabilis*), a rare species in the Bay of Fundy, was seen on 30 April 2011.

Diversity

Spring and fall migration each contributed a large fraction of the 46 species recorded at the site, with 16 to 19 species per 6 h survey in spring (late March to April) and 23 to 25 species (over half of the total) in late fall (late October to early November; Table 1, Figure 10). Fewer species occurred in summer (June to late August; eight to 14) and in early winter (15 to 17; Table 1, Figure 10). Differences among seasons overall were statistically significant (Kruskal Wallace [KW] one-way analysis of variance [ANOVA], P = 0.004), however the number of species in the spring (mid-March to late May, n = 7; which included the

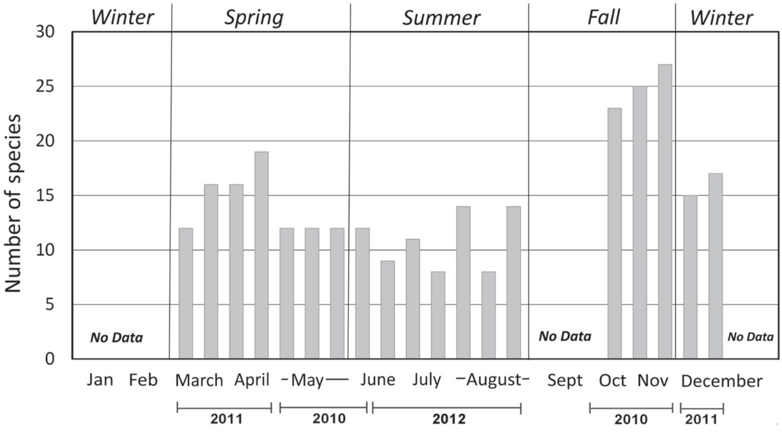

FIGURE 10. Annual cycle of species diversity in the waterbird community (total number of species per 6 h) determined from surveys conducted in Minas Passage, Nova Scotia. Year in which each survey was conducted is presented at the bottom of the figure. Supporting data are presented in Table 1.

spring migration) was not significantly different from the number of species in the summer (June to late August, *n* = 7; KW one-way ANOVA, *P* = 0.057). The number of species observed in late fall to winter (late October to mid-December, *n* = 5) was significantly greater than the numbers observed in both summer and spring (KW one-way ANOVA, *P* = 0.004 and *P* = 0.025, respectively).

Discussion

Role in migration

Minas Passage is an important although comparatively unstudied habitat and migratory route for waterbirds in the inner Bay of Fundy system, which includes Chignecto Bay and Minas Basin. Our study has shown that species and seasonal cycles of waterbirds in Minas Passage reflect patterns generally known for the inner Bay of Fundy and for the northeast Atlantic coast of North America as a whole (e.g., Tufts 1986; Hicklin and Smith 1984a; Mills and Laviolette 2011). Occurrences of large numbers of migratory species in Minas Passage in spring and relatively large numbers in fall demonstrate that the system comprised of Minas Passage, Minas Channel, and Minas Basin forms an important part of the migration pathway for seabirds and waterbirds along the East Coast of North America.

Prominent spring migrants in Minas Passage included sea ducks (Black Scoter, Surf Scoter, White-winged Scoter, and Long-tailed Duck), and Red-throated Loon. The latter was also relatively abundant in our study area in fall, in parallel with peak fall movements of the species in the outer Bay of Fundy (Dietz and Chiasson 2000). Occurrence of peaks in scoter abundance in spring at the study site shows that some scoters from the major March to May northward scoter migration through the Bay of Fundy (Bond *et al*. 2007) and seen in large numbers moving along the north side of the outer Bay of Fundy in spring (Dietz and Chiasson 2000; Bond *et al*. 2007, 2009; MacKinnon and Kennedy 2011; Cameron 2014), pass through Minas Channel and Minas Passage. Bond *et al.* (2007) inferred that some northward-migrating scoters may move along the south side of the Bay of Fundy (which includes our study area), and scoters are commonly seen in spring in outer Minas Channel areas such as Black Rock and Scot's Bay, Kings County, and spring and fall movements of scoters at the FORCE site have subsequently been observed in tidal monitoring surveys in 2017 to 2019 (P.L.S. pers. obs.).

Occurrences of all scoter species, although in lower numbers, at the site in fall suggest that some scoters pass through Minas Passage during the southward migration as well. Fall observation timing in our study coincides with scoter movement for Northumberland Strait (Hicklin and Bunker-Popma 2001) where peak movements in the vicinity of Cape Jourimain, New Brunswick, were observed from mid-October to mid-November.

Common Eider, another migrant through the Bay of Fundy, occurred in spring (i.e., April to May), a time when a strong spring movement typically occurs along the north side of the inner Bay of Fundy (Cameron 2014), and through nearby Chignecto Bay and Tantramar Marsh during April to May (Erskine and Smith 1986; MacKinnon and Kennedy 2011). A similar movement would be indistinguishable in our data from the arrival of locally-breeding birds. Common Eider observed in mid-March are probably local breeders. The species has previously been reported to arrive in Minas Basin in March (Erskine and Smith 1986) and nests in the area (Allard *et al.* 2014). Occurrence of Common Eider in small numbers at the site in two fall surveys (late October and mid-November 2010; Table 1, Figure 4) coincides with the early-October to mid-December southward migration of Common Eider through the northern Bay of Fundy (Erskine and Smith 1986; MacKinnon and Kennedy 2011; Goudie *et al*. 2020). Common Eider have been known to reach Minas Basin during their southerly fall migration (Erskine and Smith 1986), but it does not appear to be a main route, and the birds observed in Minas Passage are likely local breeders moving out of the area.

Occurrences of Long-tailed Duck in some early-spring and late-fall to early-winter surveys coincided with the species' March to early-April northerly East Coast migration (Robertson and Savard 2020). Timing of occurrences of Red-breasted Merganser and Common Merganser reflects typical migration patterns (e.g., Craik *et al*. 2020).

Migration brings a higher species diversity as migrants co-occur briefly with resident species. The highest species diversity in our study was observed during spring and fall migration when waterbirds of various kinds were moving to coastal areas or migrating through. These numbers (16 to 19 and 23 to 25 species in spring and fall surveys, respectively) are comparable to lists from shore-based point surveys conducted during migration periods in 1997 at Cape Jourimain, New Brunswick, on Northumberland Strait, Gulf of St. Lawrence, where 20 and 26 species of waterbirds were observed in spring and fall, respectively (Hicklin and Bunker-Popma 2001). Although both studies showed a similar cross-section of migrating species, they differed in levels of effort (49.8 and 156.0 h in spring and fall respectively, versus 17.5 h in our study) over roughly the same periods in both spring and fall.

Use of the study area by migrating waterbirds may reflect the geography of the Minas Channel-Minas Passage system, causing it to act as geographic trap for birds (see Figure 1). This is similar to the Bay of Fundy as a whole that is a funnel for northerly spring migratory movements of waterbirds and landbirds (Dietz and Chiasson 2000; Mills and Laviolette 2011; Cameron 2014). The tidal current regime in Minas Passage also represents a unique aspect of the site that could draw birds resting on the water into the area, as the tidal excursion, which can be upwards of 20 km, can potentially transport birds on the water significant distances both into and out of the area.

Waterbird community

Relationship to other areas—This study provides a representative list of species for almost the entire year; we did not survey in early fall (September and early October) and mid-to-late winter. Sampling in December and mid-March captured occurrences of many species typically seen in winter, such as most alcids (with the exception of Dovekie [*Alle alle*]) and some waterfowl including Harlequin Duck which overwinter in the Bay of Fundy (Dietz and Chiasson 2000). The 46 species recorded represent about a third of waterbirds likely to occur in the Bay of Fundy, based on 154 species of waterbirds in the list for Brier Island (Mills and Laviolette 2011). Moderate diversity compared with the outer Bay of Fundy is consistent with the opinion of Hicklin and Smith (1984a) who suggested that diversity and abundance in mid-portions of the Bay of Fundy are likely to be lower than Minas Basin mudflats and marshes, and the outer Bay of Fundy upwelling areas between Brier Island and Grand Manan.

Gulls—Presence of Herring Gull and Great Black-backed Gull year-round and timing of peak counts was coincident with the breeding period in the area (e.g., MacKinnon and Kennedy 2014). Both species sometimes nest on Black Rock, and lower numbers in late summer and fall suggest a movement by both species away from nesting sites post-breeding to other offshore and more southerly areas as is typical for the area (Wong *et al.* 2018; Good 2020; Weseloh *et al.* 2020). Ring-billed Gull sightings through August 2012 and in late-fall and early-winter surveys in 2010 to 2011 are consistent with southerly and easterly post-breeding movements from eastern Canadian and inland colonies (Lock 1988; Cotter *et al.* 2012; Pollet *et al.* 2020). Occurrences of Black-legged Kittiwake reflect the species' winter nearshore distribution in northeastern North America (Cotter *et al.* 2012; Hatch *et al.* 2020a), but the gap in our surveys in September and early October may have missed fall post-breeding occurrences of outer Bay of Fundy breeders observed in the Gulf of Maine (Wong *et al.* 2018). Of the occasional uncommon gulls observed (Table 1), Iceland Gull is an Arctic breeder and sightings on the Atlantic coast reflect southerly movements in winter (Snell *et al.* 2020), Laughing Gull breeds on the east coast from the Gulf of Maine southward and wanders post-breeding before moving south in winter (Burger 2020), and European Common Gull has a widespread distribution in the North Atlantic, occurring as a casual winter visitor along the Atlantic seaboard (Moskoff and Bevier 2020). Occurrences of Lesser Black-backed Gull (seen on four surveys at different times of year) reflect the widespread distribution of this European species along the east coast of North America.

Cormorants—Occurrences of Double-crested Cormorant and Great Cormorant reflected pre-breeding aggregation and occurrence during the normal breeding periods of both species in the area (Lock and Ross 1973; Dorr *et al.* 2020; Hatch *et al.* 2020b). Low counts in late summer and early fall show movement out of the area and typically southward post-breeding, with numbers in March representing early arrivals as is typical (Dorr *et al.* 2020; Hatch *et al.* 2020b). Nearest colonies in Minas Passage are at Cape Split and Spencer's Island and in Minas Basin in the Five Islands area (Milton and Austen-Smith 1983; Allard *et al.* 2014).

Loons—Sightings of Common Loon were consistent with typical patterns of occurrence in the Bay of Fundy and other coastal waters of Atlantic Canada throughout the year both for overwintering and summer occupation by non-breeders (Clay and Clay 1997; Paruk *et al.* 2021). Pacific Loon, considered rare (Russell 2020), had only occasionally been reported in the Bay of Fundy previously (e.g., Mills and Laviolette 2011). Our sightings and recent (2019) sightings off southwest Nova Scotia (eBird 2019) show potential for movement through the area and perhaps indicate an increasing use of the area by this species. F.L.L. had previous experience with the species on its breeding range and mis-identification is unlikely. The spring migration peak of Red-throated Loon observed corresponds to the timing of the early-May peak movement for the species observed along the New Brunswick coast in the outer Bay of Fundy (Clay and Clay 1997; Maybank 1997; Dietz and Chiasson 2000; Rizzolo *et al.* 2020), where Red-throated Loon is the most abundant loon in the vicinity of Saint John, New Brunswick, from March to May (Dietz and Chiasson 2000). The fall peak aligns with the early-November fall migration peak observed along the northeast coast of the USA (Barr *et al.* 2000).

Alcids—Presence throughout the year and seasonal abundance of Black Guillemot was consistent with the known local nesting period in the area (e.g., May to late June in the outer Bay of Fundy to Maine; Butler *et al.* 2020) and nesting activity observed on Black Rock during the study. Occurrences of Common Murre, Razorbill, Thick-billed Murre, and Atlantic Puffin are consistent with use of waters in the area by overwintering birds from east coast colonies and winter coastal aggregations in the Outer Bay of Fundy (e.g., Huettmann *et al.* 2005; Wong *et al.* 2018), and east coast winter distributions from October to April (Ainley *et al.* 2020; Gaston and Hipfner 2020; Lowther *et al*. 2020). Occasional sightings of Common and Thick-billed Murre (Table 1) reflect winter dispersal from northern colonies (Wong *et al.* 2018; Ainley *et al.* 2020; Gaston and Hipfner 2020). Lack of surveys in late winter (late December to early March) in our study, a period when many alcids overwintering in the Bay of Fundy may be present, is a data-gap in estimating the potential occurrence of those species in the area.

Miscellaneous seabirds—Occurrence of Northern Gannet at the site is consistent with the species' use of the Bay of Fundy in summer (Huettmann and Diamond 2011; Mills and Laviolette 2011; Mowbray 2020) and seasonal movements through the area to and from colonies in the Gulf of St. Lawrence and Newfoundland. However, occurrence of fall southerly movements in the lower Bay of Fundy as noted by Wong *et al.* (2018) could not be determined due to the September to early October gap in coverage in our survey. Great Shearwater and Sooty Shearwater, seen in August 2012, are often seen in the outer Bay of Fundy and Gulf of Maine during their summer feeding movements in the northwest Atlantic from breeding sites in the southern hemisphere. They leave the Bay of Fundy and Gulf of Maine from early September to October–November (Huettmann 2000; Pittman and Huettmann 2006; Wong *et al.* 2018), and all three species have been recorded at Brier Island (Mills and Laviolette 2011). The occurrence of Northern Gannet, Cory's Shearwater, Great Shearwater, and Sooty Shearwater in our area reflects the close connection of the study site with the outer Bay of Fundy and Gulf of Maine, where these species occur in summer (Pittman and Huettmann 2006). The single Black Tern sighting in early July is consistent with the species' typical occurrence as a rare migrant to Atlantic Canada (Mills and Laviolette 2011; Heath *et al.* 2020).

Shorebirds and miscellaneous waterfowl—All species of shorebirds that occurred, including Ruddy Turnstone, Red-necked Phalarope, Red Phalarope, Sanderling, Semipalmated Sandpiper, Spotted Sandpiper, and Greater Yellowlegs, were expected based on known late summer southerly migration through the Bay of Fundy at this time of year (Hicklin and Smith 1984a; Hicklin 1987). American Black Duck is a regular winter coastal resident in the Bay of Fundy (Hicklin and Smith 1984a; Allard *et al*. 2014). Other species of waterfowl occurring occasionally including Northern Shoveler, Canada Goose, Common Goldeneye, and Mallard. Horned Grebe and Red-necked Grebe are expected based on their previous occurrence in the area (e.g., Mills and Laviolette 2011). Individual sightings of Harlequin Duck are consistent with the species' overwintering distribution along the east coast including in the Bay of Fundy (Dietz and Chiasson 2000; Robertson and Goudie 2020).

Study limitations

The 19 surveys in our study are insufficient to capture all the nuances of seabird seasonal and migratory cycles, which are highly variable in space and time. However, they represent a substantial source of information to profile the waterbird community (species composition and relative abundance) over the three years of our study. In particular, with reference to tidal energy development, the information has been used to assess potential impacts and to develop monitoring strategies for seabirds as well as other organisms (e.g., marine mammals and fish) in relation to tidal device installations. The study was completed over three years, with potential year-to-year variability superimposed on seasonal patterns. The sampling frequency (minimum of two to three weeks separation between surveys) could allow major brief movements of birds to be missed. For example, the expected late-summer, early-fall migration of shorebirds through Chignecto Bay and Minas Basin (Hicklin 1987) was only slightly mirrored in our observations.

This survey interval was effective for other species (e.g., scoters, Red-throated Loon), which were detected in consecutive surveys. Counts obtained in this study give a measure of relative abundance that is comparable between surveys, but which likely underestimates total numbers of birds, particularly when many birds are present, or when they occur too far in the distance. Bird behaviour, such as resting on Black Rock for long periods during the day seen in gulls, cormorants, and Common Eider, can inflate average counts relative to those of more mobile species such as migrating scoters that typically move quickly through the site.

Time of day selected for the surveys, which was mainly from mid-day to late afternoon, may also affect abundances observed. Some birds migrate mainly at other times of day (e.g., Black Scoters typically move in the early morning; Cameron 2014), and some species move at night. Birds on Black Rock were incompletely censused, as the far side of the island was not visible from shore but likely supported some birds. All observations were made on the ebbing tide; while the tide affects flying birds only to a limited degree, birds remaining on the water on an outgoing tide also move past the site. Future studies at the site should address these issues if possible.

Author Contributions

Project Administration: P.L.S.; Investigation & Field Observations: F.L.L. and P.L.S.; Data Compilation & Analysis: H.A.L. and P.L.S.; Formal Analysis: P.L.S.; Writing – Original Draft: P.L.S.; Writing – Review & Editing: P.L.S., F.L.L., and H.A.L.

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An overview of experimental Gray Wolf (*Canis lupus*) poisoning programs in northern Ontario, 1956 to 1964

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Abstract

In the late 1950s, the Ontario Department of Lands and Forests commenced an experimental Gray Wolf (*Canis lupus*) poisoning program in northern Ontario, the results of which were documented in a series of unpublished reports. Most projects consisted of distributing baits poisoned with strychnine on frozen lakes in late winter; 12 were conducted by district staff and typically consisted of <10 bait stations monitored for two to four months. An intensive three-year program was completed in the Allanwater area, about 250 km north of Thunder Bay, where up to 56 bait stations were distributed on a grid covering >25 000 km^2. Thirty eight wolf kills were reported in the district projects and 81 in the Allanwater study. In total, where sex was identified 56% were male and 44% female. Adults made up 51% of the kill in the Allanwater study, subadults (<2 years old) 44%, and 5% were of unknown age. Two hundred and sixty five kills of species other than wolves were documented from all studies, comprising 10 mammal and nine bird species. Common Raven (*Corvus corax*) and Red Fox (*Vulpes vulpes*) made up 54% and 24% of the non-target mortality, respectively, and were recorded in most studies. Kills of wolves and non-target species were probably under-reported because animals left bait stations before dying, were buried by snow, were removed by bounty hunters, or monitoring for non-target species was poor. Although completed over 50 years ago, the studies summarized here provide context on the ecological impacts and ethics of poison use to control wolves.

Key words: Predator control; poison; strychnine; Ontario; non-target mortality; Gray Wolf; Common Raven; Red Fox

Introduction

Gray Wolves (*Canis lupus*) are broadly distributed across northern Ontario, occurring from the Manitoba to the Quebec border, and from the Upper Great Lakes north to the Hudson Bay coast (Ontario Ministry of Natural Resources 2005; Naughton 2012). During the late 19th century and well past the mid-20th century, Gray Wolves were considered a significant predator that needed to be controlled due to perceived impacts on populations of Moose (*Alces americanus*), White-tailed Deer (*Odocoileus virginianus*), and livestock (Pimlott 1961). Control programs included year-round hunting seasons, bounties, shooting from aircraft, and poisoning. Wolf poisoning was widely conducted in Ontario in the 1800s and early 1900s (Omand 1950; Kolenosky 1983). Prior to 1911, poisoning was the "most usual and effective method for the destruction of wolves" (Anonymous 1912: 215). By 1911, the use of poison to kill wolves remained legal, but placing poison where other furbearers could be killed was illegal, effectively limiting its use (Anonymous 1912). Poisoning was the principal means of wolf control in Algonquin Provincial Park from 1893 until about 1933 when it was replaced by snaring (Pimlott *et al.* 1969). By the late 1960s poisoning wolves was discouraged by the Ontario Department of Lands and Forests (Kolenosky *et al.* 1978) and by the early 1980s, the use of strychnine, sodium fluoroacetate ("Compound 1080"), and cyanide was prohibited (Kolenosky 1983). Bounties for wolves were initiated in Ontario in 1793 (Theberge 1973) and phased out in 1972 (Cluff and Murray 1995). Predator control for wildlife management has not been conducted in Ontario since the mid-1980s (Ontario Ministry of Natural Resources 2005). Wolves are classified as furbearers in Ontario and the use of poison to control them is now prohibited under the 1997 *Fish and Wildlife Conservation Act*.

Although no longer occurring in Ontario, wolf poisoning programs continue to be used elsewhere in North America and remain controversial (Proulx *et al.* 2015). Despite being widely used across northern Ontario in the past, there is little published

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documentation of the history and possible legacy of Gray Wolf control programs.

In the late 1950s, the Ontario Department of Lands and Forests initiated an experimental Gray Wolf poisoning program in northern Ontario. The initial programs (1956–1961) were conducted by district staff under a directive from the Division of Research (Pimlott *et al.* 1961). The objectives were generally to determine (1) the effectiveness of various poisons on wolves, (2) the impacts on non-target species, (3) the effectiveness of different baits and methods of deployment, and (4) cost.

Some studies were more specifically intended to increase local abundance of Moose or White-tailed Deer populations (e.g., Turner 1959) or reduce livestock depredation (e.g., Chrysler 1960).

A more systematic study was conducted between 1960 and 1964 in the Allanwater area about 250 km north of Thunder Bay (Pimlott *et al.* 1961). The objectives of that study (Pimlott *et al.* 1961: 1) were:

1) To obtain specific information on the mechanics of controlling a Timber Wolf population in a forested habitat.
2) To determine the effect that poison baits placed on lakes will have on other mammals and birds.
3) To determine the type of situation and type of poison baits that minimize the loss of other mammals and birds.
4) To determine the economics of a poisoning program conducted in a large area.
5) To obtain detailed information on the sex and age composition of wolf packs.

Many of the data from these studies were included in unpublished Ontario Department of Lands and Forests reports but have not been reported in peer-reviewed literature. We present the history of the Ontario experimental wolf poisoning program conducted between 1956 and 1964 and summarize data on wolves and non-target species killed during this program.

Methods

We reviewed and compiled all available Fish and Wildlife Management Reports (n = 16) describing wolf poisoning studies in northern Ontario found in the Ontario Ministry of Natural Resources Library in Peterborough, Ontario, Canada. Reports documented various regional poisoning initiatives in addition to a three-year poisoning program (Allanwater Research Study) and contained varying levels of detail on study methods and results.

District studies 1956 to 1961

We found reports of 12 studies conducted between 1956 and 1961 by Ontario Department of Lands and Forests staff in district offices under the general direction of the Lands and Forests Research Branch (Pimlott 1961). These studies were conducted in Fort Frances, Kenora, Sioux Lookout, Port Arthur, Nipigon, and Gogama districts and included observations at 48 different bait stations (Figure 1; Table 1).

Baits were placed on frozen lakes and anchored with bricks or other weights or frozen into the ice surface, except in the Rainy River study where baits were placed on land (Chrysler 1960). Baits were generally left to sink into the lake in the spring. At Kenora in 1961, baits were covered with evergreen branches in an effort to reduce kills of non-target species (Linklater 1961). The rationale for choosing bait locations was not always provided, but sometimes attempted to eliminate specific packs of wolves found at Moose or White-tailed Deer kill sites (e.g., Swift 1959), or were arranged on a convenient route for rechecking the baits.

Baits usually included Moose, White-tailed Deer, or American Beaver (*Castor canadensis*) carcasses. Fish, Northern River Otter (*Lontra canadensis*), Domestic Sheep (*Ovis aries*), and Horse (*Equus caballus*) carcasses were used in a few instances (Table 1). Cubes of deer, rather than larger portions of carcasses, were used by Linklater (1959).

Strychnine was the most commonly used poison (11 programs) although sodium fluoroacetate was used for three seasons at Kenora, and cyanide was used along with strychnine at Port Arthur in 1957 (Table 1). Strychnine pellets or cubes were inserted into the bait and sealed with a plug of meat or fat. Powdered cyanide and strychnine were sifted into slits cut into the bait. Sodium fluoroacetate was impregnated into the bait (cubes of deer) in the laboratory and then shipped to the field (Linklater 1960). In Kenora in 1959, the study area was pre-baited with deer meat in an effort to habituate wolves to the bait (Linklater 1959).

Bait stations were checked between one and 30 days after the poison was deployed and evidence of wolf and other wildlife mortality was recorded. The frequency of checks varied within and between programs and was often unreported. Most bait stations were accessed by aircraft, but some were checked by vehicle or on foot where access was possible. Effort to document non-target (i.e., species other than wolves) wildlife mortality was highly variable within and between programs and was usually poorly documented. At Kenora, Linklater (1956, 1960, 1961) specifically indicated that methods included an attempt to determine non-target mortality, although only cursory examinations consisting of an aircraft flyover were conducted on some dates (Linklater 1959, 1960,

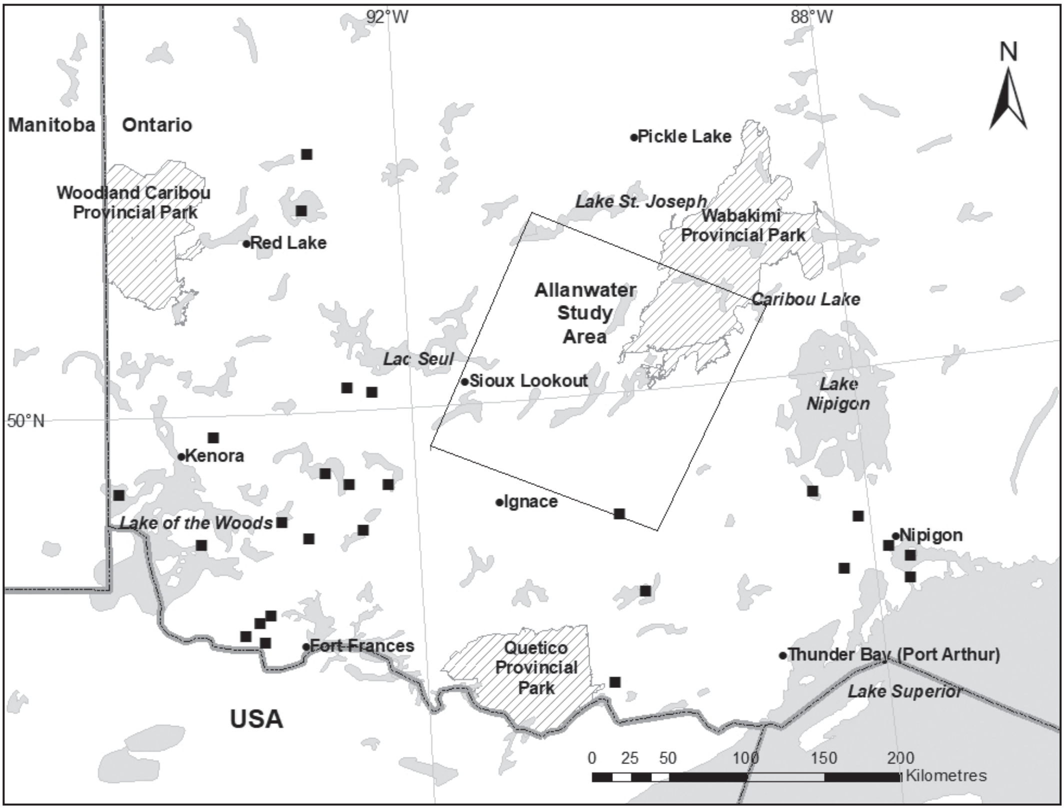

FIGURE 1. Experimental Gray Wolf (*Canis lupus*) poisoning bait locations in northwestern Ontario (1956–1964), including the Allanwater study area. Squares indicate the approximate locations of bait stations. The Gogama study area is about 430 km east of the area shown on the map.

1961). The Port Arthur program in 1959 apparently did not search for non-target mortality (Swift 1959).

Allanwater study

The Allanwater study was conducted between 1960 and 1964 by staff of the Ontario Department of Lands and Forests Research Branch under the direction of D.H. Pimlott and J. Shannon as part of the Ontario Wolf Research Program. The study area was a 161 km × 161 km (25 921 km^2) block between Sioux Lookout and Armstrong, roughly bordered by Lac Seul to the west, Lake St. Joseph to the north, Caribou Lake to the east, and Ignace to the south (Figure 1). It encompassed what is presently the southern part of Wabakimi Provincial Park. In the early 1960s, the area was a remote and undisturbed part of the Boreal Forest Region. The dominant vegetation consists of Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh), White Spruce (*Picea glauca* (Moench) Voss), Balsam Fir (*Abies balsamea* (L.) Miller), Trembling Aspen (*Populus tremuloides* Michaux), White Birch (*Betula papyrifera* Marshall), and Jack Pine (*Pinus banksiana* Lambert) forest (Crins *et al.* 2009). Moose were the most common ungulate although Caribou (*Rangifer tarandus*) were locally present and were probably more common and widespread in the early 1960s. Moose densities in the more northern portion of the study area typically remained under 0.1/km^2 in recent decades (1980–2005; Ontario Ministry of Natural Resources 2013) and were likely similar during the 1960s. Road access in the 1950s and 1960s was confined to Highway 599 extending north from Savant Lake to Pickle Lake. Industrial forestry was largely confined to areas near Sioux Lookout and Savant Lake and along the Canadian National rail line (Ontario Ministry of Natural Resources and Bowater Canadian Forest Products Incorporated 2008).

A 22.5 km × 22.5 km grid was established in 1959 with bait stations "at the most favourable locations within a 5 mile [8 km] radius" of each of the 49 intersection points (Pimlott *et al.* 1961: 5). This spacing resulted in one bait station approximately every 518 km^2 as recommended by Loughry (1958) for

TABLE 1. Details of Gray Wolf (*Canis lupus*) poisoning programs in northern Ontario, 1956–1964.

Reference	Poison	Bait	Confirmed wolf pack in area	District	Period	No. stations	Bait-days	Wolves killed
Linklater 1956	Strychnine	Moose	Unknown	Kenora	January–April 1956	2	237	3
D'Agostini 1958	Cyanide, strychnine	Deer, fish	Yes	Port Arthur	January–February 1957	2	48	0
Rettie 1958	Powdered strychnine	Deer	Yes	Port Arthur	February–March 1956	1	>30	0
Rettie 1958	Powdered strychnine	Moose	Yes	Port Arthur	January–March 1958	2	122	4
Linklater 1959	1080	Moose	Yes	Kenora	March–April 1959	1	30	0
McKeown 1959	Unknown	Moose, deer, fish, beaver	Unknown	Port Arthur	February–April 1959	3	128	3
Sayers 1959	Powdered strychnine	Whitefish, deer	Yes	Sioux Lookout	February–March 1961	5	200	8
Swift 1959	Strychnine crystals, Strychnine powder	Deer, horse, beaver	Yes	Port Arthur	February–April 1959	3	>84	7
Turner 1959	Strychnine	Moose	Yes	Gogama	December 1958–March 1959	2	256	0
Chrysler 1960	Alkaloid strychnine cubes	Beaver	No (grid)	Rainy River	February–April 1960	16	749	2
Linklater 1960	1080	Deer, beaver	Yes	Kenora	January–May 1960	1	73	0
Linklater 1961	1080 and strychnine	Deer, beaver	Yes	Kenora	January–May 1961	10	1093	11
Allanwater research study								
Pimlott *et al.* 1961	Strychnine pellets	Beaver, deer, moose	No	Sioux Lookout and Port Arthur	ca. January–April 1960	56	4843	29
Shannon *et al.* 1961			Yes		January–May 1961	21	1649	14
Shannon *et al.* 1962			No		January–April 1962	55	4757	32
Shannon *et al.* 1963			Yes		March–April 1963	6	108	6

optimal density for controlling Gray Wolves in Caribou winter range. Additional bait stations were established in 1960 (56 stations total) and 1962 (55 stations total) apparently at the discretion of the field staff conducting the study. Baits were placed on frozen lakes between 23 and 137 m from the shore and wired to scrap iron or bricks, which were frozen into the ice. Baits consisted of Moose, White-tailed Deer, or American Beaver meat. Pellets containing 0.13 g (2 grains) of alkaloid strychnine were distributed in the bait at the rate of one pellet/0.45 kg of meat. In 1961 the protocol was modified in an attempt to increase the number of wolves killed. Rather than placing bait stations on a grid, baits were placed where wolves had been observed during a reconnaissance flight. Only 21 bait stations were established due to unfavourable weather and limited aircraft availability (Shannon *et al.* 1961). In 1963, only six bait stations were established, again where wolves had been observed during reconnaissance flights. Three stations operated from 6 to 11 March and the other three from 17 February to 1 April 1963 (Shannon *et al.* 1963).

Bait stations were checked by circling the site with a De Havilland Otter aircraft and searching for carcasses of wolves and other species. Flights were initially planned weekly (Pimlott *et al.* 1961) but often had to be delayed or cancelled due to weather conditions and aircraft availability (Shannon *et al.* 1961). Wolf carcasses were counted and identified to sex and age class (adult versus subadult [<2 years old]). Carcasses were collected and submitted to the Ontario Department of Lands and Forest research laboratory in Maple, Ontario for necropsy.

Aerial wolf surveys were conducted on seven occasions between December 1960 (before the initial poison deployment) and March 1964 (at the conclusion of the study; Table 2). Survey dates were chosen based on suitable snow for observing tracks and weather conditions for flying. Transects were flown by fixed-wing aircraft on a grid with 22.5 km spacing for a total survey transect length of 2253 km. Shannon *et al.* (1963) suggested that with 22.5 km survey line spacing, about half of the total wolf population is counted based on Shannon's personal experience conducting aerial surveys for wolves in Algonquin Park. Tracks of single wolves (as opposed to packs) were not included due to the difficulty in making positive species identification.

Results

Wolf mortality

A total of 119 wolf kills was reported across all studies (Table 1). No wolf mortality was observed in the 1956 (Rettie 1958) or 1957 Port Arthur (D'Agostini 1958) projects, the 1959 (Linklater 1959) or 1960 (Linklater 1960) Kenora projects, or the Gogama (Turner 1959) project. Kill rates varied widely by study from 0.0 to 83.3 kills per 1000 bait days (Table 3). In the Allanwater study, kill rates were similar in 1960 and 1962 (6.61 and 6.73 wolves per 1000 bait-days, respectively) when numbers and distribution of baits were similar.

Of the 110 wolves where sex was identified, 56% were male (62% in the 1956 to 1961 studies; 54% in the Allanwater study). In the Allanwater study, 51% were identified as adults, 44% as subadults, and 5% were of unknown age. Ages were not reported in other studies.

Up to 10 dead wolves were found at a single bait check in the Allanwater study in 1961: three adults, five subadults, and two apparent yearlings, probably from a single pack (Pimlott *et al.* 1961). Six dead wolves (three adult males and three adult females) at Allanwater in 1963 were assumed to constitute most or all of a single pack (Shannon *et al.* 1963).

Dead wolves were found at distances ranging from 0 m (dead with mouth on the bait; Swift 1959) to over 1.2 km (Rettie 1958) from the bait. A trapper reported tracking a wolf for 1.6 km from the bait before finding it dead (Pimlott *et al.* 1961). Three incidences of wolves eating the bait but no carcass being discovered were reported by Pimlott *et al.* (1961). In several

TABLE 2. Gray Wolf (*Canis lupus*) aerial survey results for the Allanwater study area. 1960–1964.

Source	Survey dates	Estimated # wolves*	# packs †
Pimlott *et al.* 1961	16–21 December 1960	125	25
Shannon *et al.* 1961	6–10 January 1961	54	11
Shannon *et al.* 1962	19–20 December 1961, 9 January 1962	63	21
Shannon *et al.* 1963	9–11 January 1963	25	NA
Shannon *et al.* 1963	19–21 March 1963	25	NA
Shannon *et al.* 1964	13 January–February 8 1964	46	18
Shannon *et al.* 1964	17–18 March 1964	59	14

*Observed or track counts.
†Including single animals.

TABLE 3. Kill rates of Gray Wolf (*Canis lupus*), Common Raven (*Corvus corax*), and Red Fox (*Vulpes vulpes*) in poisoning programs in northern Ontario, 1956–1964.

Study area	Year	Reference	Kills / 1000 bait days		
			Gray Wolf	Common Raven	Red Fox
Port Arthur	1958	D'Agostini 1958	0.0	0.0	0.0
	1959	McKeown 1959	23.4	23.4	7.8
	1959	Swift 1959	83.3	23.8	11.9
Nipigon	1955–56	Rettie 1958	0.0	0.0	100.0
	1957–58	Rettie 1958	32.8	8.2	24.6
Gogama	1958–59	Turner 1959	0.0	3.9	0.0
Rainy River	1960	Chrysler 1960	2.7	9.3	2.7
Kenora	1955–56	Linklater 1956	12.7	0.0	0.0
	1959	Linklater 1959	0.0	0.0	0.0
	1959–60	Linklater 1960	0.0	0.0	0.0
	1961	Linklater 1961	10.1	12.8	12.8
Sioux Lookout	1959	Sayers 1959	40.0	25.0	15.0
Allanwater	1960–61	Pimlott *et al.* 1961	6.6	7.2	0.8
	1961	Shannon *et al.* 1961	8.5	10.9	1.2
	1961–62	Shannon *et al.* 1962	6.7	11.6	6.1
	1962–63	Shannon *et al.* 1963	27.8	27.8	18.5

cases bounty hunters were suspected of collecting wolf carcasses. Any wolves poisoned between the final survey in April or May and ice-out (often several weeks) were not counted (e.g., Shannon *et al.* 1962).

Wolves frequently scavenged the carcasses of previously poisoned wolves as demonstrated by partially eaten wolf carcasses, the presence of large quantities of wolf hair in scats near baits, and wolf remains in gut contents during necropsies (Shannon *et al.* 1963). Several incidences of secondary poisoning were described, including this passage from Pimlott *et al.* (1961: 9):

> One [poisoned] wolf was 30 feet [9 m] from the bait, a second had died at the same distance from the bait and then had been dragged about 80 yards [73 m] by a third wolf which then ate its intestines and lungs. This wolf then went a further 120 yards [110 m], falling repeatedly as it went, before it died; it was then 30 yards [27 m] into the forest.

Multiple authors reported wolf tracks approaching the bait but not feeding, suggesting some avoidance of bait (Rettie 1958; Sayers 1959; Linklater 1959, 1960, 1961).

Non-target species

Total observed mortality of all non-target species is summarized in Table 4. Some assumptions were made about the identity of reported non-target species, e.g., "rabbit" was assumed to be Snowshoe Hare (*Lepus americanus*), "squirrel" was assumed to be Red Squirrel (*Tamiasciurus hudsonicus*), and "seagull" was assumed to be Herring Gull (*Larus argentatus*); in all three instances, these are the sole representatives of those taxa resident in the boreal forest of northwestern Ontario in the winter or early spring. Two hundred and sixty five non-target kills were documented, comprising 10 mammal and nine bird species. Common Raven (*Corvus corax*) and Red Fox (*Vulpes vulpes*) were the most common non-target mortalities, making up 54% and 24% of the total kills, respectively, and being recorded in 69% of all studies. The kill rate for Common Raven and Red Fox increased in the Allanwater study when baits were placed near active wolf packs rather than being placed on a grid (Table 3; Shannon *et al.* 1963). At least one case of secondary poisoning of non-target species was reported; a raven which had fallen about 274 m from the bait was partially eaten by a Red Fox, which was dead about 3.1 m from the raven (Pimlott 1961).

Avian non-target mortalities increased later in the winter as migrant birds (i.e., American Crow [*Corvus brachyrhynchos*], Herring Gull, Turkey Vulture [*Cathartes aura*], and Bald Eagle [*Haliaeetus leucocephalus*]) returned to the study area.

The greatest number and diversity of reported non-target kills occurred in the Rainy River study area (Chrysler 1960). This study differed from the

TABLE 4. Non-target species killed during Gray Wolf (*Canis lupus*) poisoning programs in northern Ontario, 1956–1964.

Species	Total observed mortality (% of all birds/mammals)	No. studies (%) reported in (*n* = 16)
Birds		
Common Raven (*Corvus corax*)	144 (79.1)	11 (69)
Herring Gull (*Larus argentatus*)	14 (7.7)	3 (19)
American Crow (*Corvus brachyrhynchos*)	9 (4.9)	2 (13)
Bald Eagle (*Haliaeetus leucocephalus*)	4 (2.2)	3 (19)
Woodpecker sp. (Picidae)	4 (2.2)	1 (6)
Canada Jay (*Perisoreus canadensis*)	2 (1.1)	2 (13)
Turkey Vulture (*Cathartes aura*)	2 (1.1)	2 (13)
Raptors (“hawks”)	2 (1.1)	2 (13)
Blue Jay (*Cyanocitta cristata*)	1 (0.5)	1 (6)
Total	182	
Mammals		
Red Fox (*Vulpes vulpes*)	64 (77.1)	11 (69)
Striped Skunk (*Mephitis mephitis*)	5 (6.0)	1 (6)
Fisher (*Pekania pennanti*)	4 (4.8)	4 (25)
Canada Lynx (*Lynx canadensis*)	2 (2.4)	2 (13)
Domestic Dog (*Canis lupus familiaris*)	2 (2.4)	1 (6)
Snowshoe Hare (*Lepus americanus*)	2 (2.4)	1 (6)
Rodents (“mouse”)	1 (1.1)	1 (6)
Red Squirrel (*Tamiasciurus hudsonicus*)	1 (1.1)	1 (6)
American Marten (*Martes americana*)	1 (1.1)	1 (6)
American Mink (*Neovison vison*)	1 (1.1)	1 (6)
Total	83	

others in that it was on land rather than on a frozen lake and was in a landscape that included roads and agricultural land. Six species incidentally killed at this site were not reported elsewhere (woodpecker sp. [Picidae], Canada Jay [*Perisoreus canadensis*], Blue Jay [*Cyanocitta cristata*], Striped Skunk [*Mephitis mephitis*], Domestic Dog [*Canis lupus familiaris*], and “mouse” [Rodentia]).

Discussion

Wolf poisoning to reduce predation on wildlife was widespread in Canada for over 100 years (Cluff and Murray 1995) but there are few data on the impacts on wolf populations or non-target species, particularly in the boreal forest. Wolves were poisoned in Wood Buffalo National Park to reduce predation on Wood Bison (*Bison bison*) between 1935 and 1940 and periodically until the 1960s, but there is no available information on the numbers of wolves or other species killed (Carbyn *et al.* 1993). An experimental study to reduce wolf predation on Caribou in northern Alberta in 2005 to 2012 is probably the most well documented (Hervieux *et al.* 2014). Other studies focussed on poisoning wolves (Bjorge and Gunson 1985) or Coyotes (*Canis latrans*; e.g., Allen *et al.* 1996; Wobeser *et al.* 2004) to protect livestock.

The northern Alberta study (Hervieux *et al.* 2014) documented higher mortality rates of wolves and other species than observed in the Ontario wolf poisoning program we have summarized here. In comparison to the Alberta study, the Allanwater study reported fewer dead wolves (7.5/1000 bait-days in Ontario versus 27/1000 bait-days in Alberta). Non-target species were similar except Coyotes made up 20% of the Alberta kills, whereas Coyotes were largely absent in northern Ontario when the Ontario studies took place. Common Ravens (9.8 killed/1000 bait-days versus 15.9 killed/1000 bait-days) and Red Fox (3.3 killed/1000 bait-days versus 31 killed/1000 bait-days) were also more commonly reported in Hervieux *et al.* (2014), possibly due to higher density of wolves and other species in Alberta, and/or a more rigorous study design (Hervieux *et al.* 2014).

The effectiveness of poisoning programs for controlling wolf populations cannot be assessed from the studies summarized here. Wolf survey flights were conducted before and after the Allanwater study, but the amount of wolf immigration and emigration, the influence of bounty hunters and trappers, and the number of wolves killed but not detected remain unknown. For example, bounty hunters were killing wolves from aircraft in the Allanwater area while the study was taking place. Five wolves in one pack were killed by bounty hunters in late February 1963 (Shannon *et al.* 1963) and in Kenora District, "quite a few permits" were issued to hunt predatory animals from aircraft in 1956 (Linklater 1956: 2). Wolf mortality from poisoning would be underestimated if wolves moved into forest cover before dying, carcasses were removed by bounty hunters, or snow buried the carcasses. Most wolves likely died close to the bait stations, although one was located 1.6 km away (Pimlott *et al.* 1961). In an Alberta study most wolves died within 150 m of the bait, but some travelled up to 1 km before dying (Bjorge and Gunson 1985), while in south Texas all predators killed by strychnine were found within 188 m of the bait site, and all but one were found within 37 m (Beasom 1974). The level of search effort in many reports is poorly documented and some authors (e.g., McKeown 1959; Pimlott *et al.* 1961) acknowledged that recent snowfall compromised the search efficiency. Other factors including experience of searchers and time since carcass placement were not controlled in the studies summarized here, which could lead to highly variable results (Vyas 1999).

Weather and snow conditions probably influenced the number of wolves killed. Shannon *et al.* (1961) concluded that the low number of wolf kills in 1961 was caused by low snowfall in early winter, which allowed wolves to range freely through forested habitat rather than concentrating movements on lakes and rivers. Slush conditions in late winter may also have inhibited wolves from travelling on water bodies. In 1962, the monthly wolf kills in the Allanwater study increased between January and April, possibly due to wolves overcoming their caution about the bait, increased movements during the breeding season, and/or declining prey availability (Shannon *et al.* 1962).

Wolf poisoning in northwestern Ontario in the late 1800s and early 1900s may have contributed to declines in Common Raven populations in the region. Common Raven was by far the most common bird observed to succumb to poisoning (79% of all incidentally killed birds). In a recent western Canada study, Common Raven was also the most common non-target bird species killed (96%; Alberta Environment and Parks 2017). Ravens were reported as common in the Thunder Bay area in 1893 (Atkinson 1894) but were rare in the 1920s and 1930s (Dymond *et al.* 1928; Dear 1940; Baillie and Hope 1943; Snyder 1953). Common Raven populations in Ontario and elsewhere in North America declined in the early 20th century in part due to mortality caused by poisoning (Blomme 1987) and baited traps (Boarman and Heinrich 2020). Common Raven may be particularly vulnerable to poisoning efforts that target wolves given their propensity to follow wolf packs and feed on the kills (Stahler *et al.* 2002). This intentional association with wolf packs also serves to suppress the ravens' natural tendency to be suspicious of novel food sources (Stahler *et al.* 2002), potentially increasing their risk of consuming poisoned baits. Common Raven populations in the Kenora area in northwestern Ontario increased between the 1930s and early 1950s (Snyder 1953), following the decline in wolf poisoning. Common Raven control experiments in Nevada suggested that any reductions in raven populations were short-term and did not have long-term consequences because of the reoccupancy of vacant territories (Coates *et al.* 2007). Mortality of Common Ravens was probably under-reported in the Ontario studies because feeding activity was reported at some baits where no dead birds were observed (e.g., Linklater 1959, 1960), yet these birds likely perished. In one study, Linklater (1960: 5) concluded that "although no direct evidence of mortality in either animals or birds was found, it is felt that the ravens eventually succumbed to the poison". However, some of these Kenora studies used Compound 1080 rather than strychnine, and the former is known to be less toxic overall to birds (Connolly 2004) so there actually may have been lower raven mortality.

In contrast to Common Ravens, Canada Jays were reported as non-target mortality only in one study (at Rainy River; Chrysler 1960) although both species are distributed throughout northern Ontario and frequently feed on carrion in winter (Strickland and Ouellet 2020). Canada Jays cache food by removing pieces of carrion to be stored in trees and eaten later or fed to young (Strickland and Ouellet 2020). Kills of Canada Jays would be undiscovered if the bait is not consumed immediately and birds die after eating pieces of cached food away from the bait site, and the mortality was likely much higher than that observed.

Although Common Raven was the most common bird killed during the poisoning programs reported here, several other species of resident or early spring migrant species were also affected, principally Herring Gull, American Crow, Bald Eagle, and various woodpeckers. In contrast, in a recent wolf control study in Alberta, only 4% of birds killed were species other than Common Raven (one each of Bald Eagle, Golden Eagle [*Aquila chrysaetos*], and Canada Jay; Alberta Environment and Parks 2017). Breeding populations of Bald Eagles in northern Ontario were already depressed from the effects of dichloro-diphenyl-trichloroethane (DDT) in the 1950s and 1960s (Grier 1982), and incidental poisoning of Bald Eagle may have had an additive impact. This could be particularly so as the poisoning occurred in late winter (mid-February to late-April) when the migrant adults would have just arrived back on territory and food resources would have been limited (Armstrong 2014). A study of Bald Eagle museum specimens with a known cause of death collected from Ontario and four other North American jurisdictions (November to May, 1900 to 1980) revealed four of 21 specimens (19%) that were poisoned incidentally by strychnine from canid control programs (Bortolotti 1984). In western Canada, Bald Eagle continue to suffer incidental poisoning of an unknown magnitude as a result of the ongoing illegal poisoning of Coyote using anticholinesterase pesticides (Wobeser *et al.* 2004).

Red Fox was by far the most common mammal to be killed by poisoning (77%). In a recent western Canada study, Red Fox and Coyote were similarly the most common non-target mammals killed (42% and 45%, respectively; Alberta Environment and Parks 2017). Several other mammalian species were also killed incidentally in the Alberta study, but all at relatively low detection rates. There may also have been population-level impacts on non-target predators such as Fisher (*Pekania pennanti*; Proulx *et al.* 2015) and Wolverine (*Gulo gulo*; Slough 2007; COSEWIC 2014).

Conclusions

The projects we have described provide the only known documentation of wolf poisoning programs in Ontario. Although completed over 50 years ago, they provide some context for current discussions on the ecological impacts and ethics of the use of poison to control wolves (Musiani and Paquet 2004; Proulx *et al.* 2015). They also provide valuable context for the evaluation of past ecological effects on non-target species.

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Updated distribution of four stenohaline fish species in Labrador, Canada

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Abstract

Distributions of freshwater fish species in Labrador are poorly documented as the region is remote and sparsely inhabited. Here, we update distributions of four species native to the Labrador Peninsula based on data collected over 10 years: Burbot (*Lota lota*), Round Whitefish (*Prosopium cylindraceum*), Lake Trout (*Salvelinus namaycush*), and Slimy Sculpin (*Cottus cognatus*). In northern Labrador, our findings extend their ranges inland and northwest of their formerly reported distributions. Their presence in previously unknown locations indicates an alternative post-glacial colonization pathway to one previously proposed that suggested an isolated pocket of Lake Trout in a northern coastal area colonized through marine invasion. Instead, we suggest that overland colonization occurred when glacial Lake Naskaupi withdrew across Quebec into several northern drainages. In southern Labrador, we found Lake Trout and Round Whitefish to the southeast of their previously reported ranges. The discovery of an isolated population of Lake Trout in a remote location of southeast Labrador implies that they may have existed in the area historically (6000 years ago), but have undergone a range contraction with a warming climate. In addition, 22 new locations are documented for Lake Trout within their established range.

Key words: Burbot; *Lota lota*; Round Whitefish; *Prosopium cylindraceum*; Lake Trout; *Salvelinus namaycush*; Slimy Sculpin; *Cottus cognatus*; occurrence; Labrador; colonization; range; glaciation

Introduction

The distribution of freshwater fish species in the Labrador region of Newfoundland and Labrador, Canada, is poorly defined. This is largely because of the inherent difficulties and costs associated with sampling remote locations. Despite the paucity of data, several attempts have been made to describe fish distributions and ichthyogeographic regions for Labrador (Bergeron and Brousseau 1981; Legendre and Legendre 1984; Black *et al.* 1986). Looking at individual distributional reports collated from over 100 years of records, Black *et al.* (1986) concluded that Labrador could be divided into three ichthyogeographic regions based on species composition: the Churchill River drainage comprising three subregions; the southeastern portion of Labrador; and northern Labrador (>55°N; Table 1). Their study led to considerable advancements in our understanding of the post-glacial distribution of fish species in Labrador; however, comprehensive records were not available, particularly for the north. For example, in recent years, updated freshwater species occurrence and range adjustments for Logperch (*Percina caprodes*), Lake Chub (*Cousius plumbeus*), and Longnose Dace (*Rhinichthys cataractae*) have been reported (Grant *et al.* 2000; Perry and Joyce 2003; Michaud *et al.* 2010). These reports highlighted the necessity for further fish surveys, particularly in more northern areas.

In 2001, the Government of Newfoundland and Labrador began working on a centralized georeferenced database and archive. This new Provincial Aquatics Database and Archive (PADA) contains freshwater fish data gathered from provincial standardized stock assessments, government reports (both federal and provincial), research studies, environmental assessments, and historical documents. In general, the information housed in PADA is a synthesis of over 100 years of data collection for the period 1909 through 2015.

To augment PADA and develop a better understanding of Labrador's ichthyofauna, a standardized sampling program was initiated throughout southern Labrador in 2002. This stock assessment program was implemented by the provincial government to address

Table 1. Principal fish species present in each of the three major ichthyogeographic regions in Labrador, Canada, as defined by Black *et al.* (1986).

Order/family	Species	Southeastern Labrador	Churchill River system	Northern Labrador (>55°N)
Anguilliformes/Anguillidae	American Eel *Anguilla rostrata*	X (coastal)		
Cypriniform/Catostomidae	Longnose Sucker *Catostomus catostomus*	X	X	X
	White Sucker *Catostomus commersonii*	X	X	
	Lake Chub *Couesius plumbeus*		X	X
	Northern Pearl Dace *Margariscus nachtriebi*		X	
	Longnose Dace *Rhinichthys cataractae*		X	
Esociformes/Esocidae	Northern Pike *Esox lucius*	X	X	
Gadiformes/Lotidae	Burbot *Lota lota*		X	X
Gasterosteiformes/ Gasterosteidae	Threespine Stickleback *Gasterosteus aculeatus*	X (coastal)	X	X
Osmeriformes/Osmeridae	Rainbow Smelt *Osmerus mordax*		X	
Perciformes/Percidae	Logperch *Percina caprodes*		X	
Salmoniformes/Salmonidae	Lake Whitefish *Coregonus clupeaformis*		X	X
	Round Whitefish *Prosopium cylindraceum*		X	X
	Atlantic Salmon *Salmo salar*	X	X	X
	Arctic Char *Salvelinus alpinus*	X (coastal)	X	X
	Brook Trout *Salvelinus fontinalis*	X	X	X
	Lake Trout *Salvelinus namaycush*		X	X
Scorpaeniformes/Cottidae	Slimy Sculpin *Cottus cognatus*		X	X
	Mottled Sculpin *Cottus bairdii*		X	

the public's concern over increased anthropogenic pressures on Labrador's fish resources, including road construction, hydroelectric development, and mineral exploration. In 2007, the province also began a climate-change study to determine the potential impacts that a warming climate may have on Labrador's northern fish populations. In combination, these two programs have contributed substantially to the data contained in PADA, allowing us to refine our knowledge of species distributions for both the southeastern and northern ichthyogeographic regions. Here, we use the old and new distributional records contained in PADA to update occurrence and distribution data of four stenohaline species native to the Labrador Peninsula: Burbot (*Lota lota*), Round Whitefish (*Prosopium cylindraceum*), Lake Trout (*Salvelinus namaycush*), and Slimy Sculpin (*Cottus cognatus*). We then use this new information to update the ichthyogeographic regions proposed by Black *et al.* (1986) by offering some refinements to the colonization pathways originally proposed. We chose these four species because their newly discovered presence above the Fraser Canyon in northern Labrador has led to our hypothesis that there were multiple colonization pathways from glacial Lake Naskaupi and not just one, as previously suggested by Black *et al.* (1986).

Methods

Study area

The study area includes the entire Labrador Peninsula (Figure 1), an area of ~293 000 km², which represents 3% of Canada's total land mass (Anderson 1985). Labrador's topography was shaped by glacial activity during the Laurentide ice sheet recession of the late Wisconsinan period, which ended ~6500 years ago (Kleman *et al.* 1994). An older, undated ice sheet also contributed to these land formations (Kleman *et al.* 1994).

The provincial standardized stock assessment and climate-change studies (2007–2015) focussed on the southeastern and northern ichthyogeographic regions. The northern sample sites were situated in the high subarctic tundra (Kingurutik–Fraser River) and alpine

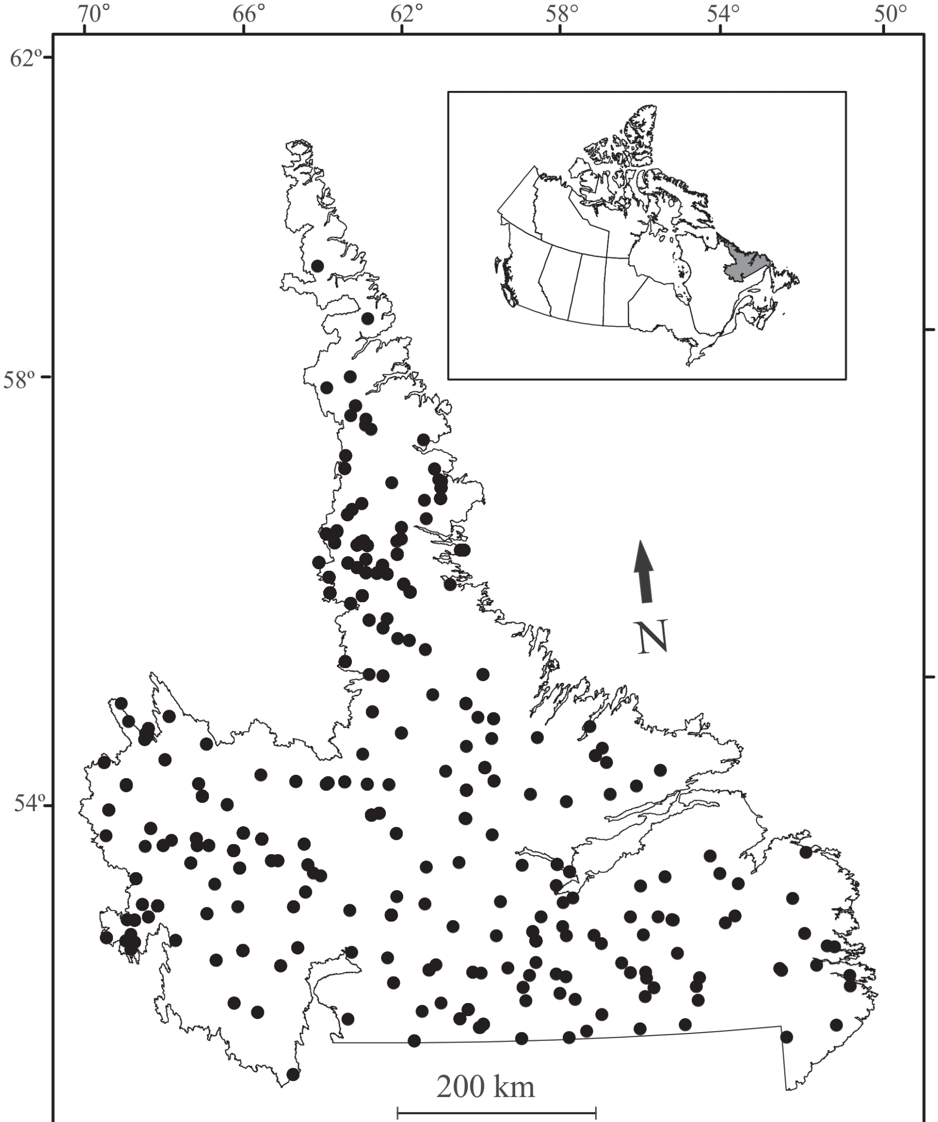

Figure 1. Location of waterbodies (solid circles) associated with freshwater fish distribution data for Labrador, Canada, collected from 1909 through 2015 from the Department of Fisheries and Oceans, Government of Newfoundland and Labrador, and Black *et al.* (1986).

tundra (Torngat) ecoregions. The southeast sites were in the low subarctic forest (Mecatina River), mid-boreal forest (Paradise River), and the string bog ecoregions (Meades 1990).

Sampling

Fish distribution data for lakes was compiled using data archived in PADA, which includes entries used by Black *et al.* (1986). However, since the publication of their paper, species occurrence records have been augmented. Collection dates for all data housed in PADA now range from 1909 through 2015.

The PADA data come from various reports and studies; therefore, the collection methods include a variety of active and passive fish-capture techniques, such as seine nets, gill nets, fyke nets, electrofishing, and angling; stomach contents of predators were also examined. Species occurrence data for all lakes were digitally georeferenced using a geographical information system (ArcMap version 10.3.1; ESRI, Redlands, California, USA).

The most recent occurrence data for Labrador were collected by the Government of Newfoundland and Labrador during both the climate-change study and index netting surveys for 2002–2015. A total of 37 lakes were selected for sampling in the northern region, and 27 lakes (representing nine major watersheds) were sampled in the southeastern region. Sampling programs used standardized multi-mesh nylon monofilament gill nets increasing in mesh size from 1.27 cm stretch to 13.97 cm, in 1.27-cm increments. Net locations were chosen randomly for each lake surveyed and all sets were placed perpendicular to the shoreline and allowed to soak overnight.

Stomach contents of sampled piscivores, such as Northern Pike (*Esox lucius*), Brook Trout (*Salvelinus fontinalis*), and Lake Trout, were also examined and prey fish species identified when possible.

Results

Burbot

Burbot was identified in 21 new locations (Tables 2 and 3; Figure 2a), 16 inside and five outside its previously known range. Four of the five lakes where Burbot was found are within the high subarctic tundra ecoregion: Langille, Iglusuatahrusuak, Alliger, and Sabrina (Table 3; Figure 2a). Burbot was also found in Lake LB50 on the southern fringe of the alpine tundra ecoregion (Table 3; Figure 2a).

Round Whitefish

We identified 13 new locations for Round Whitefish inside and six outside its previously known distribution, for a total of 19 new sites. Of the six sites outside its known range, three are in the high subarctic tundra ecoregion and three are in southern Labrador (Tables 2 and 3; Figure 2b). Two of the locations in the high subarctic tundra ecosystem, Iglusuatahrusuak Lake and Alliger Lake, are near the Labrador coastline, while the third, Lake Langille, is ~15 km north of the Fraser River, near the Labrador–Quebec border. All three new records in southern Labrador, Lac Avert, Little Guines, and Unknown Lake, are located in the low subarctic forest ecoregion (Table 3; Figure 2b).

Lake Trout

We document 22 new locations for Lake Trout inside and 10 sites outside the previously known range in Labrador (Tables 2 and 3; Figure 2c). Seven occurrences expand the known species distribution into the high subarctic ecoregion and the alpine tundra ecoregion. Lakes Sabrina, Tracy, and LB20 are found near the northeastern tip of the high subarctic tundra ecoregion, ~125 km north of the Fraser River, while Lake LB50 extends into the southern portion of the alpine tundra ecoregion (Figure 2c). Lake Tracy is part of an unnamed tributary (drainage 104; Anderson 1985) that flows northward into the Hebron Fjord. Lake LB20 (drainage 103; Anderson 1985) is also found in separate drainage that flows into the Hebron Fjord (Figure 2c).

The discovery of three previously unknown sites in southern Labrador represents expansion of the known range of Lake Trout farther into the southeast of the low subarctic forest ecoregion (Table 3; Figure 2c). Lake Trout sampled in the southeastern region were collected from Lac Mercier, Lac Avert, and Little Guines Lake. Lac Avert and Little Guines Lake are in the Little Mecatina River watershed (Table 3). Lac Mercier is ~50 km southwest of the town of Happy Valley-Goose Bay and is part of the Kenamu watershed (Figure 2c).

Slimy Sculpin

Slimy Sculpin was found at 12 new locations (Tables 2 and 3; Figure 2d), seven inside and five outside its previously reported range. New species occurrences for Slimy Sculpin were recorded in three lakes of the high subarctic tundra ecoregion in northern Labrador (Lakes Alliger, Sabrina, and Tracy) and two were in the alpine tundra ecoregion: Lake LB50 (Table 3; Figure 2d) and an unnamed stream near the Hebron Fjord (three living specimens; Table 3; Figure 2d). All Slimy Sculpin discoveries were the result of examining the stomach contents of lethally sampled Lake Trout. The specimens were not in an advanced state of decomposition and the absence of palatine teeth made it possible to identify these fish as Slimy Sculpin rather than Mottled Sculpin (*Cottus bairdii*; Scott and Crossman 1998).

Table 2. Locations of 30 lakes that highlight a new occurrence within previously established ranges* of four stenohaline freshwater fish species native to Labrador, Canada, collected during sampling by gill net from 2007 to 2015.

Lake	Latitude, °N	Longitude, °W	BUR	RWF	LT	SSC
Crystal Lake	55.5116	63.6734	X	X	X	X
Lac Joseph	52.8294	65.1878	X	X	—	X
Konrad Lake	56.2224	62.7156	X	—	X	X
Khongnekh Lake	56.3974	63.0700	X	X	X	X
Strange Lake	56.2853	63.9475	—	X	X	X
Cabot Lake	56.1500	62.6064	—	—	—	X
Genetics H†	56.6048	63.8682	X	X	X	—
Lake B6†	56.3288	63.3420	X	X	X	—
Slushy Lake†	56.4189	64.1230	X	X	X	—
Walkabout Lake†	56.3277	63.1565	X	X	X	—
WP152†	56.3779	63.4900	X	X	X	—
Hawk Lake	56.0437	63.5880	X	—	X	—
Lac Arvert	52.3020	61.7683	X	—	—	—
Little Guines†	52.1634	61.5447	X	—	—	—
Anak2†	56.5814	63.3234	X	—	X	—
Wanker Lake†	56.5828	63.4904	X	—	X	—
Lac Mercier	52.9183	60.7238	X	—	—	—
Alligar Lake	57.1074	62.0749	—	—	X	—
Unkown Lake†	52.6689	62.3518	X	—	—	—
Lake 1†	56.6817	64.0053	—	X	X	—
Esker Lake†	56.4171	63.6394	—	X	X	—
T-Bone Lake†	56.1404	63.9328	—	X	X	—
Mistastin Lake	55.8949	63.2865	—	X	—	—
Lake A4†	56.3168	62.9895	—	—	X	—
Lake B2†	56.6231	63.3826	—	—	X	—
Lake B5†	56.4531	63.3456	—	—	X	—
Genetics B†	56.1193	63.4008	—	—	X	—
Toilet Seat Lake†	55.8237	63.0595	—	—	X	—
Lake Karen†	55.7076	62.6299	—	—	X	—
Anaktalik Lake	56.5016	62.8229	—	—	—	X

Note: BUR = Burbot (*Lota lota*); RWF = Round Whitefish (*Prosopium cylindraceum*); LT= Lake Trout (*Salvelinus namaycush*); SSC = Slimy Sculpin (*Cottus cognatus*). X indicates fish present.
*Black *et al.* (1986).
†Ungazetted name.

Discussion

Our findings have extended the range of four stenohaline species (Burbot, Round Whitefish, Lake Trout, and Slimy Sculpin) northwest of their formerly reported distributions. Lake Trout is now documented ~125 km north of the Fraser River drainage (former range limit) and inland ~90 km from coastal lakes. In southern Labrador, Round Whitefish and Lake Trout, were found 65 km farther to the southeast than their formerly reported range limits.

Northern Labrador

In the north, expansion of the range for Burbot, Round Whitefish, Lake Trout, and Slimy Sculpin may indicate an alternative explanation for colonization than that described by Black *et al.* (1986) to account for the presence of an isolated pocket of Lake Trout in the Puttuaala Brook watershed, near Okak Bay.

Black *et al.* (1986) proposed that Lake Trout and other species likely dispersed through an overland pathway from Quebec that drained southward into the Fraser River watershed and on to the Labrador Sea, from where they moved northward by way of coastal invasions. Our findings show that overland invasion was likely not confined to the Fraser River drainage basin but also occurred in drainages farther north.

TABLE 3. Number of individuals of each species captured during sampling events from 2007 to 2015 at previously undescribed locations for freshwater fish species in Labrador, Canada. Location numbers correspond to points shown in Figure 2.

Location	Year	Ecoregion	Latitude, °N	Longitude, °W	Sample method	LNS	WS	LC	NP	BUR	LWF	RWF	AC	BT	LT	SSC
1. Little Guines*	2011	LSF	52.1634	61.5447	Gill net	11	69	2	18	11	59	3†	—	—	49†	—
2. Lac Avert	2011	LSF	52.3020	61.7683	Gill net	10	100	1	36	16	86	3†	—	—	66†	—
3. Unknown lake*	2011	LSF	52.6689	62.3518	Gill net	—	176	—	24	1	129	3†	—	—	28	—
4. Lac Mercier	2007	LSF	52.9183	60.7238	Gill net	66	21	—	6	2	—	—	—	12	54†	—
5. Lake Langille*	2012	HST	56.8649	63.6539	Gill net	—	—	—	—	1†	—	32†	5	—	59†	3‡
6. Lake C3*	2012	HST	56.9128	63.5762	Angled	—	—	—	—	—	—	—	—	—	1†	—
7. Lake Rhonda*	2012	HST	56.9676	63.4141	Gill net	—	—	—	—	—	—	—	1	—	119†	—
8. Lake Sabrina*	2012	HST	57.2858	63.7134	Gill net	—	—	—	—	2†	—	—	50	—	27†	—
9. Lake Tracy*	2012	HST	57.4071	63.7007	Gill net	—	—	—	—	—	—	—	5	—	59†	3‡
10. Iglusuatahrusuak	2007	HST	57.0105	62.0857	Gill net	—	—	—	—	4†	—	27†	8	—	119	—
11. Alliger Lake	2009	HST	57.1074	62.0749	Gill net	—	—	—	—	8†	—	104†	135	8	264	8‡
12. Unnamed stream*	2013	AT	57.8668	63.5386	Electro.	—	—	—	—	—	—	—	113	—	—	3†
13. Lake LB20*	2015	HST	57.7443	63.3666	Gill net	—	—	—	—	—	—	—	22	—	8†	—
14. Lake LB50*	2015	AT	57.7731	63.6157	Gill net	—	—	—	—	1†	—	—	3	3	32†	2‡

Note: LNS = Longnose Sucker (*Catostomus catostomus*); WS = White Sucker (*Catostomus commersonii*); LC = Lake Chub (*Couesius plumbeus*); NP = Northern Pike (*Esox lucius*); BUR = Burbot (*Lota lota*); LWF = Lake Whitefish (*Coregonis clupeaformis*); RWF = Round Whitefish (*Prosopium cylindraceum*); AC = Arctic Char (*Salvelinus alpinus*); BT = Brook Trout (*Salvelinus fontinalis*); LT = Lake Trout (*Salvelinus namaycush*); SSC = Slimy Sculpin (*Cottus cognatus*). LSF = low subarctic forest, HST = high subarctic tundra, AT = alpine tundra. Electro. = electrofishing.

*Ungazetted name.

†New occurrence for this species.

‡New occurrence for this species, found in stomach of Lake Trout.

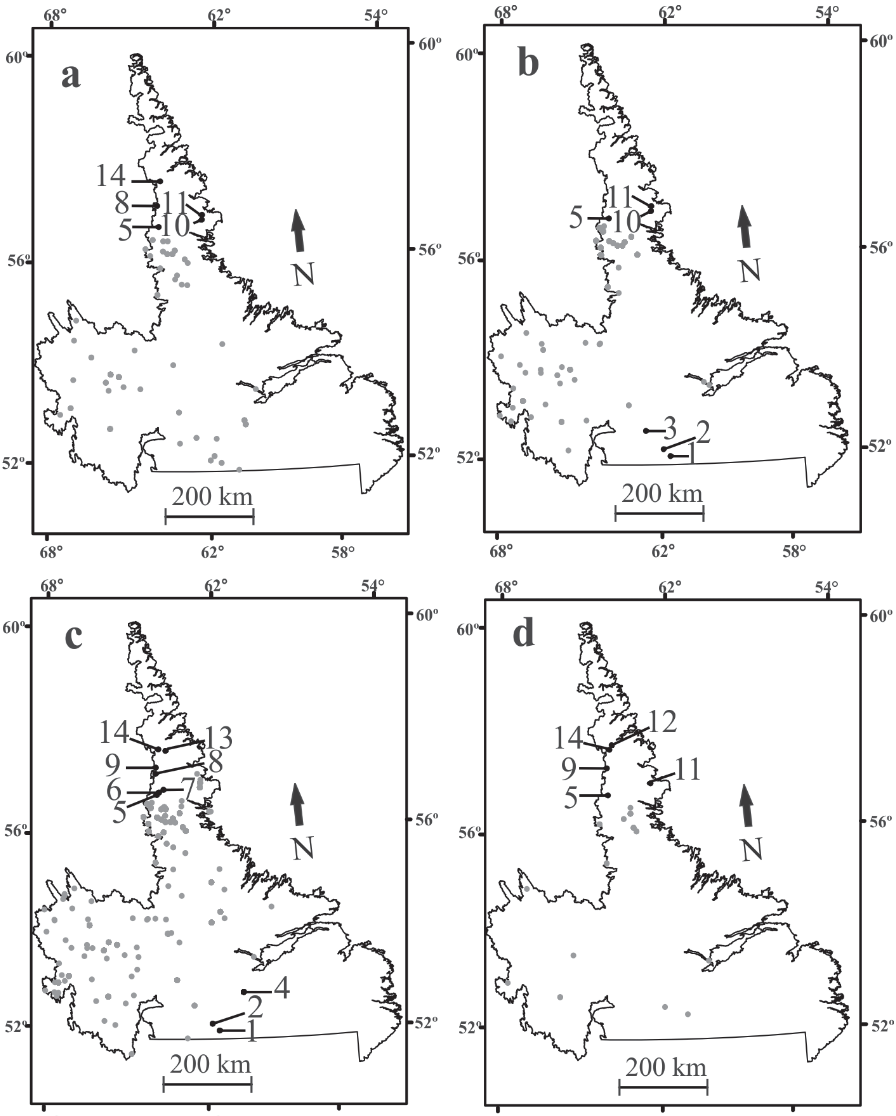

FIGURE 2. Previously known ranges (grey circles; Black *et al*. 1986) and new locations (black circles) for a. Burbot (*Lota lota*), b. Round Whitefish (*Prosopium cylindraceum*), c. Lake Trout (*Salvelinus namaycush*), and d. Slimy Sculpin (*Cottus cognatus*) in Labrador, extending species ranges north or southeast. 1 = Little Guines Lake; 2 = Lac Avert; 3 = unknown lake; 4 = Lac Mercier; 5 = Lake Langille; 6 = Lake C3; 7 = Lake Rhonda; 8 = Lake Sabrina; 9 = Lake Tracy; 10 = Iglusuatahrusuak Lake; 11 = Alliger Lake; 12 = unnamed stream; 13 = LB20; 14 = LB50.

For example, Burbot, Lake Trout, and Slimy Sculpin specimens were identified from three lakes in two unnamed tributaries (Lake Tracy, Lake LB50, Lake LB20, Rivers 103 and 104). Both of these tributaries drain northward into the Hebron Fjord, which is much farther north than the Fraser Canyon (Anderson 1985). Further, lakes Sabrina and Langille are part of the Kingurutik River drainage, which flows south into Tikkoatokak Bay, a separate watershed located above the Fraser Canyon. This finding is supported by Jansson and Kleman (2004) who determined that there were large numbers of glacial lakes present in Labrador during the retreat of the Laurentide Ice Sheet. Water spillage from these lakes led to ~30 meltwater injection events spilling into the Labrador Sea. Thus, many overland colonization events could have occurred across northern Labrador. Using geomorphic maps and the direction of esker deposits, Jansson and

Kleman (2004) described several drainage routes, in addition to the Fraser Canyon route. Some extended farther north and included the Kingurutik, Hebron, and Koruc drainage basins (Figure 3). It is noteworthy that we sampled the isolated coastal lakes, which are part of Puttuaala Brook, near Okak Bay (Lake Alliger and Iglusuatahrusuak Lake), and discovered that Burbot, Round Whitefish, and Slimy Sculpin also existed with Lake Trout. These species were also present in lakes Langille and Sabrina, located on the Kingurutik watershed, bordering Puttuaala Brook. Therefore, it is probable that all four species dispersed into Puttuaala Brook from the Kingurutik watershed when glacial lakes, such as Naskaupi, released their waters, causing spillages from the Kingurutik drainage into neighbouring Pattuaala Brook.

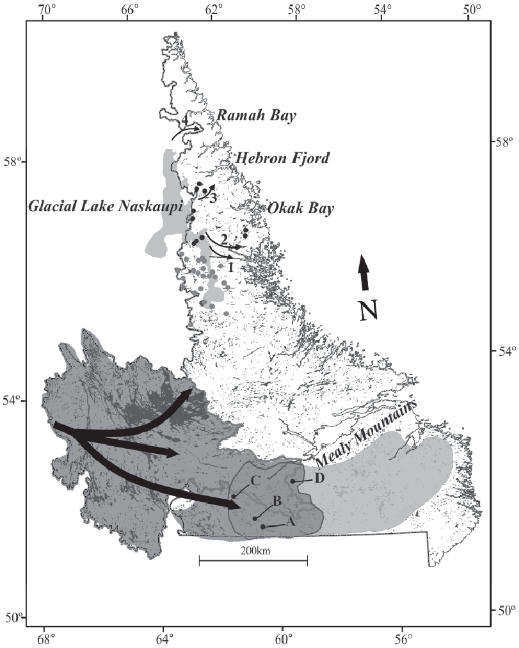

FIGURE 3. Possible colonization routes of freshwater fish species into areas of northern Labrador and location of the four sampled lakes in the transition zone: A. Little Guines Lake; B. Lac Avert; C. unknown lake; and D. Lac Mercier. The shaded dark and light grey areas represent the approximate locations of the Churchill and southeast Ichthyogeographic regions, respectively. The medium grey area, in northern Labrador represents glacial Lake Naskaupi, and the black arrows represent drainage routes adopted from Jansson and Kleman (2004): 1. Fraser River; 2. Kingurutik River; 3. Hebron Fjord; 4. Koruc River. Grey dots indicate locations of 25 lakes that highlight new occurrences within previously established ranges (Black *et al.* 1986) of four stenohaline freshwater fish species native to Labrador, Canada, collected during sampling events from 2007 to 2015. The large black arrows represent the overland dispersal routes taken by freshwater fish from Glacial Lake Barlow-Ojibway.

Waterways formerly connected following glacial retreat may have provided pathways for species dispersal into coastal areas. Thus, future investigations may extend the range of stenohaline species considerably northward. For example, we speculate that, following a pattern of drainage from Quebec, it is also likely that water spilled northward from glacial Lake Naskaupi, through the Koroc River system in Quebec, then eastward into Ramah Bay. This glacial spillway may have provided colonization routes. This is of particular interest because the lakes that may contain these species fall within the boundaries of the recently established Torngat Mountains National Park. Determining the postglacial movement of freshwater fish species in this region would provide an addition to the natural history database of the park.

Southern Labrador

The southerly collections of both Round Whitefish and Lake Trout demonstrate a range extension of ~65 km into the southeastern portion of Labrador. Of special interest is the discovery of Lake Trout in Lac Mercier, a small isolated lake that abuts the southwestern boundary of the Mealy Mountain Range and is ~50 km southeast of Happy Valley-Goose Bay. Many lakes near Lac Mercier have been sampled, and the occurrence of Lake Trout at this location represents a local anomaly. In general, the weather and geomorphology favour species tolerant of warmer waters, because most lakes are shallow and exhibit warm water temperatures in the summer (Meades 1990; Spence and Perry 2010; R.C.P. unpubl. data), and Longnose Sucker (*Catostomus catostomus*), White Sucker (*Catostomus commersonii*), Northern Pike, and Brook Trout, predominate (Black *et al.* 1986; R.C.P. unpubl. data). Lake Trout requires cold, well-oxygenated waters (Martin and Oliver 1980) with a thermal optimum of 10 ± 2°C (Magnuson *et al.* 1990).

Lake Trout in Lac Mercier are likely sustained because of a set of locally unique conditions that provide these optimal conditions. The lake is fed by three cool, well-oxygenated streams and has a small pocket of deep water that establishes a thermocline during the warm summer months (R.C.P. unpubl. data). To date, the closest lake reported to contain Lake Trout is over 100 km away from Lac Mercier. Therefore, their presence in this isolated deepwater lake suggests that, in the past, Lake Trout may have occurred across the entire region. It is possible that Lake Trout existed in southern Labrador following the final retreat of the Laurentide Ice Sheet into Ungava Bay, ~6000 years ago, when postglacial meltwaters produced cold water temperatures and much cooler mean atmospheric temperatures. Lake Trout may have been extirpated from most of this range by a warmer contemporary climate. Snucins and Gunn (1995) reported a similar situation for an isolated population of adult Lake Trout in Pedro Lake, Ontario. There, Lake Trout were sustained, in an otherwise unsuitable environment, by groundwater seepage that maintained a small pocket of cold water.

Although it is possible that Lake Trout were introduced to Lac Mercier, it is not probable. With a human population of less than 30 000, Labrador is sparsely populated (Newfoundland Labrador Census 2016). At the time of this discovery, Lac Mercier was separated from Happy Valley-Goose Bay by the Churchill River and an absence of roads. This small lake was located in an isolated area of Labrador and surrounded by pristine old-growth forest that had never been harvested. The absence of infrastructure meant that the only way into Lac Mercier was by float plane and, as Mercier is not recognized as a quality fishing destination, the potential for human introduction is minimal. Furthermore, the species complement in Lac Mercier included most of the species that co-occur with Lake Trout in the Churchill drainage, including Longnose Sucker, White Sucker, Northern Pike, Burbot, Longnose Dace, and Brook Trout.

Black *et al.* (1986) theorized that the main postglacial dispersal route into Labrador was from Quebec. The most probable pathway was via glacial Lake Barlow-Ojibway, moving across Quebec, north and south of the Otish Mountains, through proglacial lakes and watershed transfers during postglacial rebound. This route gave fish access to the headwaters of the Churchill River and to tributaries in Labrador. From there, species moved southeasterly, colonizing via tributary headwaters or through main stem migrations, moving up the Churchill drainage tributaries. At the bottom of the Churchill drainage, only a few species successfully colonized the furthest southeastern portion of Labrador, because the Mealy Mountains or sea dispersals served as barriers to most.

However, the Lake Trout population in Lac Mercier indicates another explanation is possible for the impoverished species composition in the southeast ichthyogeographic region. Black *et al.* (1986) suggested that the paucity of species found below Lake Melville and east of the Little Mecatina River could be attributed to the Mealy Mountains, which served as a barrier to species potentially arriving from the Churchill drainage.

Nevertheless, some Churchill drainage species are present, including Longnose Sucker, White Sucker, and Northern Pike. These are considered cool water species tolerant of warmer waters than Lake Trout and Lake Whitefish (*Coregonus clupeaformis*; Wismer and Christie 1987). The presence of these cool-water-tolerant species provides some indirect evidence that, at one time in the distant past, Lake Trout may have also been present in southeastern Labrador. If the Mealy Mountains were not a barrier to colonization of the area by warmer water species, it is unlikely that they were for coldwater species. The idea that the Mealy Mountains served as a barrier to some species, while allowing others to pass is predicated on varying swimming performance. The swimming ability of Lake Trout falls well within the ranges of all the warmer water tolerant species listed above and matches that of Brook Trout (Peake 2008). Therefore, it is more probable that a gradual conversion to unsuitable habitat, and not topographic barriers, led to the impoverished species complement. Supporting this assertion is the observation that lakes become shallower and summer temperatures warmer in a southwest to southeast direction (Figure 4). Thus, this combination of relatively shallow waters and warm temperatures likely created the observed species complement in southeastern Labrador.

The species complement in the deep lakes of southwestern Labrador includes both cool water and coldwater species such as Lake Whitefish, Brook Trout, Burbot, Lake Trout, Longnose Sucker, Northern Pike, Round Whitefish, and White Sucker. In contrast, we sampled many large lakes in all the major watersheds of the southeast region, including Traverspine, Kenamu, Eagle, and Paradise River watersheds, and found that most lakes were shallow (Spence and Perry 2010). The Eagle and Paradise Rivers watersheds comprise a large area of the southeastern region and drain areas of 10 824 km^2 and 5276 km^2, respectively. Both rivers have as their source shallow string bogs and glides (Anderson 1985). These shallow lakes contain fishes that have greater thermal tolerances for warmer waters or, in the case of Brook Trout, have adaptive strategies to sustain themselves during critically warm events (Petty *et al.* 2012). Thus, cool water species such as Longnose Sucker, White Sucker, Northern Pike, and Brook Trout were present while Burbot, Lake Whitefish, and Lake Trout were absent.

Lac Mercier is situated at a longitude that we consider to be part of a larger transition zone between the Churchill and southeast ichthyogeographic regions. In this zone, the topography of the land begins to change, with lakes becoming shallower from west to east (Government of Newfoundland and Labrador unpubl. data). In the area, coldwater species persist only in lakes that consistently maintain the appropriate thermal properties, while species with higher thermal tolerance are present in most lakes. For example, Lac Mercier was not the only location where we found a remnant population of a coldwater species. To the south of Lac Mercier, we sampled two lakes

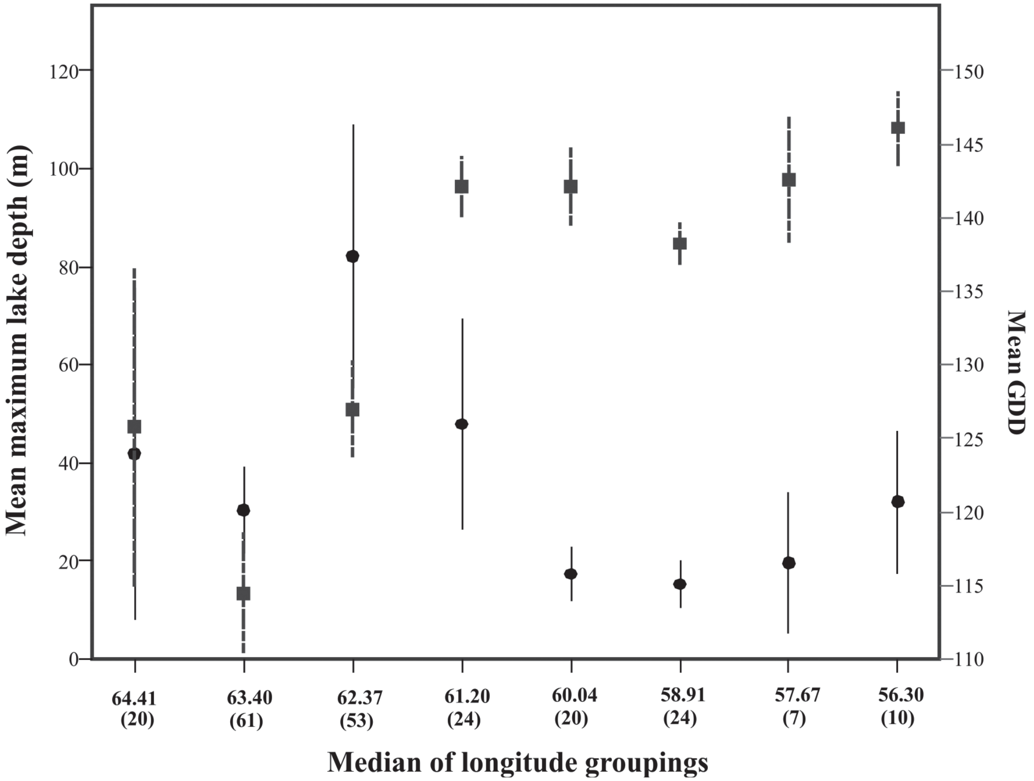

FIGURE 4. Mean maximum lake depths (●; calculated using model of Hollister *et al.* 2011) and mean growing degree-days (■; GDD; NRCan 2020), with 95% CI, for lakes in southern Labrador (all sampled lakes were below 53° latitude). Lakes were grouped longitudinally by depth (from west to east); number of lakes in each grouping is shown in parentheses under median for lakes in the group. Shape data from Natural Resources Canada (http://cfs.nrcan.gc.ca/projects/3) were used to assign mean annual temperature norms to each lake.

that contained Lake Whitefish and Round Whitefish, but not Lake Trout. Both species of whitefishes have slightly higher optimum thermal growth temperatures than Lake Trout (Hasnain *et al.* 2010). To the east of Mercier, we sampled several lakes that had Burbot but no other coldwater species. Burbot has a warmer optimum thermal growth temperature than either the whitefishes or Lake Trout (Hasnain *et al.* 2010).

Our study supports the hypothesis of three ichthyogeographic regions formulated by Black *et al.* (1986). However, our discovery of Burbot, Round Whitefish, Lake Trout, and Slimy Sculpin in other drainages above the Fraser River watershed in northern Labrador suggests that an alternative explanation of colonization pathways may be required. Rather than marine dispersal accounting for the presence of stenohaline species in coastal lakes near Okak Bay, it is more probable that an overland pathway led to their presence.

In southern Labrador, Round Whitefish and Lake Trout have been found farther to the southeast, beyond their formerly reported range limits. In addition, the discovery of an isolated pocket of coldwater species in Lac Mercier suggests that Lake Trout were present in the region since the last ice age, but environmental warming might have led to range contraction. This contraction may have led to the impoverished species complement currently found in the southeastern portion of Labrador. The isolation of this Lake Trout population (~100 km from the nearest Lake Trout lake population) may indicate that it is genetically distinct and deserves special conservation status. Future studies investigating the genetic structure of Lake Trout in Labrador may provide insights into this interesting fish population. Furthermore, the examination of genetic structure across all freshwater species would assist in validating colonization patterns as well as help identify evolutionarily distinct lineages.

Author Contributions

Writing – Original Draft: R.C.P. and D.G.K.; Writing – Review & Editing: R.C.P. and D.G.K.;

Conceptualization: R.C.P.; Investigation: R.C.P. and D.G.K.; Methodology: R.C.P. and D.G.K.

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Data accessibility

The Government of Newfoundland and Labrador Provincial Aquatics Database and Archive (PADA) houses the data contained in this manuscript. Access to data contained in PADA may be gained by submitting a written request to the Department of Fisheries, Forestry and Agriculture, Forestry and Wildlife Branch, P.O. Box 2006 Corner Brook, Newfoundland and Labrador A2H 6J8.

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Vocal repertoire, harmonic structure, and behavioural context in Red-throated Loon (*Gavia stellata*)

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Abstract

Among the five loon species (Gaviidae), Red-throated Loon (*Gavia stellata*) is the oldest lineage and is the most divergent in morphology and vocalizations. We substantially expand earlier description of calls for a nesting pair and non-breeding birds on Haida Gwaii, British Columbia, Canada. Three major calls used by the nesting pair (Quack, Wail, Plesiosaur) were all low frequency (700–3000 Hz) with multiple harmonics, calls that were also used by non-breeding birds without territories that overnight on freshwater lakes. Call duetting in the Wail and Plesiosaur, as well as sexually dimorphic frequencies and structure within the duets, typically occur in territorial display or pair interactions. The nesting pair used several calls audible only at short distances (Coo, Extended Coo, Staccato, Soft Raack) that were low frequency (200–1200 Hz), graded in behavioural intensity and that resulted in chick responses, including feeding or return to nest. A high amplitude Loud Raack was used by the female and is associated with flight incentives for pre-fledged chicks. Vocalizations of chicks, usually feeding solicitations to the adults, develop from simple chirps in the first week following hatch to more complex calls resembling the Wail and the Plesiosaur calls just prior to fledging. Although the majority of our acoustical descriptions are limited to a single nesting pair where sexes could be differentiated, these represent the first quantification of sound frequency, harmonic structure, and duration, most often associated with context-specific responses, and are suggestive of syntactical content to the vocal repertoire of this basal taxon.

Key words: Avian song; duetting; Drizzle Lake Ecological Reserve; *Gavia stellata*; Gaviidae; Haida Gwaii; harmonic structure; sexual dimorphism; sonogram; vocalizations

Introduction

The widely recognizable vocalizations of loons (Gaviidae) commonly define the acoustic landscape of northern hemisphere lakes and, as with many avian species, calls have multiple functions (Catchpole 1982; Wiley and Richards 1982). In addition to territoriality, studies in Common Loon (*Gavia immer*), the most southerly of the loon species, demonstrate that their vocalizations also include information such as levels of aggression (Rummel and Goetzinger 1975; Mager and Walcott 2014), body condition (Mager *et al.* 2010), competitive ability (Walcott *et al.* 2006), and possibly individual recognition (Walcott *et al.* 1999, 2006; Mager *et al.* 2010). Such characteristics support emerging views in animal communication that intraspecific variation in call structure can have referential or syntactical context (Templeton 2005; Wilson and Evans 2012; Suzuki 2016).

Red-throated Loon (*Gavia stellata*) is the most northerly of the loons; they are ecologically distinct in nesting on ponds or small lakes, often without fish, and flying to larger water bodies to capture and return fish to the territory (Huxley 1923; Reimchen and Douglas 1984a). This species appears to be the least derived morphologically from fossil loons and is considered the sister group to all other Gaviidae, possibly with a 20 million year separation time from other loons (Sprengelmeyer 2014). Consequently, the vocalizations of this basal taxon are of considerable interest for comparative analyses. Early investigations were descriptive (Selous 1912; van Oordt and Huxley 1922; Huxley 1923; Johnson and Johnson 1935; Keith 1937). Sjölander (1977), provided the first sonogram sketches and situational information for vocalizations and visual displays, and offered a framework for comparisons among loon species (Sjölander 1972, 1976, 1978). We provided audio tapes, basic call descriptions, and information on behaviour associated with several calls of Red-throated Loon on Haida Gwaii, British Columbia as personal communications which were then included in summaries of Red-throated Loon life history (Barr *et al.* 2000; Rizzolo *et al.* 2020). In the current manuscript, we present additional data on vocal repertoire, acoustic structure of calls, and behavioural contexts of vocalizations of a breeding pair of Red-throated Loons on an ecological reserve during the nesting period, as well as vocalizations of non-breeding birds that occupied the reserve nocturnally during the summer (Reimchen and Douglas 1980). Because the sexes exhibit differences in behaviour in feeding the young, in territorial defense, and in responses to territorial intrusions (Reimchen and Douglas 1985), we give special attention to differences between the sexes in calls. We document duetting behaviour of nesting pairs and examine some of the ontogenetic changes in vocal structure.

Methods

During biophysical surveys of 184 ponds and lakes on Haida Gwaii, British Columbia, Canada (1976–1989), we located 34 nesting territories of Red-throated Loons (Douglas and Reimchen 1988a). While the vocal behaviour was generally comparable among breeding pairs throughout this area, the diversity and specificity of calls encouraged closer study. Consequently, on an ecological reserve in the same archipelago, we collected observational, video, and audio data on nesting and non-breeding Red-throated Loons, which allowed us to broaden their described repertoire, characterize the contexts of calls and the extent of sexual dimorphism, and document the ontogeny of vocalizations. Simultaneous studies on the parental contribution to feeding regime throughout the seven-week pre-fledging period (Reimchen and Douglas 1984a) and on differential roles of the sexes in feeding and territorial defence (Reimchen and Douglas 1985) allowed a broad ecological context to the structure and function of calls.

Drizzle Lake Ecological Reserve is located on a broad expanse of *Sphagnum* bog, ponds, and lakes on the north-eastern region of Haida Gwaii, British Columbia (53.934056°N, 132.072184°W). Thirty-six species of aquatic birds have been observed on this 110 ha dystrophic lake, the majority showing regular seasonal and numerical abundance, of which Red-throated Loon and Common Loon accounted for the greatest yearly numbers (Reimchen and Douglas 1984b). Non-breeding Red-throated Loon, usually in pairs, occupied the lake from April to August, generally flying in from adjacent marine waters at dusk and leaving at dawn, with maximum evening numbers (19) occurring in July (Reimchen and Douglas 1980, 2021). Common Loons, none of which nest on this lake, were daily visitors, primarily diurnal, with peak numbers (83) in July (Reimchen and Douglas 1980, 2021). Nesting Red-throated Loons laid 14 clutches in the watershed (1976–1986; Douglas and Reimchen 1988b, 2021).

Non-breeding Red-throated Loons were observed from an elevated platform on the lake shore while breeding birds were observed from blinds within 8 m of the nests. General observations of abundance and distribution of non-breeding loons were maintained during 1977–1985 (Reimchen and Douglas 1980, 1984b). Three types of data were used for analysis: written observations, audio recordings, and video recordings.

Written observations

A total of 3620 written observational records consisted of (a) 2913 records of the breeding pair and pre-fledged young at Drizzle Lake (27 July–14 September 1982, 348.5 h), (b) 606 records of non-breeding birds (4 April–13 September 1980, 101.6 h; 14 April–14 May 1983, 21.3 h), and (c) 101 records of the pair with young on the bog pool (1 August–8 August 1981, 22.7 h). Each record contained date, time, location, identity (species), chick age, sex (when possible), breeding or non-breeding, type of vocalization or visual display and its context, the behaviour of other species that the birds interacted with and, for breeding birds, behaviour related to feeding or to infringements into the territory (~50 m radius from the shoreline nest) by other species. In written records, calls of breeding adults to pre-fledged young were grouped as "low calls", although later analysis with audio and video showed four distinct calls.

Audio recordings

Audio recordings were made in 1984 to quantify call structure. Vocalizations of a single pair of breeding Red-throated Loon and their two chicks and several non-breeding birds on Drizzle Lake were recorded using a Uher 4000 Report Monitor Tape Recorder (München, Germany) and a Dan Gibson parabolic microphone (EPM 200). Recordings were made on 24 days from 11 June to 2 August, for a total of 217 min covering 118 vocal bouts (89 bouts of the breeding pair and their two chicks, 29 of non-breeding, and six of both groups together). Playback of audio recordings was measured for duration of bouts, and in some cases, call durations and call interval lengths. Sonograms of recorded calls were made on a Kay Elemetrics Digital Sonagraph 7800 Analyzer and 7900 Printer (Lincoln Park, New Jersey, USA). Several calls from different bouts for each call were analyzed over the 8000 Hz range at both 45 Hz (for frequency discrimination) and 150 Hz (for time discrimination) bandwidth filters. For comparison of successive calls, a frequency range of 4000 Hz was used to extend the sonogram to 5.12 s duration. Frequency and duration data were obtained from sonograms using grids marked in Hertz (Hz) or in mm (converted to ms). The margin of error is ± 60 Hz and ± 0.008 s. The term “amplitude” is used in a relative sense because amplitude was not quantified on sonograms.

Video recordings

Video recording using a Sony Portable Videocorder (AV-3400, Japan) equipped with an f 12.5–75 mm zoom lens or 1000 mm fixed lens were made of non-breeding loons in 1981 and two breeding pairs in 1980–1984, including recordings of two chicks in 1984 (1050 min). For breeding birds, recordings were primarily made of feeding of young by adults; in most feeding bouts, vocalizations were recorded with the videorecorder microphone. Video recordings of visual displays were analyzed to produce descriptions of displays and to link vocal and visual displays. Contexts of different low amplitude calls were obtained from video recordings. Because sex of the adult birds was known for each recorded feeding bout, verification of sexual dimorphism in calls was possible.

Representative audio recordings were uploaded to the Macaulay Library at the Cornell Lab of Ornithology (see Appendix 1 for accession numbers and hyperlinks). Quantitative data of vocalizations (duration, intervals, sound frequencies) were compared with unpaired *t*-tests and analysis of variance (ANOVA; SPSS v25, IBM, USA).

Results

Vocalizations of nesting and non-breeding adult Red-throated Loon had dominant frequencies from 700 to 3000 Hz and all showed harmonics in at least one segment of the call. Although the different calls shared characteristics and sometimes were continuous, we recognized nine calls based on their acoustic characteristics, five of which were higher amplitude (Quack, Wail, Plesiosaur, Kark, Loud Raack) and four lower amplitude calls (Coo, Extended Coo, Staccato, Soft Raack) that were used in adult-chick interactions.

Quack

Context—The Quack was used almost exclusively in flight (99.3%, $n = 292$ bouts comprised of about a dozen birds every night throughout the breeding season) by nesting and non-breeding adult Red-throated Loons of both sexes during lake arrivals, departures, and over-flights. This call was also heard in flight over marine waters. Conspecifics on the surface responded to the in-flight Quack with surface vocalizations and displays (Wail, Plesiosaur).

Acoustic structure—The basic Quack is a single syllable call averaging 99 ms (range 72–112, SE 2.9) in duration ($n = 19$) between 1000 and 2000 Hz with approximately two or three dominant harmonics within each call, repeated about three to four times per second (Figure 1, Appendix 1). Quacks occurred in all birds and were given repeatedly in flight; we quantified this call in the nesting pair. The calling rate increased towards the end of each bout as the birds approached the lake but they did not Quack as they descended to the surface. Average intervals between Quacks (149 ms) varied within and among bouts (range 106–277, SE 8.3, $n = 33$ intervals in four call bouts from the breeding pair). During the final approach to the lake, the loons often (proportions not recorded but heard many times over many years) gave a distinctive extended Quack, approximately three times the duration of a single Quack, ending in a short (~100 ms) ‘note’ of a single dominant harmonic rising and falling near 1700 Hz.

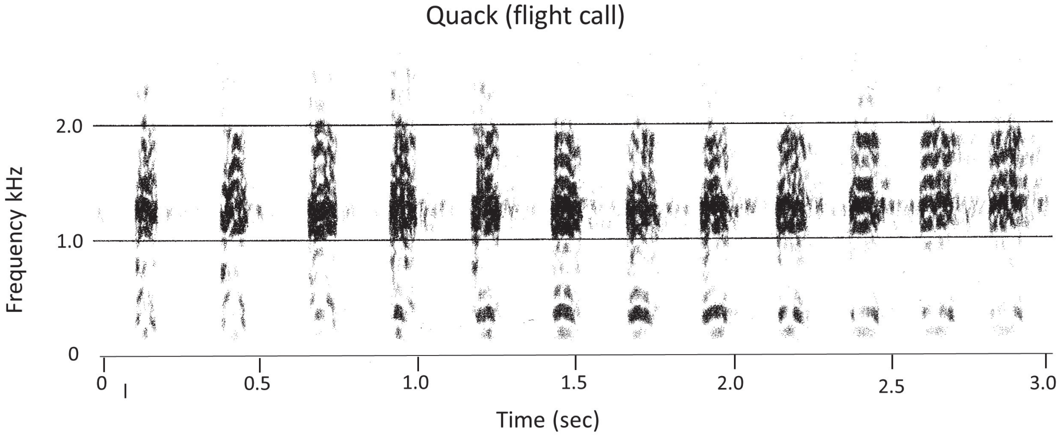

Figure 1. Representative Quack sequence of the dominant (99%) flight call given by Red-throated Loon (*Gavia stellata*) on Haida Gwaii, western Canada. Bandwidth filter: 150 Hz.

Kark

Context—This is a warning call and made primarily on water (78%, $n = 83$, other 12% in flight) by nesting Red-throated Loons, either singly or in pairs in response to lake or shoreline intrusions into the territory.

Acoustic structure—The Kark is a single syllable call, averaging 204 ms (range 152–240, SE 7.4, $n = 14$ from the nesting pair) between 1000 and 2000 Hz, similar in structure to the Quack, but audibly distinct in having significantly longer durations (unpaired t_{31}=14.1, $P < 0.001$) and arrhythmic repetition within bouts (Appendix 1). Numbers of harmonics ranged from three to five in 10 different Kark calls. Unlike the Quack, intervals between Karks were highly variable, both within and between bouts, ranging from single to multiple calls. The maximum recorded rate was 23 Karks in 27 s by the nesting pair when a Bald Eagle (*Haliaeetus leucocephalus*) perched on a tree near the nest. In a Kark bout by the male of the nesting pair, intervals between eight calls varied from 1.5 to 8.6 s, with intervals increasing between each successive call. During execution of the call, the neck was vertically extended, with the head held horizontal to the water or angled slightly up.

Wail

Context—The Wail includes a diversity of closely-related calls that are voiced on the lake surface both by nesting pairs, singly or as a duet (cooperative vocalizations by pair-mates), or by non-breeding individuals. The most consistent use was in response to conspecifics in flight that were vocalizing Quacks above the lake. The actual number heard would be in the thousands as this was the most common vocalization on the lake and was heard in response to approaching Red-throated Loons in flight and occurred for every arriving pair throughout the summer each year. Of 113 bouts of Wails in the nesting territory, 53% were performed as duets. Wail duets were in some cases antiphonal (calls of the two birds alternating and non-overlapping). For example, following the flight of a Bald Eagle over the territory the male and female nesting pair performed an antiphonal Wail bout lasting 245 s, in which the female wailed 32 times and the male 37 times. As well, the pair had duets of overlapping wails (e.g., in a 54 s bout, the female made three calls while the male made nine calls; in a 120 s bout, the female made 42 calls while the male made 22 calls). Nesting pairs also used the call on detection of potential threats including overflight of Bald Eagles and Common Raven (*Corvus corax*) near nesting territories. Loons displayed a distinctive posture during the Wail (Figure 2 inset drawing). From a head up position, the head and neck move forward and down. By the middle of the call, the head and bill are parallel to the water and the lower part of the neck is immersed; the bird remains in that posture until the end of the call. When the neck is outstretched, the throat directly below the rictus is distended. During parental feeding, the fish held in the adult's bill did not appear to alter the posture or sound characteristics of the Wail. This call was never observed with the neck and head in a normal upright position.

Acoustic structure—The Wail, ~1 s in duration (details below), has two dominant harmonics near 1000 Hz and 2000 Hz, initial frequencies rising ~300 Hz in the first quarter of the call and gradually decreasing towards the end (Figure 2, Appendix 1). The female of the nesting pair (Figure 2a) produced Wails that are ~150 Hz higher frequency than the male (Figure 2b) during the central (average 1100 versus 965 Hz, unpaired $t_{17} = 2.51$, $P < 0.02$) and terminal phase (average 880 versus 720 Hz, unpaired $t_{16} = 2.43$, $P < 0.05$) of the call and marginally, but not statistically higher, during the onset (average 960 versus 800 Hz, unpaired $t_{17} = 1.46$, $P < 0.25$). The beginning of the call had the highest variability in number of harmonics (2–8 for the female and 2–13 for the male). The female occasionally had a "croaking" quality evident as an ~1000 Hz band of noise around the dominant harmonic. Duration of the individual Wails was marginally, but not significantly, longer in the female (average 1266 ms, range 1161–1663, SE 56.7, $n = 9$; male 1158 ms, range 714–1471, SE 66.4, $n = 10$; unpaired $t_{17} = 1.29$, $P = 0.23$). Individual Wails were often given in succession, the length of which varied with the context: several Wails occurring with the over-flight of other Red-throated Loons to continued Wailing when Bald Eagles were present in the territory.

Plesiosaur

Context—The Plesiosaur is a high amplitude call and stereotypic display used by both nesting and non-breeding loons. For nesting birds it was performed, individually or in duet, when the partner arrived in the territory or prepared to depart; a Plesiosaur bout was often a progression from a Wail duet elicited by in-flight Quacking of a loon over the territory (Appendix 1). We heard this often (not quantified but less than frequent and more than occasional) when watching nesting pairs on multiple years. It was also used during territorial intrusions from Common Loons and conspecifics. In the latter case, intruders occasionally (not quantified) participated in the Plesiosaur calling. Non-nesting birds in the centre of the lake commonly performed the Plesiosaur call and display, individually or in groups, usually directly following a Wailing bout in response to conspecific overflights. We were not always able to determine the stimulus for Plesiosaur calls in these loons because they occupied the lake in low light conditions during twilight.

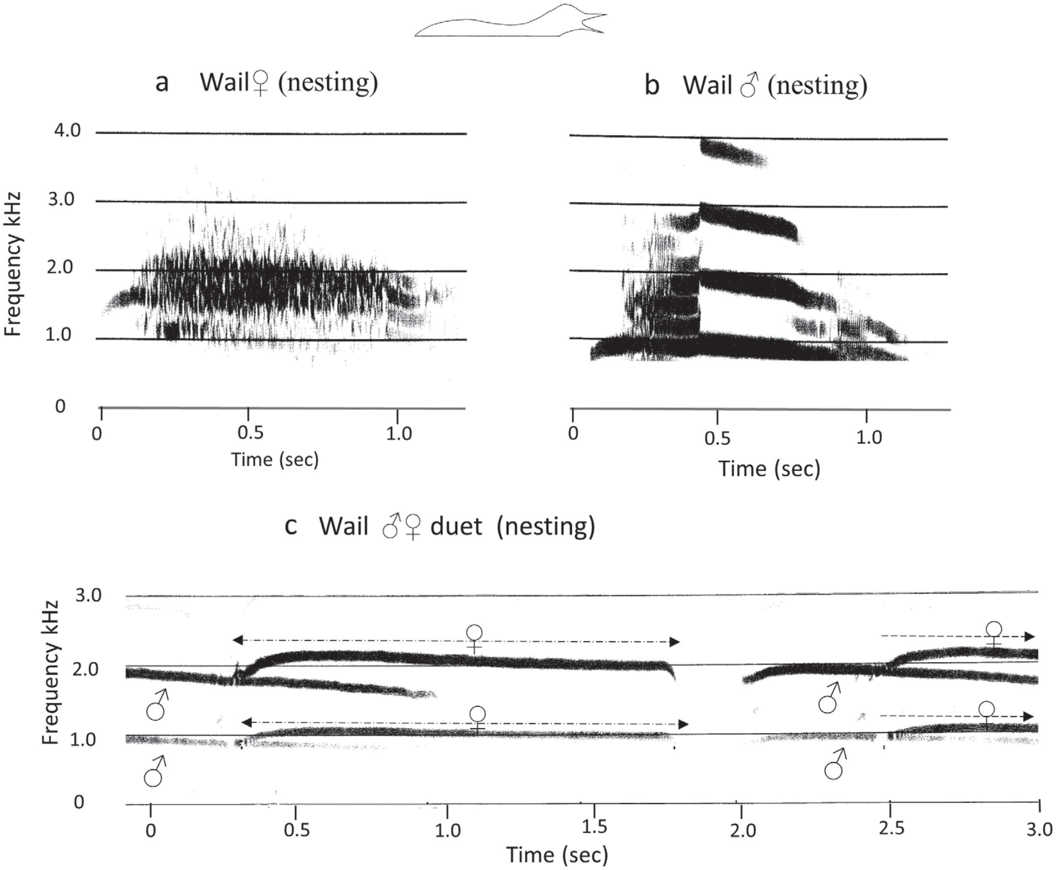

FIGURE 2. Variation in Wail calls given by a nesting pair of Red-throated Loon (*Gavia stellata*) on Haida Gwaii, western Canada. a. female, b. male, c. female/male duet. Drawing at the top of the figure shows body position during vocalization. Bandwidth filter: 150 Hz.

Acoustic structure—The Plesiosaur is a structurally complex sexually dimorphic call (Appendix 1). The female call (Figure 3a) consisted of broadband noise in the range of 1000–2500 Hz that had a growling or rattling quality. Underlying harmonics show a dominant mean frequency near the central part of the call at 1610 Hz (range 1500–1825, SE 46.5, n = 6 from the nesting pair) and the call terminated in a short, ascending phrase that lacked a noise overlay (dominant frequency average 1459 Hz, range 1375–1500, SE 56.8, n = 7). Durations of the female Plesiosaur call and intervals between calls in a bout were relatively consistent (duration: average 435 ms, range 400–576, SE 9.14, n = 24; intervals: average 213 ms, range 160–272, SE 11.2, n = 11). The male of the nest pair Plesiosaur call (Figure 3b) had a dominant frequency that ranged from 750 to 1160 Hz (average 963, SE 41.7, n = 18) throughout most of the call, with a rapid increase in frequency at the end of the call (range 950–1500 Hz; average 1123, SE 88.6, n = 6). Superimposed on this was a band of rapid sound pulses covering a frequency range of 750–2750 Hz; this made the vocalization appear like rhythmic pulses of noise rather than a structured call. Durations of the call by the nesting male (average 821 ms, range 71–959, SE 15.3, n = 18) were about twice as long as those of the female (note that all sonograms did not have complete information hence the different sample sizes from the nesting pair). Plesiosaur calls by a non-breeding bird (Figure 3c) showed comparable structure to that of the nesting male, differing primarily in its frequency range. Individual Plesiosaur calls by non-breeders were difficult to isolate aurally and in sonograms because the recorded birds were usually in groups and at a distance. In the nesting pair, the call and display occurred primarily (81%, n = 100) as a duet, in which there were few silent segments (Figure 4). In groups of non-breeding birds that

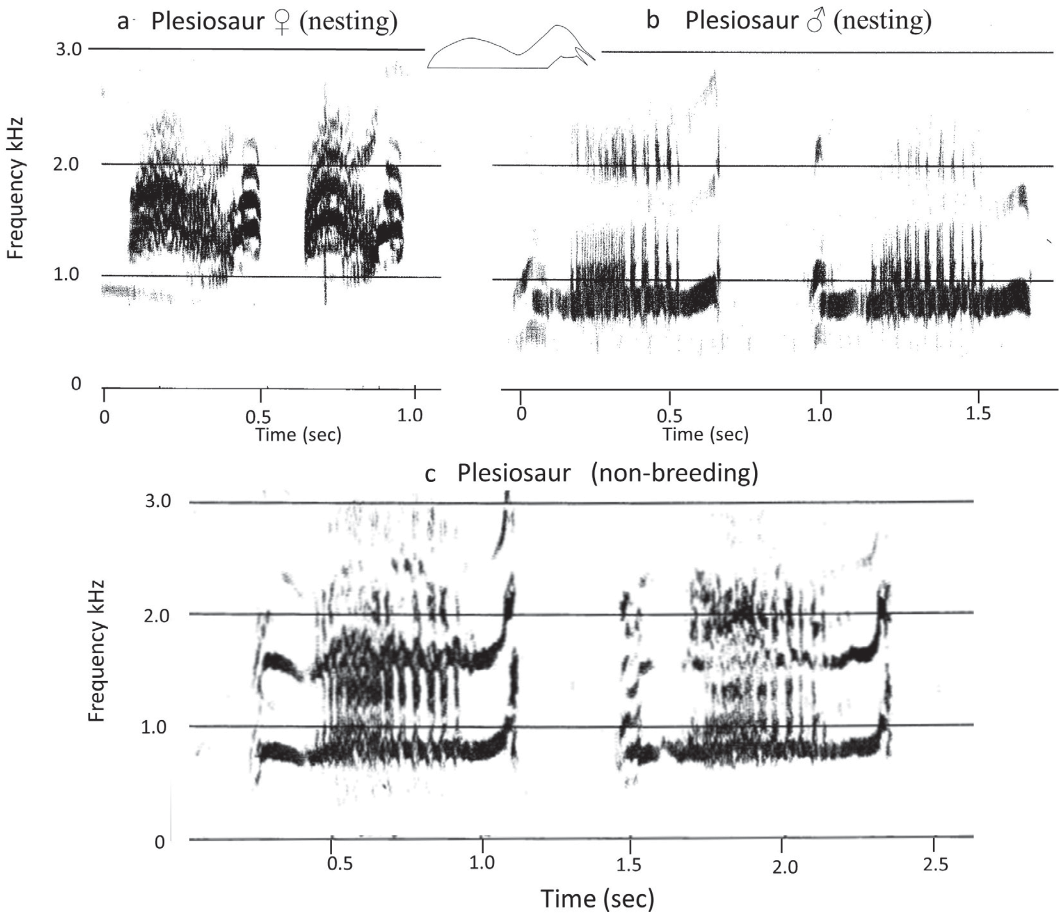

FIGURE 3. Variation in Plesiosaur calls of a nesting pair and non-breeding Red-throated Loon (*Gavia stellata*) on Haida Gwaii, western Canada. a. female and b. male of nesting pair. c. Non-breeding adult Red-throated Loon (similar to male call but sex could not be reliably determined). Drawing at the top of the figure shows body position during vocalization. Bandwidth filter: 150 Hz.

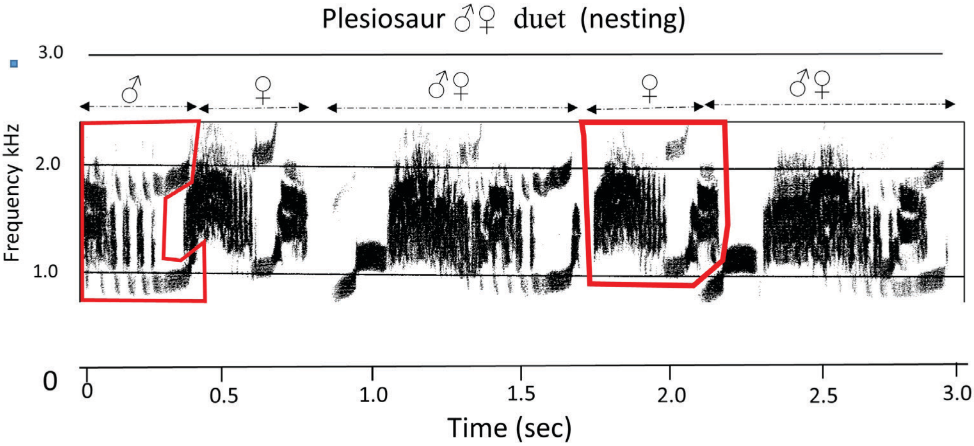

FIGURE 4. Duetting Plesiosaur call of a nesting female/male pair of Red-throated Loon (*Gavia stellata*) on Haida Gwaii, western Canada. Separate male and female calls are outlined. Bandwidth filter: 150 Hz.

aggregate on the lake during dusk, up to seven loons were observed participating in a Plesiosaur call and display and in most instances, these bouts were preceded by Wail bouts.

Display—The majority (97%) of Plesiosaur calls (*n* = 243, all from the breeding pair) were accompanied by the Plesiosaur display, the few exceptions occurring during calls in flight (six cases) and on the nest (one case). In the Plesiosaur display (Figure 3 inset drawing), termed the "Plesiosaur race" and "snake ceremony" by Huxley (1923), the body is held high in the water with the neck arched and the head angled downward, with the bill tip at water level or immersed. The neck appears to be contracted in length and greatly expanded in circumference; the throat immediately below the rictus is distended. After a bout or between calls the birds often shake the head and bill. The male of the nesting pair was seen to Plesiosaur call and display with a fish in the bill. A variation on the display is a "winged" Plesiosaur, where one or both of the wings are held out of the water but bent at the wrist and angled slightly backwards so that the wing tip is immersed. The bird alternately extends the left and right wings, changes in wing extension coinciding with changes in direction of movement through the water, or both wings may be extended simultaneously. Most Plesiosaur displays involved abrupt changes in direction and loons sometimes traced a zigzag path through the water.

Vocalizations by the breeding pair associated with parent-chick interactions

Context—Seven calls were used by the adults of the breeding pair to solicit responses from their chicks. Four were low amplitude (Coo, Extended Coo, Staccato, Soft Raack) and were voiced primarily during feedings. Typically, an adult returned from the ocean with a marine fish in its bill and vocalized to a chick on the nest; in response, a chick entered the water and attempted to grasp and swallow the fish, after which it would be called back to the nest by the other adult. There were also three high amplitude calls used in parent-chick interactions. Two of these, the Wail and the Kark were given during proximity of the Bald Eagle (see Table 1 for number of times), following which the chicks either dove or swam rapidly to the shoreline where they sheltered in the emergent vegetation. A third high amplitude call was the Loud Raack used by the female in flight as a flight incentive to the chick during the week prior to fledging, usually followed by the young swim-flying over the water surface and attempting to take off.

Acoustic structure—The Coo (Figure 5a), only heard and recorded for the male (but heard in all nesting years), is a short (average 82 ms, range 56–96, SE 3.3, *n* = 20) low frequency (200–1200 Hz) call with multiple harmonics that was given singly or in short bouts. Frequencies could increase by 300 Hz during the initial part of the call and there were usually at least four harmonics. The length of Coo bouts varied considerably, as did the call rate within bouts (e.g., 15 Coos in a 90 s bout and 81 Coos in a 143 s bout). Coo bouts were sometimes followed by Extended Coo or Staccato bouts. The Extended Coo (Figure 5b), also only vocalized by the male, had a frequency and harmonic structure similar to the Coo, but longer duration (average 934 ms, range 625–1175, SE 66.3, *n* = 10), and with abrupt changes in dominant frequencies and number of harmonics within the call. During the calls, the adult assumed a normal body

Table 1. Calls used by a pair of breeding Red-throated Loon (*Gavia stellata*) during interactions with conspecifics and other bird species on Haida Gwaii, British Columbia, Canada. This includes interactions within the breeding territory and instances in which calls of other birds were audible within the territory. Species with fewer than five interactions excluded. RTLO = Red-throated Loon (*Gavia stellata*); COLO = Common Loon (*Gavia immer*); CORA = Common Raven (*Corvus corax*); BAEA = Bald Eagle (*Haliaeetus leucocephalus*); GWTE = Green-winged Teal (*Anas carolinensis*); CAGO = Canada Goose; BEKI = Belted Kingfisher (*Ceryle alcyon*); RNGR = Red-necked Grebe (*Podiceps grisegena*); GLGU = Glaucous-winged Gull (*Larus glaucescens*); SCAU = scaup (*Aythya* sp). A single interaction between Red-throated Loon and Bald Eagle which might last an hour, could have 50 sequential wails but this is considered one interaction.

Species	RTLO	COLO	CORA	BAEA	GWTE	CAGO	BEKI	RNGR	GLGU	SCAU
Interactions (*n*)	405	135	129	59	33	24	13	12	8	6
Vocal bouts (*n*) comprised of the following types of calls:	91	21	32	25	3	1	2	0	1	1
Wail	36	9	24	24	1	1	2	0	0	1
Plesiosaur	31	8	0	0	0	0	0	0	0	0
Kark	16	2	8	1	2	0	0	0	0	0
Loud Raack	6	0	0	0	0	0	0	0	0	0
Low calls*	2	2	0	0	0	0	0	0	1	0

*Coo, Extended Coo, Staccato, Soft Raack.

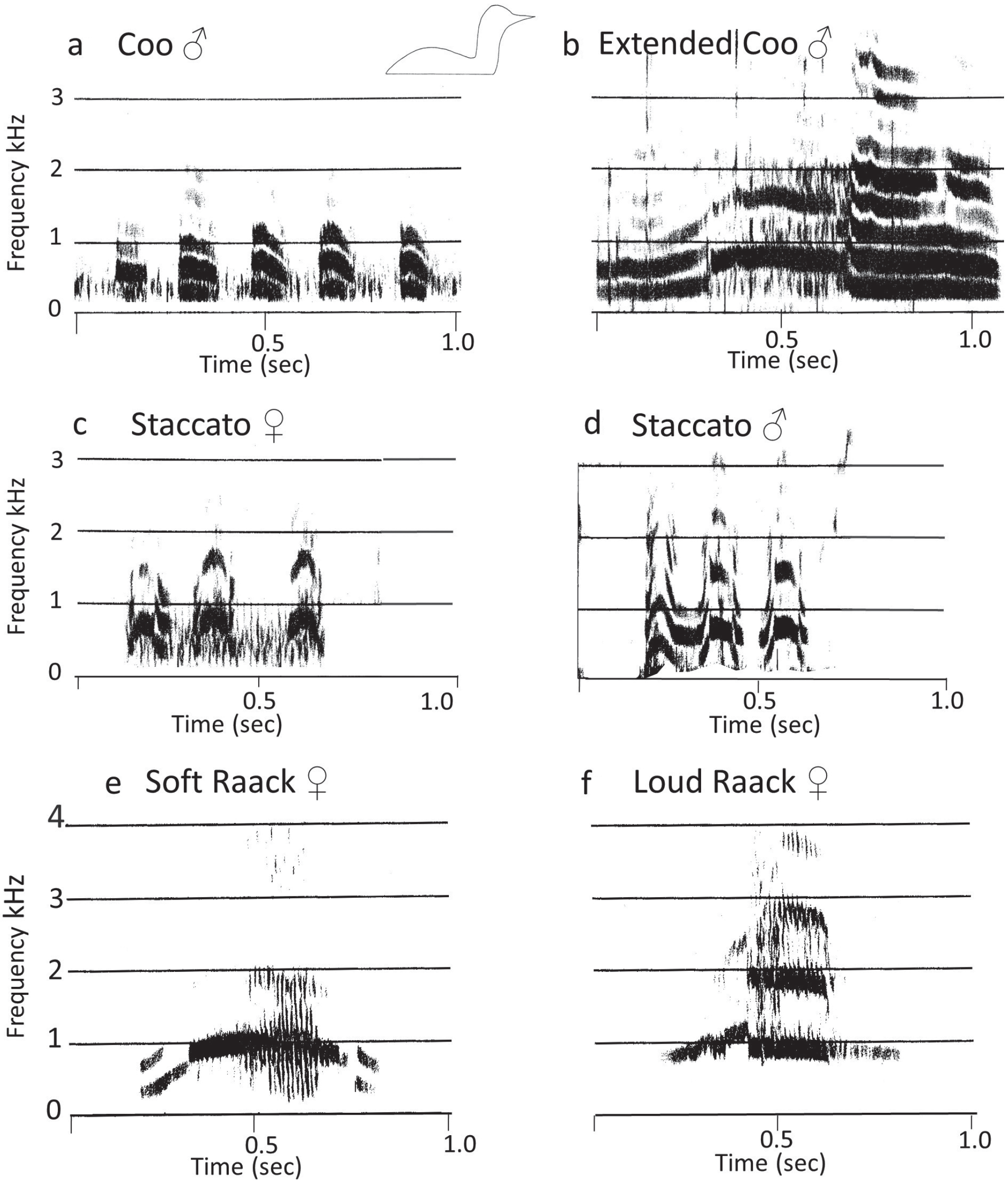

FIGURE 5. Representative vocalizations of a pair of adult Red-throated Loon (*Gavia stellata*) to their pre-fledged chicks in their nesting territory. a. Coo–male. b. Extended Coo–male. c. Staccato–female. d. Staccato–male. e. Soft Raack–female. f. Loud Raack–female. Drawing at the top of the figure shows body position during vocalization. Bandwidth filter: 150 Hz.

posture with no noticeable changes in bill opening. The Staccato, a short low frequency (500–2000 Hz) call occurring singly or in groups up to five was recorded for both the adult female (Figure 5c) and male (Figure 5d) and was the major (55%) feeding solicitation call. Number of harmonics varied from two to five, with the first harmonic the dominant frequency throughout and in each of the harmonics, the call had an initial increase in frequency, a central high amplitude phrase, and a terminal decrease in frequency. Dominant frequencies (measured in the central part of the call) were similar for the female (average 732 Hz, range 700–750, SE 11.1, *n* = 5) and male (average 756 Hz, range 680–810, SE 8.1, *n* = 19), respectively, as were the mean duration of calls (female average 90 ms, range 80–96, SE 1.5,

n = 5; male average 90 ms, range 56–138, SE 4.6, n = 24). Call rates ranged from 0.15/s to 0.73/s with total bouts ranging from 14 to 148 calls. Associated with the Staccato was a sporadic rapid bobbing of the head and bill which increased the conspicuousness of the fish to the chick; the fish was often reoriented in the adult's bill. The adult held its neck at an oblique angle and the fish's tail often dipped in the water. In the majority of cases, chicks responded to the vocalization with feeding behaviour, such as leaving the nest, swimming to the adult bird, or pecking, grasping, or swallowing the fish. The Soft Raack (Figure 5e), recorded only for the female, lasting about 600 ms, is initiated with a fundamental frequency near 325 Hz that increases gradually to a dominant harmonic near 800 Hz at a higher amplitude and ending with a short descending tone back to its initial low frequency. The call has up to three harmonics. The most distinct characteristic of the call was the superimposition of a wide-frequency band of "noise" that overlay the central part of the call, spanning frequencies of about 100–6000 Hz. The Loud Raack (Figure 5f, Appendix 1) was distinctly louder and harsher than the Soft Raack. We were only able to record several of these calls but it had a structure similar to the Soft Raack, with a low frequency onset (average 760 Hz, range 700–800, SE 27.8, n = 4), a high amplitude and frequency central phrase (average 900, range 780–970, SE 61.7, n = 3) at the beginning and a lower amplitude and frequency ending. The dominant frequency was the fundamental. Loud Raacks were most often given in short series (e.g., five calls in 34 s). Similar to the Soft Raack, the call had an overlay of noise, ranging in frequency from 625 to 4000 Hz. Gradation between the two calls was heard on one occasion, when a Soft Raack was transformed into a Load Raack by increased amplitude.

Vocalizations of chicks

Chicks of the nesting pair displayed a diversity of calls, ranging from simple chirps near hatching to calls closely resembling those of the territorial adults near fledging. The vocal repertoire (Figure 6) increased over the 46 day pre-fledging period. The simplest call was the Chirp that was used throughout and was associated with begging behaviour. The Chirp is a repeated short duration call with a dominant frequency at 2200 Hz and a second harmonic at 4600 Hz with a slight (100 Hz) ascending and descending variation over the call (Figure 6a). The Chirp, usually repeated 1/s (up to 86 Chirps/73 s) was given on the nest or in the water. By day four and five, the chicks began to vocalize a longer and more complex call that initially ascended and rapidly flipped between a dominant harmonic at 2200 and 3000 Hz in the central part of the call and descended on the 2000 Hz harmonic (Figure 6b,c). By day 27, in addition to the basic Chirps on each feeding, the chick gave a long but structurally simple call with two dominant harmonics near 1200 and 2400 Hz that were conserved throughout the duration of the call (Figure 6d). We heard a similar call again on day 44 with highly conserved frequencies throughout the duration although with each harmonic about 200 Hz less than the earlier call (Figure 6e). This call resembles the Wail that adults were vocalizing every day in response to overflights of other Red-throated Loons. On day 41, the chick gave a structurally complex call beginning with broad band noise between 1000 and 3000 Hz rising and following about 500 Hz over the broadband noise but then continuing with a single narrow band harmonic near 1100 Hz that gradually ascended to 2000 Hz (Figure 6f). This high amplitude call structurally resembles the Plesiosaur call of the adults and was used by the chick in response to flight solicitation by the adult female.

Vocal responses of the nesting Red-throated Loon pair to other species

Incursions into the nesting territory elicited varying vocal responses by the nesting Red-throated Loon pair (Table 1). The nesting pair responded vocally to 22% of birds that flew over the territory or approached the pair on the water surface (n = 824 total interactions resulted in 177 vocal bouts). The pair responded most often to Bald Eagles (42% of responses, 25/59), Common Ravens (25%, 32/129), and Red-throated Loons (22%, 91/405). Among the major vocalizations, Wails were the most frequent, with the highest response rate to Bald Eagle (96% = 24/25 vocal bouts). The Plesiosaur call was given in response to only two species, other Red-throated Loon (34%, 31/91) and Common Loon (38%, 8/21). The Kark was given in response to Bald Eagle, Common Raven, Green-Winged Teal (*Anas crecca*), Red-throated Loon, and Common Loon. Other species that intruded close to the nesting pair's territory, including Red-necked Grebe (*Podiceps grisegena*), Canada Goose (*Branta canadensis*), Green-winged Teal, scaup (*Aythya* sp.), Glaucous-winged Gull (*Larus glaucescens*), and Belted Kingfisher (*Ceryle alcyon*), received little or no vocal response from the nesting pair. Small groups of up to six Canada Goose occasionally swam within 10 m of the nesting loon pair without eliciting an obvious response. In one instance, an adult goose rested for about 5 min on the nesting platform adjacent (20 cm) to the Red-throated Loon incubating eggs, yet the loon showed no behavioural or vocal responses. As well, Red-necked Grebe foraging for fish within the nesting pair's territory (n = 12 events) elicited no vocal response or agonistic behaviour.

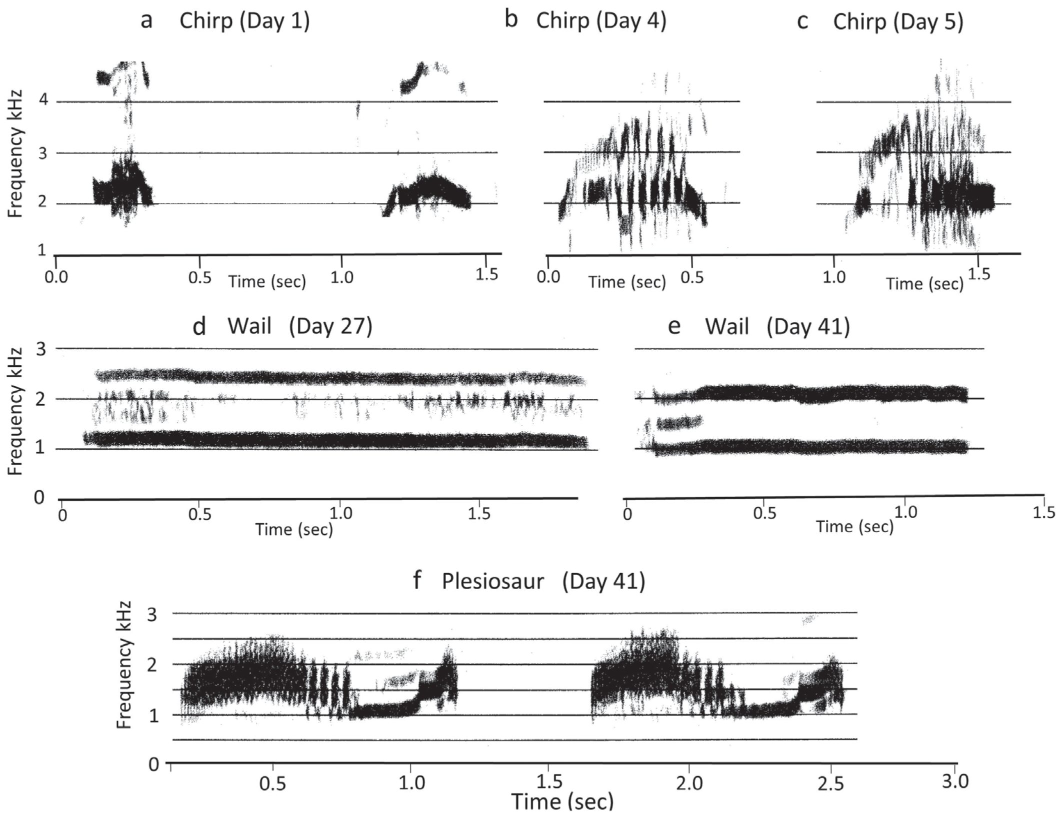

FIGURE 6. Ontogenetic variation in Red-throated Loon (*Gavia stellata*) chick vocalizations on Haida Gwaii, western Canada. a. Chirp (day 1). b. Chirp (day 4). c. Chirp (day 5). d. Wail (day 27). e. Wail (day 41). f. Plesiosaur (Day 41). Bandwidth filter. 150 Hz.

Discussion

Previous documentation of vocalizations in Red-throated Loon from northern Europe defined a repertoire of four calls, consisting of the roll-growl (Plesiosaur), mewing call (Wail), Kark, and cooing call (Coo; Huxley 1923; Keith 1937) while later studies by Sjölander (1977) in Iceland and Alaska added the cackle (Quack). Based on our audio recordings from one nesting pair and observations of numerous nesting and non-breeding pairs of loons from Haida Gwaii, British Columbia, we extend the previous studies and recognize nine calls (Quack, Kark, Wail, Plesiosaur, Coo, Extended Coo, Soft Raack, Loud Raack, and Staccato). Each of the Red-throated Loon calls has multiple harmonics, with the major harmonic between 1000 and 2000 Hz, which is the peak auditory sensitivity of Red-throated Loon (Crowell *et al*. 2015).

The major flight call of Red-throated Loon is the Quack which is used by both territorial and non-breeding pairs. This structurally simple call has no counterpart in other loon species but has some similarity in sequence, duration, and sound frequency to the 'Quack' of Mallard duck (*Anas platyrhynchos*; Abraham 1974), suggesting a common bioaccoustical adaptation among groups. Flight calls and timing are closely correlated with wing beat frequency in many bird taxa, including nocturnal flyers, and have a diversity of functions such as social positioning (reviews in La 2011; Berg *et al.* 2019). As well, the calls might act as a 'vocal altimeter' given the inner structure of the avian ear that allows sound distances to be estimated (Schnyder *et al.* 2014). Among the Gaviidae, Red-throated Loon has the highest flight requirements, making up to 1000 flights to large lakes or marine waters to obtain food for the young throughout the seven-week pre-fledging period, independent of the presence of fish in the nesting territory (Reimchen and Douglas 1984a). These flights commonly occur during twilight for both nesting and non-breeding birds when visual cues are limited (Reimchen and Douglas 1980) and where a basic flight call is important. Whatever its primary function, the Quack of

Red-throated Loon also acts as a vocal stimulus for territorial vocalizations such as the Wail and Plesiosaur from the lake surface.

The Wail was used by both nesting and non-breeding birds in response to conspecific over-flights. To birds in flight, these Wails could establish an aural map of the surface distribution of individual loons. Such an aural map could be of particular importance in this species because many flights occur at twilight where surface visual cues would be limited (Reimchen and Douglas 1980). The Wail was also used as a high amplitude alarm call by the nesting pair, most consistently in response to overflight or perching of a Bald Eagle, a predator on both young and adult loons in the study area (Douglas and Reimchen 1988a), and to a Common Raven, a potential egg predator (Ewins 1991). Loons did not Wail to territorial incursions of Canada Goose, scaup, Belted Kingfisher, or Red-necked Grebe, none of which are predators or competitors.

The Plesiosaur call and display of Red-throated Loon have been described as "courtship displays" related to establishment of territory and copulation (van Oordt and Huxley 1922; Huxley 1923) and conspecific interactions (Keith 1937). Sjölander (1977) noted that this high intensity call was used most frequently following the return of a partner and in response to conspecifics vocalizing or intruding in the territory, and attributed functions of this call to territorial defence and mate recognition. Our data are generally consistent with this and also show that the Plesiosaur was used when Common Loons entered the nesting territory and by non-breeding pairs that overnighted on the lake (Reimchen and Douglas 1980).

We recognized a group of low amplitude calls used by the nesting adults with their chicks in association with feeding. The calls (Coo, Extended Coo, Staccato, Soft Raack), usually with frequencies less than 1000 Hz, are delivered with varying amplitude and behavioural intensity; the higher intensity Staccato is given when the chicks have not taken the offered fish. Such increased vocal solicitation seems reasonable given the major energetic investment to capture and return the marine fish to the young. In addition to the low amplitude of the calls, the low sound frequencies at the water surface could also be important, as Marten and Marler (1977) have shown experimentally that low frequencies near the ground have high attenuation rates. This is functionally relevant as it would limit the sound transmission to the immediate vicinity of the nest. The much higher amplitude Loud Raack is used by the female to the chick as a flight solicitation to the young near fledging. The Extended Coo has a structure similar to the Wail and can be theoretically transformed into a Wail by damping selected harmonic frequencies and increasing amplitude. As well, the higher amplitude Loud Raack of the female is structurally derivable from the simple Soft Raack by overall increased frequency and amplitude. We consider these to comprise different calls because of their different behavioural contexts.

Comparisons among species

All loon species have a similar number of high amplitude adult calls, yet the vocal repertoire and call characteristics differ from that of Red-throated Loons. Common Loon and Yellow-billed Loon (*Gavia adamsii*) have three high amplitude calls (Sjölander and Agren 1972, 1976): the Wail and Tremolo, which have variations that are graded in intensity (Barklow 1988, 1979), and the Yodel, a male territorial call with complex structure and context (Mager *et al.* 2010; Mager and Walcott 2014). Arctic Loon (*Gavia arctica*; Sjölander 1978) and possibly Pacific Loon (*Gavia pacifica*; Russell 2020) have a Yodel that resembles Common Loon in structure and variation, the Wail, possibly a low intensity version of the Yodel and the Croak. In comparison, Red-throated Loon have no high amplitude territorial call that resembles the Yodel. Structurally, there are similarities between the Red-throated Loon Wail and sections of the Wail and Yodel of other loons, yet the Red-throated Loon has none of the elaboration and frequency changes of the other species. No other calls have shared characteristics, although there is an overall restriction in calls to frequencies less than 3 kHz and to the use of harmonics. The complex acoustic structure and overlay of noise or sound pulses in the Red-throated Loon Plesiosaur is noticeably lacking in other loons. The Quack, Kark, and Loud Raack have not been reported for other loon species although the Croak of Arctic Loon (Sjölander 1978) may be equivalent. Although vocal repertoires of loon species differ, there are parallels in the behavioural contexts of calls. All five species produced high amplitude vocal responses to extra-pair conspecifics, whether they were intruding into the territory, calling on other territories, or flying over territories. In Common Loons, there is a graded response in the Wail and Tremolo, similar to the escalation of the Wail into the Plesiosaur call and display in Red-throated Loon.

Low amplitude contact calls used by adult pairs in the nesting territory are documented for Common Loon, Yellow-billed Loon, and Arctic Loon (Sjölander 1978; Evers *et al.* 2020; Uher-Koch *et al.* 2020). In our study, we found more complexity than for the other species, recognizing four calls used in different context with the chicks. The lack of specificity of contact calls in the other loon species may simply be a data gap, although the investment that adult Red-throated Loon make in obtaining food for the young from the ocean, compared to the other loon species, may require a distinct signal to ensure that the young eat.

Ontogeny

Ontogeny of vocalizations over the pre-fledging period in loons has received limited attention. It is best described for Common Loons and ranges from a peep in hatching to adult-like Hoots and Tremolo by eight months and the iconic Yodel by birds older than two years (Evers *et al.* 2020). In our study, pre-fledged Red-throated Loon chicks used Chirps with varying complexity throughout the pre-fledging period, a harmonic call by four weeks, and recognizable Wail and Plesiosaur calls by six weeks just prior to fledging. Although speculative, our sonograms of these vocalizations for two chicks exhibit a large amount of structural variability in the calls that could encode context-specific information for the attending adults.

Duetting

In Red-throated Loons, we documented duetting in the Wail and Plesiosaur in several contexts (pair contact, territory defence) in both the nesting pair and non-breeding birds. Duetting is a habitat-dependent complex co-operative behaviour exhibited by pair-mates (Thorpe 1972 as cited in Malacarne *et al.* 1991; Falls 1982; Farabaugh 1982). Studies of duetting in Common Loon, Yellow-billed Loon, and Pacific Loon have attributed a wide range of functions to the behaviour: alerting partners to threats, distracting potential predators (Barklow 1979), as an alarm call, in territorial conflict (Russell 2020; Uher-Koch *et al.* 2020), and as contact calls in flight (Evers *et al.* 2020). In other studies, defence of a joint resource, such as a breeding territory, is an important function of duetting (Dahlin and Benedict 2014; Brumm and Goyman 2018; Takeda *et al.* 2018; Diniz *et al.* 2019), although functions such as signalling pair-bonds (Farabaugh 1982), paternity guarding (Kahn *et al.* 2018), and facilitating mate recognition (Falls 1982) have been demonstrated as well. In Red-throated Loon, the high intensity coordinated behaviours and high amplitude vocalizations demonstrated in duets may communicate to non-breeding birds and to other territorial pairs both the existence of an occupied territory and the identity of the nesters. With the multiple territories on small ponds and lakes, such as on Haida Gwaii (Douglas and Reimchen 1988b), high amplitude duets may produce an aural map of territories within the region.

Kinematics

The invariable association of Red-throated Loon postures with the Plesiosaur and the Wail indicate that the spatial positioning of the head and neck are involved in specific sound production. The oral cavity can act like an "oral bell", reducing impedance as sound transfers from the pharynx to the outside air (Gaunt *et al.* 1987); this is a likely explanation for the distended "pouch" below the base of the bill seen in the Plesiosaur posture. Distention of the neck in the Wail and the Plesiosaur call suggests an anatomical modification producing a resonant chamber, a mechanism for call amplification used by some grouse, curassows (Wiley and Richards 1982), and ducks (Brackenbury 1982). Bill gape has been found to modulate frequency in passerines (Westneat *et al.* 1993) and in geese (Hausberger *et al.* 1991). Some of these processes may be involved in the modification of calls by physical displays in Red-throated Loon.

Characteristics of the avian trachea (length, diameter, and thickness) affect the sound generated by the internal tympaniform membranes by amplifying or damping frequencies (see Brackenbury 1982 for review). Sutherland and McChesney (1965) concluded that calls in Ross' Goose (*Chen rossii*) and Snow Goose (*Chen caerulescens*) were both modulated by tracheal resonance and that the difference between the two species is related to differing tracheal length. Greenewalt (1968) analyzed the harmonics in calls of Whooping Crane (*Grus americana*), Whistling Swan (*Olor columbianus*), and Trumpeter Swan (*Cygnus buccinator*), all of which have exceptionally long tracheae coiled at their base, and found no relationship between tracheal length and harmonic frequencies. There is no evidence of tracheal coiling in Gaviidae. We found that in some of the Red-throated Loon calls (Wail, Quack, Kark, and female Plesiosaur call) the lowest harmonic was not equivalent to the intervals between the harmonics; that is, the lowest harmonic frequency was not the fundamental. In the Wail, series of harmonics both higher and lower than the dominant frequencies were completely damped in parts of the call. This, in association with display kinematics, indicates that there is considerable modulation of song characteristics, which could mean more transmission of greater content and individual information in calls.

Sexual dimorphism

Sexual dimorphism in avian vocalizations is common and represents two processes: differences in the type of calls by each sex and differences in the acoustic structure of individual calls. Both processes are known in Gaviidae. In Common Loon and Yellow-billed Loon, only the male gives the Yodel, the dominant territorial call (Sjölander and Agren 1972, 1976; Walcott *et al.* 2006). Although we have previously shown that male Red-throated Loon are largely responsible for defense, including direct attacks on intruders (Reimchen and Douglas 1985), we have not identified any male-specific vocalization associated with territoriality defense. Rather, the Wail, the most prevalent territorial call, is given by male or female either singly or in duet. Vocalizations directed to the chicks differed between the sexes for some calls, as the Coo and Extended Coo were only recorded for the male and the Low Raack for the female, although they had similar contexts in interacting with the young and each other in the nesting territory and feeding fish to the young.

Sex differences in acoustic structure of the calls have also been reported for other loon species. In Common Loon and Yellow-billed Loon, the Tremolo, the major flight call, is lower pitched in the male than in the female (Sjölander and Agren 1976), possibly associated with body size because male loons are about 10% larger than females in each species (Selander 1966; Cramp and Simmons 1977). Our acoustic data on Red-throated Loon are similar as we found that in both the Wail and the Plesiosaur, the male vocals were about 200–400 Hz lower than that of the female. We cannot assess whether this difference is a by-product of the body size or more context-specific behaviour differences in the interactions with the chicks.

Alarm calls

For species exposed to multiple predators, alarm calls distinct for each predator group would provide improved response options of the target prey (e.g., Leger *et al.* 1980; Templeton 2005). Throughout the geographical nesting range, loons overlap with a range of egg and chick predators including ravens, gulls, skuas, jaegers, foxes, wolves, and raptors (Johnson and Johnson 1935; Cyrus 1975; Bundy 1976; Furness 1983) and this might predict species-specific vocal responses. We observed that Red-throated Loon exhibited several distinctive alarm calls to predators such as the Kark towards Common Raven, which is an egg predator (Ewins 1991), and the Kark and Wail towards Bald Eagles. Solitary eagles were present in the study area almost daily throughout summer and have attacked Red-throated Loon chicks as well as adults (Douglas and Reimchen 1988b). We also observed that when chicks were present, the adult Red-throated Loon responded aggressively with the Wail or Kark to both other Red-throated Loon and Common Loon, as these are known to attack Red-throated Loon chicks in the territory (Reimchen and Douglas 1985). There were no vocal responses to the multiple avian taxa that were not a threat to the pre-fledged young.

Conclusion

Our observations of nesting and non-nesting Red-throated Loon show a diversity of vocalizations and variable responses to intra- and interspecies interactions. The Quack and the Plesiosaur are two calls that are unique to Red-throated Loon. While it is possible that these calls represent ancestral traits in this basal taxon, it is equally or more probable that their vocal repertoire is an acoustical adaptation to the distinctive life history of nesting in small lakes or ponds that require flights to and from the territory throughout the pre-fledging period. We identified nine calls, more than previously reported, but feel these might still be over-simplified categories that greatly underestimate the complexity of their vocal repertoire, given the multiple instances of context-specific behavioural responses to different vocalizations. While our data on acoustic structure are limited to a single nesting pair, these represent the first characterization of this dimorphism in Red-throated Loon and provide a basis for future comparisons. The extent to which these vocalizations comprise syntactical and referential signals (review in Smith 2017) awaits further study.

Author Contributions

Writing – Original Draft: S.D.D.; Writing, Review & Editing: T.E.R. and S.D.D.; Conceptualization: S.D.D. and T.E.R.; Investigation: S.D.D. and T.E.R.; Methodology and Analyses: S.D.D. and T.E.R.; Visualization: S.D.D. and T.E.R.

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APPENDIX 1. Accession numbers for representative audio-recordings and spectrograms of Red-throated Loons (*Gavia stellata*) at Drizzle Lake, Haida Gwaii, western Canada uploaded to the Macaulay Library at the Cornell Lab of Ornithology (https://macaulaylibrary.org). Recordings were made by S.D.D. and T.E.R. and are part of the data used in this study. Spectrograms accompanying the recordings were produced by the Macaulay Library.

Call	Hyperlink	Accession number
Adult pair with 1-day old chick	https://macaulaylibrary.org/asset/221326721	ML221326721
Kark	https://macaulaylibrary.org/asset/221510911	ML221510911
Wail and Plesiosaur, male and female duet	https://macaulaylibrary.org/asset/216337511	ML216337511
Plesiosaur, male and female duet	https://macaulaylibrary.org/asset/216348661	ML216348661
Quack	https://macaulaylibrary.org/asset/216351121	ML216351121
Loud Raack	https://macaulaylibrary.org/asset/221524591	ML221524591

The Canadian Field-Naturalist

Note

Behavioural interactions among Canada Lynx (*Lynx canadensis*) during pre-estrous

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Bailey, T.N., and B.N. Bailey. 2021. Behavioural interactions among Canada Lynx (*Lynx canadensis*) during pre-estrous. Canadian Field-Naturalist 135(2): 181–185. https://doi.org/10.22621/cfn.v135i2.2563

Abstract

Information is lacking on the behaviour of free-roaming Canada Lynx (*Lynx canadensis*) during the breeding season, likely because they are rarely observed in the wild. Other wild solitary felid males compete with each other to mate with promiscuous females. However, the behavioural context or sequence of this competition among wild male Canada Lynx remains unreported. We describe the behaviour of three adult wild lynx during the breeding season. We observed the first two lynx together; an adult male and an inferred adult female remained together non agonistically for nearly 2 h before they were interrupted by another adult male. Our observation of interaction between the two males includes agonistic behaviours, vocalizations, scent marking, fighting, and a long-distance (1.7-km) expulsion of the intruding male lynx by the first male. These observations add to the limited information available on the social ecology of lynx during the breeding season.

Key words: Alaska; Canada Lynx; *Lynx canadensis*; fighting; mating behaviour; scent marking; territoriality; vocalizations

There are few published observations of breeding and agonistic behaviour among wild Canada Lynx (*Lynx canadensis*) during the breeding season (Mowat *et al.* 2000; O'Donoghue *et al.* 2010; Stanton *et al.* 2015; Andrews *et al.* 2018; Lavoie *et al.* 2019). Most information on Canada Lynx mating behaviour comes from observations of captive animals (e.g., Anderson and Lovallo 2003; Stanton *et al*. 2015). The mating season of lynx in interior Alaska is from late March through early April (Nava 1970), and in British Columbia it apparently peaks during the second half of March (Crowley *et al.* 2013). In Alberta (Nellis *et al.* 1972) and elsewhere, it may last into May. The lynx estrus cycle lasts a month; captive female lynx are apparently in estrus only 3–5 days, and wild female lynx may be presumed to mate with only one male (Sunquist and Sunquist 2002). However, perhaps like Eurasian Lynx (*Lynx lynx*), female Canada Lynx may be promiscuous breeders and males may search widely outside their usual home ranges for receptive females and defend them during the brief breeding period (Erofeeva and Naidenko 2012).

There is no published, direct, and visually supported information on agonistic, aggressive, or fighting behaviour among wild Canada Lynx. We found four videos of vocalizing or fighting lynx posted on the internet, but they lacked behavioural context (MacKay 2014; Lewis 2018; Wiebe 2018; Wadleigh 2020). The videos were reportedly made on 1 April (Weibe 2018) and 18 May (Lewis 2018), months perhaps associated with the mating season, and on 29 May (Wadleigh 2019) and 28 October (MacKay 2014). Here, we summarize our observations of three wild adult Canada Lynx during the mating season in Alaska; detailed observations are included in Appendix S1. We took videos of segments of the interaction we observed: Video S1 and S2.

For 3 h on 14 March 2020, we opportunistically observed a wild adult lynx of unknown sex and an adult male lynx, later interrupted by another adult male, interact during the breeding season. Our observations, which were from a vehicle, occurred within the Skilak Wildlife Recreation Area (SWRA), Kenai National Wildlife Refuge, Alaska (60.44991°N, 150.2319°W), an area closed to the hunting and trapping of carnivores to increase wildlife viewing opportunities. Our observations took place along the Skilak Lake Loop Road traversing the SWRA, near a road pullout (known as Skilak Lake Overlook), which we refer to as site A.

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The 73-year-old forest in the area is dominated by Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh), Alaska Birch (*Betula neoalaskana* Sargent), and Trembling Aspen (*Populus tremuloides* Michaux). Much of the surrounding habitat was destroyed by the 2019 Swan Lake Fire, leaving an unburned area of ~41 km^2 in the eastern half of the SWRA.

The Snowshoe Hare (*Lepus americanus*) cycle was in an increase phase, near the peak (Kenai National Wildlife Refuge unpubl. data 1983–2015). Other passing vehicles did not stop or interfere with our observations until two male lynx came out of dense cover to the road. Then, almost simultaneously, two approaching vehicles stopped to allow the occupants to also observe and then closely follow the lynx for ~1.5 km down the road before they passed by them. The temperature was ~–2.8°C, snow depth ~0.5–1.0 m, and snow-plowed-berms on both sides of the road were ~1.0–1.5 m high.

We used our images (385 photographs and 17 short videos of 1–9 min duration) to confirm the sex of two of the three lynx (two males, M1 and M2; we could not visually confirm the sex of L3) and reconstruct the timing of their behaviours, even though vegetation and the vehicle windshield obscured or distorted many images. We identified three phases of the interaction and use a standardized ethogram with its terminology and behavioural definitions for the Felidae recommended by Stanton *et al.* (2015) with specific behaviours shown in italics on first use.

Phase I, duration 1 h 46 min (1708–1854), was non-agonistic interaction between M1 and L3, ~30 m from the road (Figure 1a). We did not observe L3 again.

Phase II, 35 min (1854–1929), was agonistic behaviour between M1 and M2 that began when M2 suddenly appeared, rapidly *walking* up the road behind our vehicle toward site A. After the apparently *alerted* L3 suddenly disappeared from view, M2 began interacting agonistically with M1, both frequently *vocalizing* and posturing. We did not observe any physical contact between the males even though they sometimes faced each other <0.5 m apart (Figure 1b); neither scent marked.

Phase III (Figure 1c–e), 39 min (1929–2008), was aggression, scent marking, and fighting, as M1 closely followed and aggressively escorted M2 from site A (perhaps from M1's territory) back along the road on which M2 arrived, to a point 1.7 km east of site A. Then, each male separately disappeared into dense vegetation on opposite sides of the road.

Lynx L3 was only observed during phase I; from the interactions with M1 and the behaviours observed, L3 was probably an adult female in pre-estrus. She tolerated M1's close (<1 m) presence, allowed M1 to closely follow for at least 20 m, and did not exhibit any agonistic behaviour toward M1. We speculate that L3 did not encourage physical contact because she was not yet ready to breed and did not exhibit other "typical" female felid behaviours in estrus, such as urine spraying, head rubbing, the "*flirting run*", or *avoiding* approaches of the male with her paws or loud shrieks (Leyhausen 1979). Furthermore, we did not observe "typical" male felid behaviour with a female in estrus, such as vocalizations, head rubbing, scent marking with urine or feces, or attempted copulation (Leyhausen 1979). Instead, the behaviours we observed were comparable to the courtship or pre-estrus behaviour before mating or copulation described in Domestic Cats (*Felis catus*; Leyhausen 1979; Yamane *et al.* 1996; Petersen 2015) and captive and other wild felids (Leyhausen 1979; Sunquist and Sunquist 2002; Andrews *et al.* 2018). Alternatively, the long non-agonist interaction between M1 and L3 may have had nothing to do with breeding: L3 was an adult female merely associating with M1. However, because we observed M1 and L3 in the early breeding season and adult lynx generally do not travel with other adults outside the breeding season (O'Donoghue *et al.* 2010), we probably observed pre-breeding behaviour. We also discount a third possibility: L3 was an adult male travelling with M1. Adult lynx are known to sometimes travel together when prey densities are low (O'Donoghue *et al*. 2010); however, hare densities were rapidly increasing near their peak, not low, during our observation (Kenai National Wildlife Refuge unpubl. data 1983–2015). Finally, based on other solitary felid behaviour during the breeding season, it appears unlikely that two adult male lynx would travel non-agonistically together.

We interpret phase II of the behavioural sequence as attempts by newly arriving M2 and M1 to establish territorial dominance or to mate with L3. They displayed their body size by posturing, their facial expressions by the position of their ears and facial ruffs, and their temperament by their loud and piercing vocalizations. The most notable aspect of their behaviour was the highly variable, loud, vocalizing that most closely met Stanton *et al.*'s (2015) criteria for yowling in felids. It varied rapidly in frequency and at least two-fold in intensity. It is believed that female Eurasian Lynx can estimate, from a distance, the "quality" of a potential mating partner by his long distance calls, because they are correlated with the level of testosterone in his blood plasma (Rutovskaya *et al.* 2009). During the mating season, humans are reported to hear the long distance calls of Eurasian

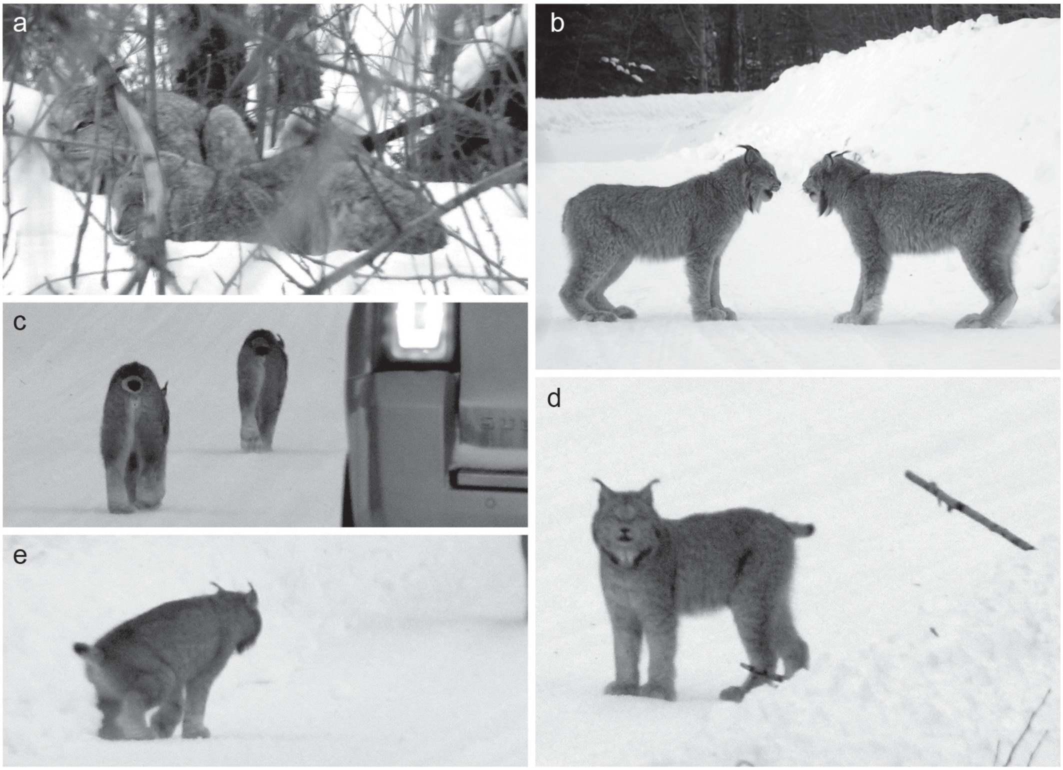

FIGURE 1. Interactions between Canada Lynx (*Lynx canadensis*). a. Lynx M1 crouches in the left background; lynx L3 with eyes closed crouches in front of him. b. Lynx M1 (right) and M2 (left) face each other, yowling, after entering the road. Note white markings on feet of M1. c. Lynx M1 walks closely behind M2 down the road, both lynx ignoring two vehicles driving closely behind them. Note the positions of their tails (M1's tail is held straight out, M2's tail down). d. After scent marking and head rubbing against a branch sticking out of the snow berm, lynx M2 looks back up the road at following M1. e. Lynx M1 scraping his hind feet after scent marking over ("overmarking") a scent mark just left by M2, still partly visible at upper right. Photos: T.N. Bailey and B.N. Bailey.

Lynx from 2 km away (Erofeeva and Naidenko 2012) and those of Bobcat (*Lynx rufus*) from 1.6 km (Young 1958).

From our photographs and videos, it appeared M1 was perhaps the calmer, more secure in temperament, of the two males. M2 appeared more agitated, at first unwilling to move but also the first to eventually leave site A. It also exemplified a general pattern of aggressive behaviour among male felids during the mating season, which usually, but not always, suggests that males attain dominance by ritualized vocal and visual displays and avoid actual fighting (Leyhausen 1979).

We interpret phase III of the behavioural sequence as M1's successful attempt to drive M2 out of its territory and perhaps prevent M2 from mating with the presumed female L3. Among Domestic Cats, fighting rarely occurs near a receptive female (Bradshaw 2016); when it occurs between two males, the heaviest male most often wins (Yamane *et al.* 1996). Physically, M2 appeared younger and perhaps slightly smaller than M1. Behaviourally, M1 appeared more confident (calmer) and less aggressive than M2, who more often appeared more aggressive (position of ears, retreating). Of interest, M1 did not *chase* M2, nor *run* or *trot* after him. M1 merely walked behind him at a steady pace as M2 retreated.

We are not certain whether M1 escorted M2 from his territory. Several observations favour this interpretation: (1) M1's persistence to drive away M2 ~1.7 km back down the road (the direction M2 apparently came from); (2) M1's behaviour to overmark M2's frequent scent marks as they retreated and, thus, reaffirm his social status; and (3) M1's possible "status as winner" after their brief physical fight. Although fighting is apparently rare among Canada Lynx (Sunquist and Sunquist 2002; Poole 2003), torn ears and broken canines indicate that male lynx sometimes fight (Mowat and Slough 1998; T.N.B. unpubl. data). In a study of Iberian Lynx (*Lynx pardinus*), one suffered serious injury during an apparent territorial fight (Ferreras *et al.* 1997). A resident female Eurasian Lynx fought and drove away an unidentified lynx (Wölfl and Wölfl 1996). Amongst male Eurasian Lynx, in four aggressive encounters among five males over a 9-year study period, two were fatal, all occurred during the mating season, and three involved the takeover of a home range by the intruder (Mattisson *et al.* 2013). Male Eurasian Lynx also intensively mark their territories during the breeding season (Schmidt *et al.* 1997). Bobcats also visited scent-marking sites ("community sites") most frequently during January, presumably at the peak of their courtship and mating (Allen *et al.* 2015). We note that despite about 1 h of sometimes close (<0.5 m) contact, fighting between the two males lasted only about 3 s without any apparent physical injuries, suggesting that these two adult male Canada Lynx resolved their conflict mostly by ritualized, non-injurious behaviour.

As reported for other wild solitary felids (Bailey 1993; Krofel *et al.* 2017; Rafiq *et al.* 2020), our observation supports the view that human infrastructure, such as roads and trails, may serve as important pathways for the maintenance of home ranges, social cohesion, and the exchange of olfactory information among Canada Lynx and, by coincidence, make them more vulnerable to human exploitation.

Author Contributions

Writing – Original Draft: T.N.B.; Writing – Review & Editing: T.N.B. and B.N.B.; Methodology: T.N.B. and B.N.B.

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SUPPLEMENTARY MATERIALS:

APPENDIX S1. Detailed field observations of three Canada Lynx (*Lynx canadensis*), 14 March 2020, in the Skilak Wildlife Recreation Area, Kenai National Wildlife Refuge, Alaska, USA.

VIDEO S1. Male Canada Lynx (*Lynx canadensis*) M1 and M2 agonistically interacting after emerging from dense vegetative cover and before entering the road. Sequence begins with M1 sitting in the snow on the right. Videographer: Brian Bailey. Location: Kenai National Wildlife Refuge, Alaska. Date taken: 14 March 2020. https://vimeo.com/414965666.

VIDEO S2. Male Canada Lynx (*Lynx canadensis*) M1 and M2 interacting on the road before M2, final frame on the left, leaves site A. Videographer: Brian Bailey. Location: Kenai National Wildlife Refuge, Alaska. Date taken: 14 March 2020. https://vimeo.com/414994144.

The Canadian Field-Naturalist

Overall and repeated floral visitation by insects suggests flower flies (Syrphidae) as the major pollinator group of Alaska Wild Rhubarb (*Koenigia alaskana* var. *glabrescens*; Polygonaceae) in Northwest Territories, Canada

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Abstract

Alaska Wild Rhubarb (*Koenigia alaskana* var. *glabrescens*; Polygonaceae) is a native Arctic, subarctic, and alpine plant of northwestern North America. Although the plant has some economic and ecological importance, its biology is poorly known. At 11 sites in the northeast corner of its range in Northwest Territories, we found that 87% of its floral visitors were flies, mostly Syrphidae, a diverse family known to be important pollinators. Insects visiting consecutive flowers on different plants and, thus, likely effecting pollination were also flies (78.6%) and also mostly Syrphidae (72.7%) followed by Hymenoptera (20%). Although syrphids were the dominant potential pollinators at most sites, there was some variation among sites. Our results provide quantitative support for pollinator diversity and the major role of Syrphidae in pollination of Alaska Wild Rhubarb. We suggest that pollination is not a limiting factor in this plant's spread, nor its rare and local occurrence and restricted distribution, because the majority of its pollinators are widespread.

Key words: Alaska Wild Rhubarb; *Koenigia alaskana* var. *glabrescens*; pollination; crop; flies; Syrphidae; Northwest Territories

Introduction

Alaska Wild Rhubarb, *Koenigia alaskana* (Small) T.M. Schuster & Reveal var. *glabrescens* (Hultén) T.M. Schuster & Reveal (previously recognized as *Polygonum alaskanum* (Small) Wright var. *glabrescens* Hultén and *Aconogonon alaskanum* (Small) Sojak var. *glabrescens* (Hultén) H.R. Hinds; Shuster *et al.* 2015), known as Quaugaq in Gwichin, has a restricted distribution in northwestern North America, being largely confined to the unglaciated subarctic and alpine regions of Beringia in Alaska, Yukon, and Northwest Territories (NWT; e.g., Porsild and Cody 1980, map 455; Hinds and Freeman 2005). In NWT, it occurs only in the extreme northwest from the Richardson Mountains and the Husky Lakes (Eskimo Lakes, known as Imaryuk in Inuvialuktun) region north of Inuvik and the tree line and south along the Mackenzie River and in the Mackenzie Mountains to the latitude of Tulita (64.9132°N; P.M.C. pers. obs.).

All plants of Alaska Wild Rhubarb that we have seen in NWT are var. *glabrescens*, which is glabrous instead of densely retrorsely pubescent on the stems and also glabrous instead of densely pubescent on the leaves (Hinds and Freeman 2005).

The flowers, 8–10 mm in diameter, have five white tepals, 6–8 well-developed stamens, and three stigmas on top of a superior ovary (Figure 1a; Hinds and Freeman 2005). Inflorescences comprise hundreds of flowers (Figure 1b), and there may be up to 5000 flowers on a plant (Figure 1c). Plants reach more than 2 m (6.6 ft) in height in a single growing season (Figure 1c).

The plants are confined to areas of substrate disturbance, such as eroding banks, rockslides, landslides, roadsides, piles of rich organic debris, and bulldozed or dumped substrate (Figure 1d). Currently, most known locations and most plants are associated with human disturbance (P.M.C. and B.K. pers. obs.). *Koenigia alaskana* var. *glabrescens* is rare on the

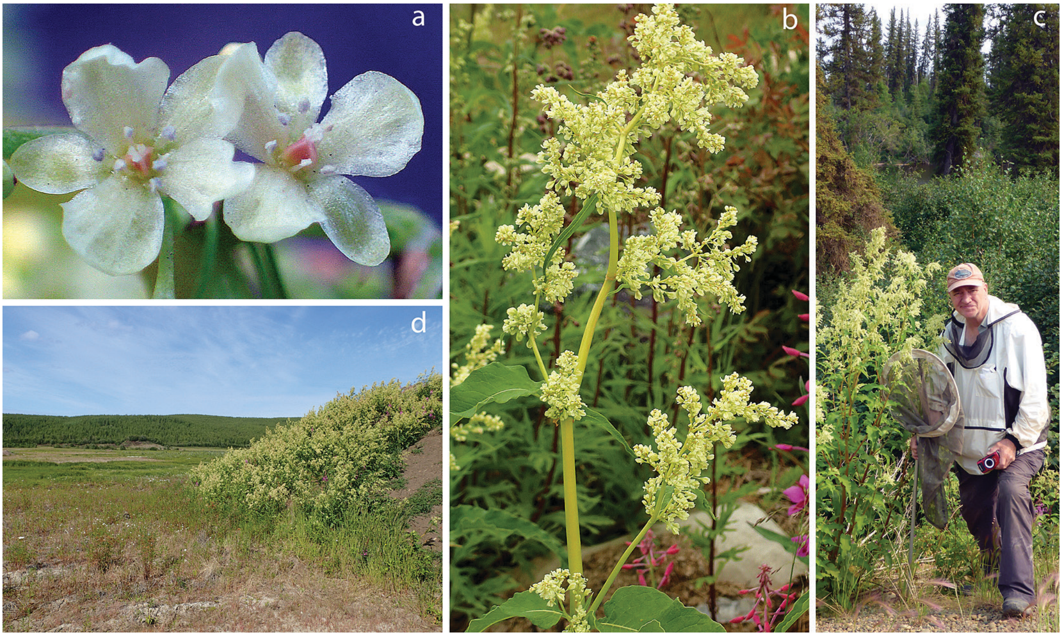

FIGURE 1. Alaska Wild Rhubarb (*Koenigia alaskana* var. *glabrescens*). a. Flowers, 8 mm in diameter. b. Inflorescence, ~20 cm in length with ~400 flowers. c. Plant, 1.83 m tall. d. Population of over 100 plants on a pile of bulldozed and fertilized topsoil. Photos: P.M. Catling and B. Kostiuk.

NWT landscape in its general region of occurrence, which is dominated by boreal forest and shrub tundra. It is restricted to landslides along the Mackenzie River, steep slopes in the Richardson Mountains, roadsides, and disturbed areas in towns (P.M.C. and B.K. pers obs.). Where it occurs, there may be a few, hundreds, or even many thousands of plants (P.M.C. and B.K. pers. obs.).

This perennial plant has been used as a food source and medicine by Indigenous People and early explorers (e.g., Porsild 1953; Kuhlein and Turner 1991). Characteristics, such as its hardiness in the north (P.M.C. pers. obs.), substantial annual productivity (P.M.C. pers. obs.), and frequent tendency to produce pure stands (P.M.C. pers. obs.), suggest ease of cultivation as a northern crop. A potential limitation to its production, the availability of pollinators, is understudied but explored here.

Methods

Sampling

During sunny, mild (15–23°C) periods of low wind (0–15 k/h) in the second week of July 2019, P.M.C. and B.K. spent 1 h near midday at each of 11 sites in the Mackenzie Delta region (Table 1) recording all individual insects visiting flowers of *K. alaskana* var. *glabrescens* and collecting as many as possible of the insects that visited two flowers on two different plants consecutively. These insects were potentially carrying pollen from one plant to another.

Identification

Flies were identified by J.H.S. The moth *Scopula seritinaria* (Geyer) was identified by C. Schmidt. The two Ichneumonidae: *Itoplectis viduata* (Gravenhorst) and *Exyston chamaeleon* Mason were identified by A. Bennett. The sawfly, *Tenthredo piceocincta* (Norton), was identified by H. Goulet. Other insects were identified by P.M.C. using Environment and Natural Resources (2017) and Williams *et al.* (2014) for species of *Bombus*, Bohart (1976) for *Crabro latipes* F. Smith, and Buck *et al.* (2008) for *Dolichovespula norwegica* (Fabricius) = *D. pallida* Sladen. Vouchers of all insects (57 individuals, listed in Table 1) were placed in the Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa (CNC). Not all of these insects have common names.

Where identification of flies to species was not possible using morphological characters (e.g., male *Syrphus rectus* Osten-Sacken 1875 and *Syrphus vitripennis* Meigen 1822 specimens cannot be separated morphologically) or identification was outside our area of expertise (non-syrphid Diptera), we generated DNA barcodes from specimens and matched them against the BOLD database using the BOLD identification engine (available at http://v4.boldsystems.org/

Table 1. Sites in Northwest Territories, Canada, where floral visitors to Alaska Wild Rhubarb (*Koenigia alaskana* var. *glabrescens*) were recorded and collected. Plant voucher accessions are indicated.

Site no.	CAN plant accession no.	Site name	Latitude °N	Longitude °W
1		Tuktoyaktuk highway	68.3476	133.6830
2		Tuktoyaktuk highway	68.6284	133.6777
3		North Inuvik, industrial area, Navy Road	68.3758	133.7511
4		North Inuvik, industrial area, Navy Road	68.3706	133.7459
5		North Inuvik, industrial area, Navy Road	68.3664	133.7410
6		Inuvik community garden refuse pile	68.3596	133.7188
7		South Inuvik, west side of golf course	68.3483	133.6911
8	10104548	South Inuvik, east of driving range	68.3505	133.6849
9	10104545	Fort McPherson, along road 27 km east of town	67.4067	134.3575
10	10104547	Fort McPherson town site	67.4322	134.8816
11	10104546	Richardson Mountains	67.1509	135.9213

index.php/IDS_OpenIdEngine). All but two taxa were identified to species in this way. The other two were identified to genus.

Four voucher specimens (listed in Table 1) of *K. alaskana glabrescens* were deposited in CAN (Canadian Museum of Nature, Aylmer, Quebec).

Generating DNA barcodes

A single leg (the right midleg where possible) was removed from specimens and the 5′ end of the cytochrome *c* oxidase I mitochondrial gene (COI) was sequenced at CNC. Extraction, cycling, and sequencing conditions are available from Motamedinia *et al.* (2019). For DNA amplification and sequencing, we largely used primers developed for use in Diptera (Table 2). Barcodes were variously recovered in a single fragment or in three smaller segments that were assembled as a full barcode.

All sequence data are stored on the BOLD website (http://www.boldsystems.org/) in the Pollinators of Alaska Wild Rhubarb, *Koenigia alaskana* var. *glabrescens* dataset (BOLD n.d.). All complete sequences used in this project are also available on GenBank (https://www.ncbi.nlm.nih.gov/genbank/); accession numbers are listed in Table 3.

Results

General observation of flower visitation by insects

In the 161 insect visits (Table 4), 31 species of potential pollinators were identified (Table 5) representing three major insect families. Twenty-six individuals of at least 12 species (Table 3) were identified or confirmed using barcode data and the remainder using morphology. Flies (Diptera) were present on flowers at most sites and represented 87% of insects recorded on flowers (Table 4). Most of the fly visitors were Syrphidae (73%) and they were primary visitors at most sites (Table 4). This large group of insects (over 6000 species), usually called flower flies, feed mostly on nectar and pollen as adults. Wasps were the next largest group, representing 10.3% of insects on flowers, and were the largest group of floral visitors at a site in the Richardson Mountains.

Collections of insects moving between flowers on different plants

Fifty-seven insects were collected after moving from a flower on one plant to a flower on another (Table 5). These were mostly flies (45 of 57, 78.9%), and most of them were among the 13 species of syrphids recorded (33 of 45, 73.3%). The second largest group

Table 2. Primers used to sequence the cytochrome *c* oxidase (COI) barcoding region of insects collected when visiting Alaska Wild Rhubarb (*Koenigia alaskana* var. *glabrescens*) in Northwest Territories, Canada.

Primer name	Primer design	Primer sequence
Heb-F	Folmer *et al.* 1994	GGT CAA CAA ATC ATA AAG ATA TTG G
COI-Fx-A-R Kelso	Young *et al.* 2020	CGD GGR AAD GCY ATR TCD GG
COI-Fx-B-F Kelso	Young *et al.* 2020	GGD KCH CCN GAY ATR GC
COI-Fx-B-R Kelso	Young *et al.* 2020	GWA ATR AAR TTW ACD GCH CC
COI-Fx-C-F Kelso	Young *et al.* 2020	GGD ATW TCH TCH ATY YTA GG
COI-780R	Gibson *et al.* 2011	CCA AAA AAT CAR AAT ARR TGY TG

TABLE 3. Species of insects collected when visiting Alaska Wild Rhubarb (*Koenigia alaskana* var. *glabrescens*) in Northwest Territories, Canada, specimen identification (unique identifiers), GenBank number, and sequence lengths for species identified or confirmed using DNA barcoding. There were no ambiguous base calls in any of the sequences. Available common names are provided.

Species	Specimen ID	GenBank number	Sequence length
Cheilosia sp. NWT1*	CNC1078275	MT216206	662
Cheilosia sp. NWT1	CNC1078267	MT216195	645
Cheilosia sp. NWT1	CNC1078265	MT216190	662
Delia fabricii (Holmgren, 1872)	CNC1078279	MT216193	662
Delia fabricii	CNC1078278	MT216209	662
Eristalis obscura (Loew, 1866) (Dusky Drone Fly)	CNC1078269	MT216201	662
Graphomya sp.	CNC1078280	MT216200	662
Hydrotaea pilitibia Stein, 1916	CNC1078274	MT216197	662
Lispe tentaculate (De Geer, 1776)	CNC1078266	MT216189	662
Phaonia hybrida Schnabl, 1888	CNC1078242	MT216192	662
Phaonia lugubris Meigen, 1826	CNC1078277	MT216204	662
Phaonia lugubris Meigen, 1826	CNC1078276	MT216211	662
Protophormia terraenovae Robineau-Desvoidy, 1830	CNC1078251	MT216210	662
Protophormia terraenovae	CNC1078241	MT216203	662
Stratiomys normula (Loew, 1866)	CNC1078240	MT216194	662
Syrphus vitripennis Meigen, 1822 (Black-legged Flower Fly)	CNC1078262	MT216213	662
Syrphus vitripennis	CNC1078261	MT216196	662
Syrphus vitripennis	CNC1078260	MT216198	659
Syrphus vitripennis	CNC1078258	MT216214	419
Syrphus vitripennis	CNC1078257	MT216207	662
Syrphus vitripennis	CNC1078255	MT216199	662
Syrphus vitripennis	CNC1078252	MT216191	661
Syrphus vitripennis	CNC1078249	MT216208	662
Syrphus vitripennis	CNC1078248	MT216202	662
Syrphus vitripennis	CNC1078247	MT216212	659
Tetanocera sp.	CNC1078270	MT216205	662

**Cheilosia* (Blacklets) requires revision. We could not place this definitively to species so gave it a morphospecies name.

TABLE 4. Numbers of individuals of various insect groups seen on flowers of Alaska Wild Rhubarb (*Koenigia alaskana* var. *glabrescens*) in Northwest Territories, Canada, at sites indicated in Table 1. This table includes unidentified floral visitors of single flowers, visitors of two or more plants that were not caught and specifically identified (counted as single individual visits), and captured insects visiting flowers on two consecutive plants that were specifically identified (also counted as a single individual visit).

Insect group	Site											Total
	1	2	3	4	5	6	7	8	9	10	11	
Diptera—flies												
Syrphidae	13	16	10	4	15	11	24	3	3	3	6	108
Other Diptera		6	2		7	5	8	6				34
Hymenoptera—bees and wasps												
Apidae	1					1	1					3
Crabronidae	1											1
Ichneumonidae		1		1			1	4				7
Vespidae	1								1	1	7	7
Lepidoptera—moths												
Geometridae								1				1

of potential pollinators was Hymenoptera (11 of 57, 19.3%). The potential pollinators, and notably those more frequently recorded, are widespread species.

Discussion

Our results provide quantitative support for a major role of Syrphidae in pollination of *K. alaskanum* var. *glabrescens*. Flower flies play a major role as pollinators in Arctic and boreal regions (e.g., Larson *et al.* 2001) and have also been reported as important pollinators in other species of Polygonaceae. For example, Chen and Zhang (2010) reported flower flies as the principal floral visitors of *Polygonum jucundum* Meisner (no English common name) from east-central China, a heterostylous species with flowers similar in morphology to those of *K. alaskanum* var. *glabrescens*. They noted that the flies harvest pollen from *P. jucundum* with their mouthparts from short-styled

TABLE 5. Identification of 57 specimens collected after moving from a flower on one plant of Alaska Wild Rhubarb (*Koenigia alaskanum* var. *glabrescens*) to a flower on another plant, thus indicating potential pollination. The rows are in alphabetical order by family, subfamily, then species.

Group/family	Subfamily	Taxon (common names provided where possible)	No.
Diptera—flies			45
Anthomyiidae		*Delia fabricii* (Holmgren 1872)	2
Calliphoridae	Chrysomyiinae	*Protophormia terraenovae* (Robineau-Desvoidy 1830)	2
Muscidae		*Graphomya* Robineau-Desvoidy 1830	1
		Hydrotaea pilitibia Stein 1916	1
		Lispe tentaculata (De Geer 1776)	1
		Phaonia hybrida (Schnabl 1888)	1
		Phaonia lugubris (Meigen 1826)	2
Sciomyzidae		*Tetanocera* Dumeril 1800	1
Stratiomyidae		*Stratiomys normula* (Loew 1866)	1
Syrphidae	Eristalinae	*Cheilosia* sp. NWT1	3
		Eristalis (*Eoseristalis*) *anthophorina* (Fallén 1817) (Orange-spotted Drone Fly)	2
		Eristalis (*Eoseristalis*) *obscura* (Loew 1866) (Dusky Drone Fly)	1
		Eristalis (*Eoseristalis*) *rupium* (Fabricius 1805) (Spot-winged Drone Fly)	1
Syrphidae	Syrphinae	*Epistrophe* (*Epistrophe*) *nitidicollis* (Meigen 1822) (Straight-banded Smoothtail)	2
		Eupeodes (*Metasyrphus*) *curtus* (Hine 1922) (Comma-spot Aphideater)	1
		Eupeodes (*Metasyrphus*) *perplexus* (Osburn 1910) (Bare-winged Aphideater)	1
		Meligramma guttata (Fallén 1817) (Spotted Roundtail)	4
		Meligramma triangulifera (Zetterstedt 1843) (Variable Roundtail)	1
		Meliscaeva cinctella (Zetterstedt 1843) (Common Thintail)	1
		Parasyrphus tarsatus (Zetterstedt 1838) (Holarctic Bristleside)	1
		Sphaerophoria (*Sphaerophoria*) *abbreviata* (Zetterstedt 1849) (Variable Globetail)	1
		Sphaerophoria sp. 1828 (*S. abbreviata*, *S. asymmetrica* Knutson 1972 or *S. philanthus* (Meigen 1822) females)	3
		Syrphus (*Syrphus*) *vitripennis* Meigen 1822 (Black-legged Flower Fly)	11
Hymenoptera—bees and wasps			11
Apidae	Apinae	*Bombus bifarius* (Cresson 1878) (Black-notched Bumble Bee)	1
		Bombus occidentalis Greene 1858 (Western Bumble Bee)	1
Crabronidae	Crabroninae	*Crabro latipes* F. Smith 1856	1
Ichneumonidae	Pimplinae	*Itoplectis viduata* (Gravenhorst 1829)	1
Ichneumonidae	Tryphoninae	*Exyston chamaeleon* Mason 1959	1
Tenthredinidae	Nematinae	aff. *Tenthredo piceocincta* (Norton 1860)	2
Vespidae	Vespinae	*Dolichovespula albida* Sladen 1918) (Arctic Yellowjacket)	4
Lepidoptera—moths			1
Geometridae	Sterrhinae	*Scopula sentinaria* (Geyer 1837)	1

morphs while hovering for 2–8 s, during which time some pollen sticks to their legs, thorax, and abdomen. This pollen is later deposited on flowers of other *P. jucundum* plants. Our observations of potential pollination in *K. alaskanum* var. *glabrescens* involved many cases of insects landing on flowers, rather than hovering. The predominance of flies as visitors across most of our sites reinforces their importance as potential pollinators, but the slight predominance of vespid wasps at one site in the Richardson Mountains also suggested some local variation.

In a study of dimorphic heterostyly in the related Bellflower Knotweed (*Koenigia campanulata* (Hook. f.) T.M. Schuster & Reveal (previously *Aconogonum campanulata*)), Hong (1991) observed that small solitary bees were the primary pollinators of its campanulate flowers. He considered these flowers shape-adapted to melittophily. He further noted that most other species of *Aconogonon* are pollinated to a large extent by flies and have non-campanulate flowers agreeing with a general syndrome of fly pollination. He finally noted, based on his general observations, that the flowers of species of *Aconogonon* may attract a large number of different insects to feed on their nectar. Hong's (1991) suggestions regarding fly pollination and pollinator diversity are supported by the 31 species of potential pollinators reported here for Alaskan Wild Rhubarb.

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Salt marsh width positively affects the occurrence of Least and Pectoral Sandpipers in the St. Lawrence River Estuary during fall migration

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Abstract

Salt marshes are vulnerable to climate change-associated sea-level rise and storm-induced surges. Their degradation will likely affect shorebirds relying on this ecosystem. Least Sandpiper (*Calidris minutilla*) and Pectoral Sandpiper (*Calidris melanotos*) migrating along coastline habitats typically use salt marshes to rest and replenish their body reserves. Our objective was to test if width of the different vegetation zones within salt marshes affects the occurrence of Least and Pectoral Sandpipers stopping along the St. Lawrence River Estuary, Quebec, Canada, during fall migration. We established 26 survey sites, each 600 m in length, along the shoreline. Shorebird surveys were conducted in 2011 and 2012. We characterized salt marshes by measuring the width of each vegetation zone (lower marsh and upper marsh). We analyzed shorebird presence/not detected data with generalized estimating equations to test the predictions that occurrence of Least Sandpipers and Pectoral Sandpipers increases with width of both the lower and upper marsh. Upper marsh width was positively associated with probability of occurrence in each species. Our results highlight the importance of protecting the integrity of salt marshes for these two species. In the St. Lawrence River Estuary, where landward migration of salt marshes is no longer possible (coastal squeeze), effective management of shorelines is much needed. Otherwise, salt marshes and these two species could be locally jeopardized.

Key words: Least Sandpiper; Pectoral Sandpiper; shorebird migration; stopover site, salt marsh, St. Lawrence River Estuary

Résumé

Les marais salés sont menacés par la hausse du niveau des océans et par les tempêtes côtières associées aux changements climatiques. Leur dégradation aura vraisemblablement un impact négatif sur les oiseaux de rivage qui les fréquentent. Le bécasseau minuscule (*Calidris minutilla*) et le bécasseau à poitrine cendrée (*Calidris melanotos*) migrant le long des côtes utilisent de manière importante cet habitat pour le repos et l'acquisition de réserves corporelles. Nous avons voulu vérifier si la largeur du bas marais et celle du haut marais avaient un effet sur l'occurrence de ces deux espèces dans l'estuaire St-Laurent au cours de la migration automnale. Nous avons disposé 26 sites d'inventaire d'une longueur de 600 m le long du littoral. Des inventaires d'oiseaux de rivage y ont été réalisés, en 2011 et en 2012. Nous avons mesuré dans ces sites la largeur du bas marais et celle du haut marais. Nous avons analysé des données de présence/absence pour le bécasseau minuscule et le bécasseau à poitrine cendrée à l'aide d'équations d'estimations généralisées, afin de vérifier si leur probabilité de présence augmentait avec la largeur du bas marais et celle du haut marais. La largeur du haut marais avait un effet positif sur l'occurrence de ces espèces. Ces résultats démontrent l'importance de protéger les marais salés pour celles-ci. Dans l'estuaire du fleuve St-Laurent, là où la migration vers l'intérieur des marais salés n'est plus possible (coincement côtier), des mesures de conservation sont requises. Sans ces mesures, les marais salés et ces deux espèces pourraient être localement menacés.

Mots-Clés: Bécasseau minuscule; Bécasseau à poitrine cendrée; migration des oiseaux de rivage; halte migratoire; marais salé; estuaire du fleuve St-Laurent

Introduction

Climate change impacts on coastal ecosystems, adjacent infrastructure, and low-lying communities is one of the most significant challenges of our time (United Nations 2020; World Wildlife Fund 2020). Indeed, the effects on coastal ecosystems of climate change-associated sea-level rise, as well as increasingly severe and frequent storm-induced surges, are now well documented (Hoegh-Guldberg and Bruno 2010; Passeri *et al*. 2015; Campbell and Wang 2020). Unfortunately, based on greenhouse gas emission scenarios, this situation is unlikely to improve in the short term (Nicholls and Cazenave 2010; Hinkel *et al*. 2014; Taherkhani *et al*. 2020). In salt marsh ecosystems, wave lateral erosion on the seaward edge and drowning, due to insufficient vertical surface accretion to compensate relative sea-level rise, both contribute to salt marsh degradation or losses (Watson *et al*. 2017; Cahoon *et al*. 2019; Payne *et al*. 2019).

Increasingly severe weather events and salt marsh degradation will likely affect animal populations, including shorebirds (Hunter *et al*. 2015; Correll *et al*. 2017; Von Holle *et al*. 2019). Unfortunately, many shorebird populations worldwide are already declining (Andres *et al*. 2012; Sutherland *et al*. 2012; Galbraith *et al*. 2014). In North America, shorebird populations have decreased since 1970 (Rosenberg *et al*. 2019). Some species are now considered Endangered in Canada (e.g., Piping Plover [*Charadrius melodus*], Red Knot rufa subspecies [*Calidris canutus rufa*]; SARA Registry 2021a,b). The underlying causes of global shorebird decline are not fully understood, but several mechanisms are likely involved (Munro 2017). On their subarctic and Arctic breeding grounds, rapidly changing climate conditions and associated mismatch between chick needs and peak insect emergence (van Gils *et al*. 2016; Kwon *et al*. 2019), degradation of tundra breeding sites by now overabundant Snow Goose (*Anser caerulescens*; Koons *et al*. 2014; Flemming *et al*. 2016), and increased predation of shorebird nests by Arctic Fox (*Vulpes lagopus*), and aerial predators attracted by conspicuous Snow Goose nests (Lamarre *et al*. 2017; Flemming *et al*. 2019a,b) have been invoked. Further south, hunting in the Caribbean and northern South America (Watts and Turrin 2016; Reed *et al*. 2018), human disturbance (Finney *et al*. 2005; Liley and Sutherland 2007), harvesting of marine resources (van Gils *et al*. 2006; Atkinson *et al*. 2007), pollution (Hua *et al*. 2015; Perkins *et al*. 2016; Pratte *et al*. 2020), and coastal development (Piersma *et al*. 2016; Chan *et al*. 2019; Mu and Wilcove 2020) are other likely drivers of shorebird decline.

Climate change effects on salt marsh integrity may exacerbate this ongoing decline if migrating shorebirds relying on salt marshes can no longer find adequate stopover and staging habitats. Stopover and staging sites are essential to migrating shorebirds to rest and replenish their body reserves throughout their route on predictable and abundant prey (Warnock 2010). Least Sandpiper (*Calidris minutilla*) and Pectoral Sandpiper (*Calidris melanotos*) migrating along coastline habitats typically use salt marshes (Bent 1962; Farmer *et al*. 2020; Nebel and Cooper 2020). Along the St. Lawrence River Estuary shoreline during fall (post-breeding) migration, Least Sandpiper and Pectoral Sandpiper *en route* to their wintering grounds, located mainly in South America, are observed almost exclusively in, or close to, salt marshes. While Pectoral Sandpiper populations are considered stable (BirdLife International 2020a), Least Sandpiper populations are decreasing (BirdLife International 2020b). Therefore, it is essential to readily identify salt marsh characteristics selected by these species during migration to achieve proper protection or restoration of these ecosystems where needed. These actions would help meet shorebird conservation objectives (North American Bird Conservation Initiative Canada 2019; North American Bird Conservation Initiative 2020).

The main objective of our study was to identify salt marsh characteristics affecting the occurrence of southbound Least and Pectoral Sandpipers stopping along the St. Lawrence River Estuary during fall migration. We hypothesized that the presence of these two species is associated with salt marsh width. More specifically, we addressed this hypothesis by testing the following predictions. Because width of another type of relatively narrow habitat (beaches) has been associated with shorebird use during migration (Murchison *et al*. 2016), we predicted that their occurrence at the survey site scale would increase with the size and therefore the width of the Smooth Cordgrass (*Sporobolus alterniflorus* (Loiseleur-Deslongchamps) P.M. Peterson & Saarela) lower marsh covered, at least partially, twice daily by tides. We also predicted that their occurrence at the survey site scale would increase with the size of the more diversified upper (or higher) marsh, flooded only during the highest tides, hence providing refuge to these species in most tidal conditions.

Study Area

This study was conducted on the south shore of the St. Lawrence River Estuary, along a 130 km stretch of shoreline between St-Roch-des-Aulnaies (47.311°N, 70.177°W) and St-Simon-sur-Mer (48.205°N, 69.082° W), Quebec, Canada (Figure 1a). Within the study area, water circulation is dominated by semidiurnal

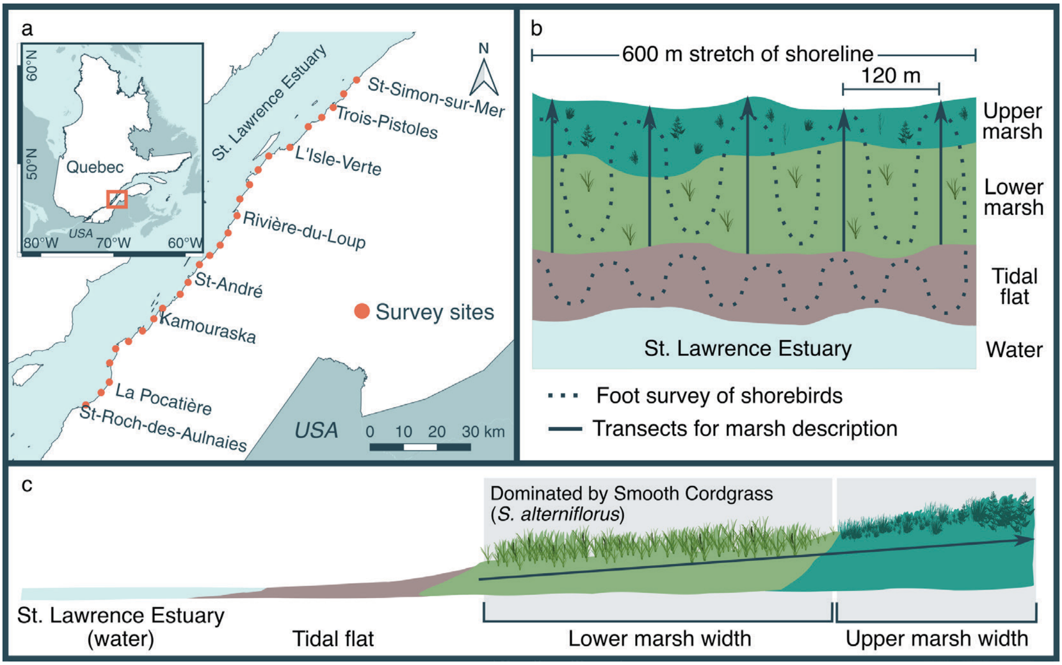

FIGURE 1. Study site locations and physical characteristics of areas surveyed. a. Location of survey sites on the south shore of the St. Lawrence River Estuary, Quebec, Canada; b. A typical foot survey of shorebirds and transects for marsh description; c. A transect for marsh description and zonation of salt marsh vegetation.

tides that can reach over 5 m in height (Fisheries and Oceans Canada 2011–2012). Intertidal substrates are highly variable, ranging from boulders, bare rock, and beaches at exposed sites to mudflats adjacent to salt marshes on more protected shorelines. Additional details on the study area can be found in Turcotte *et al*. (2017).

Salt marshes in the St. Lawrence River Estuary show the typical plant zonation resulting from tidal flooding and reported in other locations along the Atlantic Coast (Bertness and Ellison 1987; Kunza and Pennings 2008; Smith 2015). The lower marsh is covered, at least partially, twice daily by tides and is almost exclusively occupied by the native Smooth Cordgrass. Above the lower marsh, the upper marsh's seaward edge is generally dominated by Saltmeadow Cordgrass (*Sporobolus pumilus* (Roth) P.M. Peterson & Saarela). Upslope from Saltmeadow Cordgrass zone, the upper marsh vegetation becomes highly diversified and includes species such as Prairie Cordgrass (*Sporobolus michauxianus* (Hitchcock) P.M. Peterson & Saarela), Saltmarsh Bulrush (*Bolboschoenus maritimus* (L.) Palla), Seaside Plantain (*Plantago maritima* L.), and Virginia Glasswort (*Salicornia depressa* Standley; Dionne 1989; Coulombier *et al*. 2012).

Methods

Shorebird surveys

We established 26 survey sites 5 km apart along the shoreline (Figure 1a). Each survey site corresponded to a 600 m stretch of shoreline (Figure 1b), the length of which was measured with a handheld global positioning system unit at mean high tide level. Mean high tide level coincides with the upper limit on the shore of Smooth Cordgrass (Gauthier 1982; Smith 2015). Survey sites included all shorebird habitats above and below the shoreline (tidal flats, marshes, beaches, rocky shores). A first survey site was randomly selected to the nearest metre along a longitudinal axis within the study area. The other sites were thereafter positioned progressively every 5 km along the shoreline (systematic random sampling). In some cases, survey sites were relocated in similar habitat type, as close as possible from the selected site when, chiefly due to duck hunting activity, observer safety was compromised.

Surveys were conducted in 2011 and 2012 from early July through late November, corresponding to the migration period of all shorebird species observed annually in the study area. Surveys were conducted every week in 2011 (21 survey weeks) and every other week in 2012 (11 survey weeks). During precisely 30 min, each 600 m survey site was walked

(Figure 1b) by one or two nearby comoving observers (same observers in both years) to maximize visual coverage and induce flight of birds hidden in vegetation otherwise difficult to detect (Farmer and Durbian 2006; Andres *et al.* 2012). Shorebirds were identified with 60× spotting scopes or 8× binoculars when on the ground, or by their calls when in flight. Although each survey site corresponded to a 600 m stretch of shoreline, their widths were highly variable. It follows that in extensive marshes, complete surface coverage was challenging, and some birds likely remained undetected (see *Statistical analyses*). Sites were surveyed in different tidal conditions during consecutive weekly (2011) or biweekly surveys (2012). Tidal conditions may constrain habitat availability for birds feeding in intertidal habitats (Calle *et al.* 2018; Horn *et al.* 2020). Thus, we determined the relative water level at the time of the survey for each site, using predicted hourly heights for the nearest water level station located along the coast (Fisheries and Oceans Canada 2011–2012; distance to survey site: mean 9.5 km, SD 6.6 km). We defined the relative water level as the difference (m) either above or below the mean high tide level established for the nearest water level station. We used relative water level rather than absolute water level because the half funnel shape of the St. Lawrence River Estuary resulted in the mean high tide level increasing progressively going upriver in our study area (1.1 m difference).

Survey site descriptions

We selected the two most likely salt marsh characteristics based on species' natural history (Bent 1962; Farmer *et al.* 2020; Nebel and Cooper 2020), to explain occurrence at the survey site scale. We measured to the nearest metre with a measuring tape the width of each vegetation zone (lower marsh and upper marsh) from its lower edge to its upper edge along five evenly spaced (120 m) transects (two or three per year; Figure 1b). We did not notice perceivable habitat change between years. A first transect location was randomly selected to the nearest metre along a longitudinal axis within each survey site. The other transects were thereafter positioned every 120 m along the shoreline. Thus, the lower marsh width was measured from Smooth Cordgrass's appearance on the mudflat to the upper marsh's seaward edge (Figure 1c), typically occupied by Saltmeadow Cordgrass. The upper marsh width was measured from the lower marsh's upper edge to halophyte vegetation's disappearance. A mean lower marsh width and a mean upper marsh width were averaged from the five transects measures for each survey site.

Statistical analyses

There can be no certainty that all birds hidden in vegetation, along tidal pools, or drainage channels, were detected during surveys, particularly in extensive marshes. Therefore, for each species, we analyzed presence/not detected data rather than abundance. We acknowledge that even with equal effort, there would be a greater chance of missing birds on wider marshes. Also, we are unaware of a procedure to detect hidden birds other than using well-trained dogs or several people walking side-by-side; therefore we concentrated on presence/not detected.

Data collected at the same survey site over several weeks were not independent (repeated measurements design). Thus, we used generalized estimating equations (GEE) to test the predictions that occurrences of Least Sandpipers and Pectoral Sandpipers increase with: 1) the width of the lower marsh and, independently, 2) the width of the upper marsh. We looked at residual autocorrelograms to identify, for each species/year combination, the most suitable correlation structure to include in our models. In each of these four combinations, the correlation between any pair of observations declined with survey week. Thus, we used autoregressive models of a 1st order correlation structure (AR1). Because we had a small number (<30) of survey sites, we used the jackknife variance estimator. We ran separate analyses for each species.

During fall migration, Least Sandpipers are present in the study area from early July through early October (peak abundance around mid-August), while Pectoral Sandpipers were present from late August through late October (peak abundance around late September; Turcotte *et al.* 2017). Hence, we considered only survey weeks for each species during which at least one individual was detected in one of the 26 survey sites (as a result, one week was not considered in the analysis of Least Sandpiper occurrence in 2011). Preliminary models included one categorical predictor variable (study year), three continuous predictor variables (mean lower marsh width, mean upper marsh width, relative water level during the survey), and Least Sandpiper or Pectoral Sandpiper occurrence as response variables. Final models included predictor variables for which $P < 0.05$ in the preliminary model. All statistical analyses were carried out using package "geepack" (Halekoh *et al.* 2006) with R version 4.0.2 (R Core Team 2020).

Results

Shorebird surveys

Out of the 26 survey sites, Least Sandpipers were present at 23 survey sites in 2011 (from 4 July to 9 October, for a total of 963 birds detected) and 16 survey sites in 2012 (from 3 July to 22 September, for a total of 512 birds detected). Pectoral Sandpipers were present at 10 survey sites in 2011 (from 2 September to 23 October, for a total of 68 birds detected) and nine survey sites in 2012 (from 25 August to 22 October, for a total of 108 birds detected). Least and Pectoral Sandpipers were never detected at three and 13 survey sites, respectively. Total number of birds detected per survey site in 2011 and 2012 were positively correlated in both species (Least Sandpiper: Pearson $r = 0.69$, $t_{24} = 4.69$, $P < 0.0001$, $n = 26$; Pectoral Sandpiper: Pearson $r = 0.97$, $t_{24} = 18.97$, $P < 0.0001$, $n = 26$).

Survey site descriptions

Among the 26 survey sites, 14 included both a lower and an upper marsh, five contained only a lower marsh adjacent to a beach, and one included only an upper marsh because the lower marsh was completely eroded. Six survey sites were devoid of salt marsh vegetation. Lower marsh width (average of the five transects) ranged from 1.0 to 318.8 m (mean 93.8, SD 86.9, $n = 19$) while upper marsh width (average of the five transects) ranged from 4.4 to 357.8 m (mean 91.4, SD 107.8, $n = 15$). Lower marsh width and upper marsh width were not correlated in the 14 marshes where both types were present (Pearson $r = −0.27$, $t_{12} = −0.97$, $P = 0.35$, $n = 14$).

Survey site occupancy by Least and Pectoral Sandpipers

Neither year nor relative water level was associated with occurrence in either shorebird species (Table 1). However, lower marsh width and upper marsh width were both positively associated with Least and Pectoral Sandpipers' occurrence (Table 1). Six of the 26 survey sites were devoid of salt marsh vegetation. Hence, these results may be driven by the simple absence of marsh vegetation at these sites (Least Sandpiper: never detected at two of these six survey sites; Pectoral Sandpiper: never detected at any of the six survey sites). Therefore, to test if marsh width *per se* affected occurrence, we reanalyzed the data considering only the 20 sites where marsh vegetation was present. Again, upper marsh width was positively associated with Least and Pectoral Sandpipers' occurrence (Table 2). However, lower marsh width was no longer associated with Least and Pectoral Sandpipers' occurrence using the conventional criterion of $P < 0.05$ (Table 2). Nevertheless, we cannot rule out the possibility that this last result could be due to low sample size and associated reduced statistical power. Thus, it may represent a Type II error (incorrectly failing to reject a false null hypothesis). If we apply the precautionary principle of environmental decision-making, we should not readily conclude that lower marsh width has no effect on occurrence of these species.

Indeed, Figure 2 suggests that both species used salt marshes as long as a minimum width of either the lower marsh, the upper marsh, or both, was available. At survey sites where these species were observed during both study years, lower and upper marsh's total width reached at least 39 m and 106 m for Least and Pectoral Sandpipers, respectively (Figure 2). Based on CIs, mean total width was greater at those sites with our focal species than at survey sites where these species were never detected (Figure 3). Correspondingly, although we did not analyze abundance data due to possible detection issues, we found a positive trend between the maximum number of birds detected during a survey per survey site and salt marsh total width for both years and species (Figure 4).

Discussion

Our study presents, to our knowledge, the first investigation of habitat requirements for two south-

TABLE 1. Relationships between salt marsh characteristics, relative water level, year, and occurrence of Least (*Calidris minutilla*) and Pectoral (*Calidris melanotos*) Sandpipers on the south shore of the St. Lawrence River Estuary, Quebec, Canada, during fall migration, 2011 and 2012. Preliminary models include lower marsh width, upper marsh width, relative water level, and year as predictor variables. Final models include only lower marsh width and upper marsh width.

Species	Predictor variable	Preliminary model				Final model			
		β	SE	Wald statistic	P	β	SE	Wald statistic	P
Least Sandpiper	Lower marsh width (m)	0.005	0.001	12.97	0.0003	0.005	0.001	11.50	0.0007
	Upper marsh width (m)	0.008	0.001	46.92	<0.0001	0.008	0.001	50.70	<0.0001
	Relative water level (m)	−0.032	0.111	0.08	0.7755				
	Year	−0.192	0.294	0.43	0.5134				
Pectoral Sandpiper	Lower marsh width (m)	0.006	0.002	11.13	0.0009	0.007	0.002	9.86	0.0017
	Upper marsh width (m)	0.008	0.003	5.80	0.0160	0.008	0.003	6.47	0.0110
	Relative water level (m)	0.226	0.230	0.97	0.3242				
	Year	0.263	0.647	0.17	0.6841				

TABLE 2. Relationships between salt marsh characteristics, relative water level, year, and occurrence of Least (*Calidris minutilla*) and Pectoral (*Calidris melanotos*) Sandpipers on the south shore of the St. Lawrence River Estuary, Quebec, Canada, during fall migration, 2011 and 2012. Data only include the 20 survey sites where marsh vegetation was present. Preliminary models include lower marsh width, upper marsh width, relative water level, and year as predictor variables. Final models include only upper marsh width (Least Sandpiper) or lower marsh width and upper marsh width (Pectoral Sandpiper).

Species	Predictor variable	Preliminary model				Final model			
		β	SE	Wald statistic	P	β	SE	Wald statistic	P
Least Sandpiper	Lower marsh width (m)	0.002	0.001	2.64	0.1043				
	Upper marsh width (m)	0.006	0.001	29.64	<0.0001	0.006	0.001	30.04	<0.0001
	Relative water level (m)	0.001	0.118	0.00	0.9961				
	Year	−0.104	0.278	0.14	0.7079				
Pectoral Sandpiper	Lower marsh width (m)	0.005	0.002	4.33	0.0375	0.005	0.002	3.84	0.0500
	Upper marsh width (m)	0.007	0.003	4.20	0.0404	0.006	0.003	4.47	0.0350
	Relative water level (m)	0.253	0.231	1.21	0.2720				
	Year	0.273	0.621	0.19	0.6608				

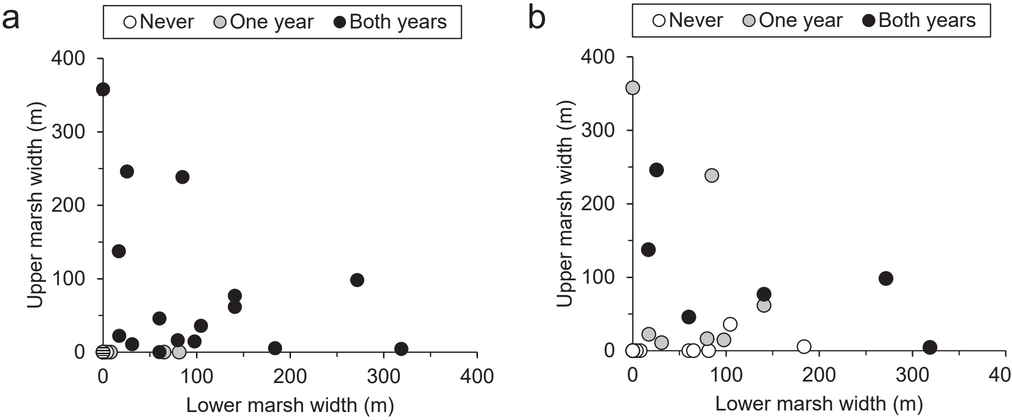

FIGURE 2. Salt marsh characteristics and occurrence of a. Least (*Calidris minutilla*) and b. Pectoral (*Calidris melanotos*) Sandpipers on the south shore of the St. Lawrence River Estuary, Quebec, Canada, during fall migration. Black circles are survey sites where species were detected during both years of the study, grey circles are survey sites where species were detected one year only, and white circles are survey sites where species were never detected. The cross-hatched circle represents six survey sites where Least Sandpipers were either detected one year only (four sites) or never detected (two sites).

bound shorebird species using salt marshes as stopover sites along the Atlantic seaboard. The fact that total number of birds detected per survey site in 2011 and 2012 was positively correlated in both species suggests that these birds' stopover site selection was not random but rather driven by habitat requirements. Indeed, we found that their occurrence along the St. Lawrence River Estuary was associated with marsh width, in particular upper marsh width. Because the upper marsh floods only during the highest tides, it provides refuge to these species in most tidal conditions. Our results highlight the importance of protecting the integrity of salt marshes for these two species. These marshes are likely highly relevant for migrating juveniles that far outnumber adults in our study area for both species (Turcotte *et al*. 2017).

Salt marshes are relatively narrow habitats that, in many places, became narrower due to the development of dikes, roads, and other civil development. Indeed, in our study area, in addition to road construction at the edge of salt marshes, extensive salt marsh diking was initiated in the mid-19th century to expand arable land (Hatvany 2002). In all of these locations, salt marshes are threatened by sea-level rise and storm-induced surges because, where landward migration becomes impossible, a coastal squeeze can occur (Torio and Chmura 2013; Watson *et al*. 2017; Mitchell and Bilkovic 2019). The upper marsh is especially at risk as it is expected to decline faster than the lower marsh (Valiela *et al*. 2018).

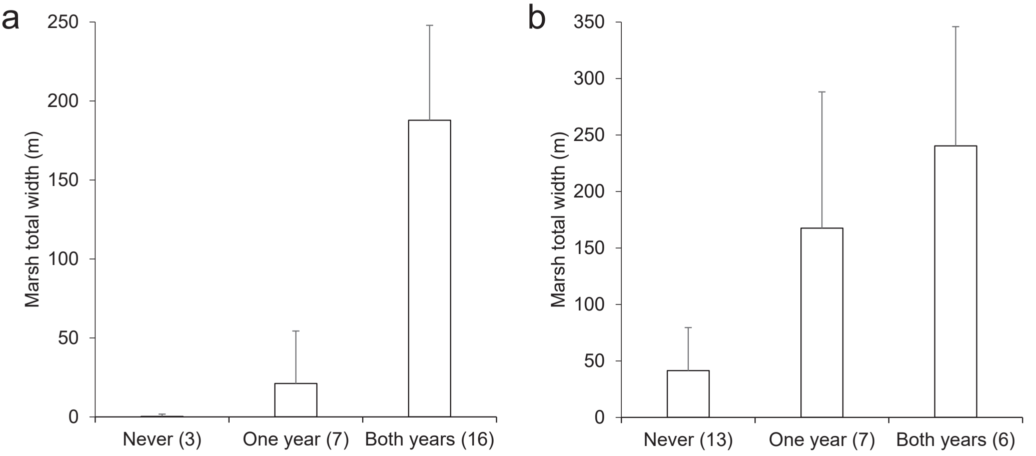

FIGURE 3. Mean salt marsh total width (+ 95% CI) in survey sites where a. Least (*Calidris minutilla*) and b. Pectoral (*Calidris melanotos*) Sandpipers were detected during both years of the study, detected one year only, or never detected on the south shore of the St. Lawrence River Estuary, Quebec, Canada, during fall migration.

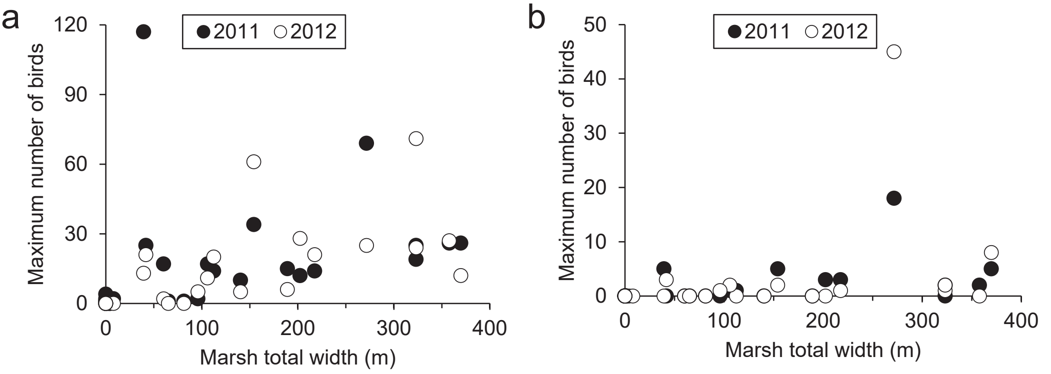

FIGURE 4. Relationship between the maximum number of a. Least (*Calidris minutilla*) and b. Pectoral (*Calidris melanotos*) Sandpipers detected per survey site per year, and salt marsh total width on the south shore of the St. Lawrence River Estuary, Quebec, Canada, during fall migration.

Degradation of stopover habitat has been linked to declines in migrating shorebird populations (Studds *et al*. 2017). However, effective management of shorelines such as realignment (e.g., moving of a coastal defense line inland to allow the re-inundation and development of an intertidal habitat [Shepard *et al*. 2011]) or climate-resilient, living shoreline design (e.g., use of stabilizing structures to protect the shoreline and enhance marsh establishment [Mitchell and Bilkovik 2019]) could increase salt marsh resilience through wave attenuation and higher accretion rate (Möller *et al*. 2014; Zedler 2017; Cahoon *et al*. 2019). We need such climate-resilient adaptation strategies. It is especially true where, due to glacial isostatic rebound (e.g., Magdalen Islands in the Gulf of St. Lawrence [Rémillard *et al*. 2016]) or compaction of Holocene strata (e.g., Mississippi Delta [Törnqvist *et al*. 2008]), subsidence exacerbates the effects of sea-level rise (Koohzare *et al*. 2008; Kirwan and Megonigal 2013; Piecuch *et al*. 2018). In areas such as the St. Lawrence River Estuary, where landward salt marsh migration is no longer possible, effective management is needed. Otherwise, salt marshes and associated salt marsh shorebirds could be locally jeopardized.

Author Contributions

Conceptualization: Y.T.; Methodology: Y.T.; Investigation: Y.T. and J.-F.L.; Data Curation: Y.T.; Formal Analysis: Y.T.; Writing – Original Draft: Y.T.; Visualization: Y.T. and É.D.; Writing – Review & Editing: Y.T., J.-F.L., É.D., and J.B.; Funding Acquisition: Y.T. and J.B.

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The Canadian Field-Naturalist

Changes to the Book Reviews and New Titles Sections

As of the publication of Issue 135, Volume 2, our Book Review Editor will be stepping down. We have been unable to find a replacement to date; thus, this section will undergo several changes. Until we find a new editor, William Halliday (wdhalliday@gmail.com), our Online Journal Manager, will take over the New Titles list and Amanda Martin (canadianfieldnaturalistae@gmail.com), the Assistant Editor, will manage the Book Reviews. William Halliday will focus on titles of books that are available for review. Readers of this journal are invited to request titles they are willing to review from the list from William and, if still available, copies will be sent directly to them by the publisher. Readers will still be able to submit reviews of books they have on hand, provided that reviewed books have a Canadian connection, including those on any species (native or non-native) that inhabits Canada, as well as books covering topics of global relevance, including climate change, biodiversity, species extinction, habitat loss, evolution, and field research experiences. Book reviews will be submitted through the online submission system https://www.canadianfieldnaturalist.ca/index.php/cfn/about/submissions. All received reviews will undergo editing, and prospective reviewers are encouraged to check our book review guidelines at https://www.canadianfieldnaturalist.ca/index.php/cfn/about/submissions. These changes will be fully in place as of Issue 135, Volume 3 and continue until a new Book Reviewer Editor is found.

We wish to thank each of you who has provided reviews in the past, and encourage all of you to continue to keep this section going. Lastly, are there any volunteers willing to assume the full role of the Book Reviewer Editor? If so, please contact the Editor-in-Chief (editor@canadianfieldnaturalist.ca) for more information.

Book Reviews

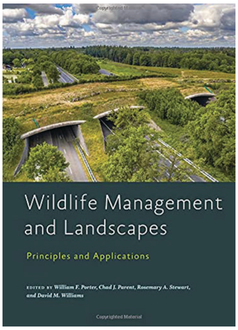
Book Review Editor's Note: *The Canadian Field-Naturalist* is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those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

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

ECOLOGY

Wildlife Management and Landscapes: Principles and Applications

Edited by William F. Porter, Chad J. Parent, Rosemary A. Stewart, and David M. Williams. 2021. John Hopkins University Press (in association with The Wildlife Society). 360 pages, 74.95 USD, Cloth or E-book.



The landscape ecology concept, which became established in the 1990s, was a great idea, but suffered from a lack of evidence. The idea that species may require habitat beyond the size of their home range or territory, or that populations may actually be metapopulations, or some areas that look ideal were actually mortality sinks was compelling, but few studies had been conducted, typically because of limitations in project design and a too-narrow spatio-temporal scale. Thirty years later, enough evidence exists that managers readily apply larger-scale thinking into resource management, urban/rural planning, endangered species recovery plans, and protected areas. Parallel with this evidence has been the delivery of books promoting landscape ecology and advising on how to better incorporate the landscape into management.

Wildlife Management and Landscapes is a compilation of existing knowledge, followed by applications to real management problems. The first two of four parts, with three and six chapters, respectively, establish a link between traditional wildlife management (i.e., local or stand-scale and short-term demographics) and landscape-scale thinking. Well-used terms such as island biogeography, metapopulation, corridor, matrix, patch, and habitat fragmentation are covered. The term 'habitat', misused by nearly everyone, is explained because habitat is the foundation for all wildlife management. Other chapters cover metadata and geographic information systems, both obvious components when considering patterns over a large and small spatial extent. Parts 3 and 4 are more interesting for advanced readers who already have a foundation in landscapes and wildlife. Because large areas typically involve more stakeholders, and sometimes competing land-use priorities, much of these chapters focus on cooperative ventures between disparate groups, the role of non-government organizations, and conservation incentives.

The authors, over 40, are mainly academics at American universities or government departments. Several well-established Canadian academics are involved but the examples and case studies are nearly all American. The ideas though would apply just as well to Canadian situations. Case studies include managing for Gunnison's Sage Grouse over four American states, prioritizing waterfowl habitat in the American section of the Great Lakes, mapping warbler habitat over the Appalachian Mountains range, and corridor and conservation planning in the Yellowstone to Yukon Initiative. I will note though that corridor planning is not a significant component of this book, even though corridors often are associated with landscape-scale conservation planning, and the book cover shows a wildlife overpass over a highway. Other books dwell more on corridors and connectivity planning. This book is well-suited to researchers and as an upper-level university textbook in wildlife management, although the first half of the book would be of interest to a wider audience because it does a nice summary of the evolution of the concepts over the last 30 or so years.

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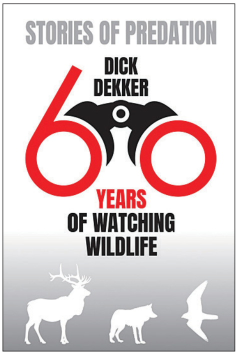
ZOOLOGY

Stories of Predation: 60 Years of Watching Wildlife

By Dick Dekker. 2021. Hancock House Publishing. 240 pages, 34.95 CAD, Cloth, 19.95 CAD, Paper.



Dick Dekker is a remarkable individual, and *Stories of Predation* is a remarkable book. Dekker is a largely self-taught "independent naturalist", but unlike thousands of other birders and wildlife watchers, he has taken it upon himself to carefully collect, analyze, and synthesize his many endless observations. He tells us that "the first science paper I had ever read ... opened my eyes to what could be done by just watching hawks in the field" (p. 210), and that his "methods were simple and required no more than patience and luck to be in the right place at the right time" (p. 61). Dick Dekker is not just a hobbyist; he is a researcher, and this book is a summary of his studies. I have to admit: such things fascinate me.

The tagline, *60 Years of Watching Wildlife*, gives away the fact that this is actually an autobiography, summarizing Dekker's accomplishments over the years. On page 209, he can't resist letting us know that this was his original choice for the book's title. Still, this volume is indeed about predators, mostly, and there are plenty of well-told stories here about wolves, falcons, and eagles. But the book also contains reflections on the natural history of shorebirds, ungulates, forests, and water levels and, on another level, it chronicles Dekker's opinions on various aspects of park management (and mismanagement), conservation, experiences in the backcountry, and life as a Dutch immigrant to Canada.

It is important to realize that in many ways, Dick Dekker's perspective is singular. He is unlike a university academic, or a government biologist, or a typical environmental journalist. However, he now holds a Ph.D., awarded by the University of Wageningen in the Netherlands, where they invited him to submit a thesis based on his falcon studies. In 2009, at age 75, he became the oldest person ever to receive a doctorate from that institution.

So what does an "independent naturalist" do for 60 years, free of the shifting research priorities of government, and the grant politics and publication pressures experienced by university academics? Well, for one thing, Dekker publishes extensively in specialist venues tightly appropriate to his work (e.g., the *Journal of Raptor Research* and *Waterbirds*). He has also been a regular contributor to *The Canadian Field-Naturalist*. One gets the impression that to him, all publications should be considered equally important, refereed or not, local or international. I agree, at least in principle, and I wish that universities shared this view.

Do I have anything to criticize about this book? Well, I could nit-pick about various aspects of Dekker's ecological worldview, and point out some misspelled scientific names, but these concerns do not diminish my approval of the book. I did, however, find it curious that Dekker mentions all of the people he agrees with by name, but treats his rivals and detractors anonymously. This comes across as gentlemanly, but it also makes one want to uncover the identities of the anonymous bad guys.

He does seem to have some valid complaints about some of his colleagues, though. For example, on pages 54 and 55, we learn that the ecological dynamics involving Elk, wolves, and aspen trees were first elucidated by Dekker in Jasper National Park, and published in the *Alberta Naturalist*, only to be seen and then reworked in Yellowstone by professional scientists, who failed to credit Dekker's original studies.

Twice in the book (pp. 97, 201), Dekker bemoans the fact that scientists are not always objective and fair, and credits none other than David Suzuki for this insight. What a contrast to life in the academic sphere, where one continually encounters scepticism regarding the objectivity of science, with Suzuki as a frequent target of such criticisms. In a world where scientists are typically considered guilty of bias and spin, until proven innocent, it is refreshing to encounter Dekker's somewhat old-fashioned ideals, and his genuine desire to remain objective and dispassionate.

Perhaps Dekker's sense of etiquette is also the reason that it is rather difficult to identify many of his major conclusions. For example, he seems convinced that the oil and gas industry is reducing water levels in Central Alberta lakes, but he mentions it only as an aside. Even after reading the book cover to cover, I still had to go back to figure out what "the Peregrine's paradox" was all about and, despite an entire chapter on the subject, I'm still not clear what the adaptive value of melanism is for wolves (but I can guess, from the title of one of Dekker's co-authored papers).

When you read the works of professional scientists, the conclusions are almost too bold, but with Dekker, they take some sleuthing to uncover.

Dekker's scientific style makes sense when one considers his overall approach. In a world where most biological studies take place over one or two "field seasons", using tightly-focussed "hypothesis testing", Dekker's datasets were amassed over decades, and he is relentlessly inductive, mulling over thousands of observations before tentatively suggesting a general explanation for what he has seen. When it comes to statistics, he keeps it simple, using only sums, means, and the occasional linear regression, performed by his brother, "a mathematician". Jumping to conclusions is simply not Dekker's style.

Stories of Predation is as close as we can get to an independent, carefully researched perspective on the topics addressed in this book. As such, it should be right there on the bookshelf of anyone interested in the natural history of Western Canada, be they professional or amateur. Recognizing the importance of diverse perspectives on all environmental issues, a voice as unique and powerful as Dick Dekker's deserves to be heard, and this book will ensure his legacy as a classical, careful, and very literate outdoor naturalist.

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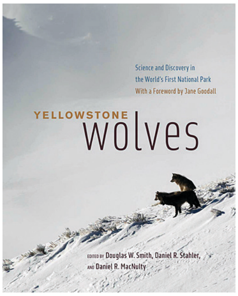
Yellowstone Wolves: Science and Discovery in the World's First National Park

Edited by Douglas W. Smith, Daniel R. Stahler, and Daniel R. MacNulty. 2020. University of Chicago Press. 358 pages, 35.00 USD, Cloth.



Yellowstone Wolves is a comprehensive, important, and authoritative text that summarizes the major findings of the first 25 years of wolf recovery in one of the world's first national parks. Given that the vast majority of people (79 to be exact: pp. 321–326) involved with the restoration have contributed to this massive six-year undertaking (p. 285), it will definitely be the ultimate reference on wolves in Yellowstone and beyond for years to come. While L.D. Mech and L. Boitani's *Wolves: Behavior, Ecology, and Conservation* (2003, University of Chicago Press) might be considered the definitive work on wolves to date, *Yellowstone Wolves* is the most detailed text published on the species in a specific location. The book is more academic than most previous publications on Yellowstone wolves so it is perfect for biologists, die-hard fans, and travellers to Yellowstone; as a text in college wildlife biology courses; and for the layperson with a keen interest in Yellowstone or wolves. It is a bit technical, however, so might not be suitable or of interest to the casual tourist who visits the park. For them, I might suggest easier reads, such as Rick McIntyre's books on Yellowstone wolves (Way 2019, 2020a).

While not an informal, page-turning read like others that have come from the park, *Yellowstone Wolves* tells the complete story of the species' recovery, starting with 14 wolves reintroduced from Canada in 1995 and then with 17 more in 1996 (pp. 23–24). Their subsequent ecological impact over the last two and a half decades is presented in an accessible, scientific way through anecdotes, many pictures, and other stories (including guest essays). It is illustrated with loads of colour images and impressive graphs and tables (many of which I have seen in previous publications), making it a good book for one's coffee table. Plus, a 68-minute accompanying online video, produced by cinemaphotographer extraordinaire Bob Landis, shares original wolf footage and interviews with some of the main players of this collaborative effort. I have read dozens of peer-reviewed scientific articles, books, and popular (magazine and online) articles and have watched numerous documentaries on Yellowstone's wildlife. This book is a summary of all those sources, from the wolf's perspective. The authors' goal was clearly to put the results of all of the impressive research into an organized volume. For that, they did a fantastic job! Furthermore, the price is very reasonable, especially for a large, heavy (4–5 pounds [2 kg]), double-columned book printed entirely on glossy paper.

The book is divided into six major sections: the history and reintroduction process; behavioural and population ecology; genetics and disease; wolf–prey relationships; ecosystem effects and species interactions; and conservation, management, and the human experience. We gain knowledge of individual wolves, family dynamics, population dynamics, territoriality, effects of disease, genetics and the rise of the black wolf (Chapter 8), wolf–Elk relationships, scavenging on bison carcasses (pp. 166, 174), management and various stakeholders involved, interspecies interactions, and the 'trophic cascades' that wolves have (purportedly) caused. My favourite part was Chapter 18, The Wolf Watchers, because I am part of that loose collection of folks (e.g., Way 2020b) and believe that this eclectic group has been critical for helping to give widespread attention to individual wild wolves which helps garner support to better protect them (p. 257). This is important because wolves are estimated to generate $65.5 million USD a year in the Yellowstone region (pp. 260–261).

Chief among the many themes in this wide-ranging book is the importance of radio-collaring wolves (pp. 32, 139, 269). This was apparent throughout the text, with just about every research finding predicated on using marked animals—including the wolves' prey (deer, Elk, and bison) and competitors (bears, Cougars, Coyotes)—to track and determine home range and territory size, habitat selection, movement and activity patterns, food habits, mortality causes, and sociality. Yellowstone is unparalleled because biologists and tourists alike most often observe wolves easily from the park's roadways, giving the animals more space in the backcountry to behave naturally (p. 248). This spectacular visibility has made Yellowstone the best place in the world to observe wolves, a central tenet of the book (e.g., pp. 26, 261). Wolves in Yellowstone are also one of the least persecuted populations in North America, providing a benchmark to compare other populations (p. 267). The park is also an ideal natural 'laboratory' for conducting valuable long-term studies that provide researchers a deep knowledge of the system and their study subjects (p. 143).

Yellowstone Wolves demonstrates in detail that while Elk are the main prey and food source of wolves, scavenged bison has become an increasingly large percentage of their diet as bison numbers have increased and Elk have decreased in the park (Part 4: Wolf-Prey Relationships). Wolf predation attempts usually fail, even for Elk, and bison are about three times more difficult to kill (p. 149). Wolves are a generalist species, a jack of all trades, so are not particularly adept at killing large prey (pp. 32, 187) and are usually only able to kill the young, old, and weak (pp. 162–163). However, with a full suite of carnivores presently on the landscape, the ecosystem has been at least partially restored with improved willow and aspen regeneration in many parts of the park, although it is difficult to distinguish between behavioural (landscape of fear) versus demographic (i.e., reduced numbers) changes in Elk (Chapter 15).

We learn in *Yellowstone Wolves* that males are the better hunters and defenders of their family's territory while females are the social glue of the pack and are most involved in leading pup-rearing activities (Part 2: Behavioral and Population Ecology). With an average pack size of 10 (pp. 46, 59), wolf family structure in Yellowstone is more flexible and diverse than previously described elsewhere, with packs often starting from groups, not pairs (p. 43). In fact, this 'group dispersal' was often mentioned in the text and is unique to wolves in Yellowstone who live in a saturated population that requires strength in numbers to claim an area (pp. 44, 60, 75, 89). I also found the discussion of black wolves, about 50% of the colour morphs in the park, fascinating because they likely arose in northwestern North America (i.e., Yukon region) via introgression with Domestic Dogs (pp. 112–113). Black wolves have better immunity than grey-coloured wolves and are thus more adept at surviving disease epidemics, while greys are more aggressive and have about 25% better litter survival than their melanistic counterparts (pp. 116, 119). To balance these life history factors, a disproportionate number (64%) of pairs are mixed colours; this disassortative mating is rare in nature (p. 115; also see online video).

The book's 19 chapters serve as standalone manuscripts written by various combinations of the 79 different contributors. A robust 31-page, double-columned Literature Cited section accompanies the text. *Yellowstone Wolves* need not be read completely and in order as it can be used as much as a reference as anything else. However, I did read the entire book from cover to cover and found that it had many repetitive sections owing to this format. While it certainly stressed the importance of many key concepts described above, it also became confusing to remember where certain passages appeared even though I created two pages of detailed notes. For instance, habituated wolves were mentioned often (e.g., pp. 247, 252, 269), as were the open landscape of the park permitting year-round observation (e.g., Chapter 18 and just about every other chapter), wolf reintroduction coinciding with the natural recovery of Grizzly Bears and Cougars (especially Chapters 10–16), and the natural regulation philosophy occurring in national parks (literally throughout the book, but especially in the five chapters of Part 4; also see p. 267). This similarity and repetitiveness in text, not surprisingly, was most pronounced in related chapters that were within the same section (e.g., within Part 4) because their data collection methods were similar. However, each chapter also presented important and different research results; for instance, wolf–Elk populations have appeared to stabilize in the park and the diverse number of predators and prey species, as well as other factors such as human hunting and climate change, make it difficult to predict what may happen in the future (Part 4).

There is no doubt that this is one of the most significant and impressive volumes ever written on wolves and I wholeheartedly recommend it. The main value of this book is to serve as a baseline to which other manuscripts and wolf populations will be compared. For example, I envision future studies citing this book when comparing their research results to average packs sizes where wolves are not readily killed by people, prey selection in a natural versus human-influenced system, wolf behaviour and interspecific relationships in diverse ecosystems, or the ability to study wolf behaviour directly for an extended length of time, which is unparalleled in Yellowstone (Chapters 17 and 18). To that end, *Yellowstone Wolves* has set the standard for a tome on a wildlife species in a specific area. Kudos to all of the authors involved in this endeavour!

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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

The Atlantic Walrus: Multidisciplinary Insights into Human-Animal Interactions. Edited by Xénia Keighley, Morten Tange Olsen, Peter D. Jordan, and Sean P.A. Desjardins. 2021. Academic Press. 344 pages, 102.00 USD, Paper or E-book, 120.00 USD, bundled.

A History of Biology. By Michel Morange. Translated by Teresa Lavender Fagan Joseph Muise. 2021. Princeton University Press. 448 pages, 29.95 USD, Cloth.

†Male Choice, Female Competition, and Female Ornaments in Sexual Selection. By Ingo Schlupp. 2021. Oxford University Press. 176 pages, 65.00 CAD, Cloth. Also available as an E-book.

Mammalian Paleoecology: Using the Past to Study the Present. By Felisa A. Smith. 2021. Johns Hopkins University Press. 280 pages, 79.95 USD, Cloth or E-book.

†Medicinal Mushrooms of Western North America. By Robert Rogers and J. Duane Sept. 2020. Calypso Publishing. 96 pages and 87 colour photos, 14.95 CAD, Paper.

Mushrooms of British Columbia. Royal BC Museum Handbook. By Andy MacKinnon and Kem Luther. 2021. Royal BC Museum. 504 pages, 34.95 CAD, Paper. Also available as an E-book.

Myxomycetes: Biology, Systematics, Biogeography, and Ecology. Second Edition. Edited by Carlos Rojas Alvarado and Steven L. Stephenson. 2021. Academic Press. 566 pages, 127.50 USD, Paper.

In Search of Mycotopia: Citizen Science, Fungi Fanatics, and the Untapped Potential of Mushrooms. By Doug Bierend. 2021. Chelsea Green Publishing. 336 pages, 24.95 USD, Cloth.

Secret Worlds: The Extraordinary Senses of Animals. By Martin Stevens. 2021. Oxford University Press. 272 pages, 25.95 CAD, Cloth. Also available as an E-book.

The Theory of Ecological Communities. Monographs in Population Biology Series. By Mark Vellend. 2020. Princeton University Press. 248 pages, 49.95 USD, Cloth, 35.00 USD, Paper. Also available as an E-book.

Understanding Animal Behaviour: What to Measure and Why. By Sergio Pellis and Vivien Pellis. 2021. Cambridge University Press. 166 pages, 84.99 USD, Cloth, 34.99 USD, Paper, 28.00 USD, Adobe eBook.

BOTANY

†Ash. By Edward Parker. 2021. Reaktion Books. 224 pages and 80 colour plates, 27.00 USD, Cloth.

Evolution Made to Order: Plant Breeding and Technological Innovation in Twentieth-Century America. By Helen Anne Curry. 2021. University of Chicago Press. 295 pages, 36.00 USD, Paper.

Finding the Mother Tree: Discovering the Wisdom of the Forest. By Suzanne Simard. 2021. Allen Lane. 368 pages, 34.95 CAD, Cloth, 41.00 CAD, Large Print Paper, 15.99 CAD, E-book.

†Flora of North America: Volume 10, Magnoliophyta: Proteaceae to Elaeagnaceae. By Flora of North America Editorial Committee. 2021. Oxford University Press. 488 pages, 95.00 CAD, Cloth.

Lives of Weeds: Opportunism, Resistance, Folly. By John Cardina. 2021. Cornell University Press. 296 pages, 24.95 USD, Paper, 11.99 USD, E-book.

The Nature of Oaks: The Rich Ecology of Our Most Essential Native Trees. By Douglas W. Tallamy. 2021. Workman. 200 pages, 27.95 USD, Cloth, 21.95 USD, E-book.

Nature Remade: Engineering Life, Envisioning Worlds. Edited by Luis A. Campos, Michael R. Dietrich, Tiago Saraiva, and Christian C. Young. 2021. University of Chicago Press. 320 pages, 135.00 USD, Cloth, 45.00 USD, Paper or E-book.

Roots to Seeds: 400 Years of Oxford Botany. By Stephen A. Harris. 2021. Bodleian Library, University of Oxford. Distributed by University of Chicago Press. 224 pages and 80 colour plates, 60.00 USD, Cloth.

Treepedia: A Brief Compendium of Arboreal Lore. Pedia Book Series. By Joan Maloof. Illustrated by Maren Westfall. 2021. Princeton University Press. 152 pages, 16.95 USD, Cloth. Also available as an E-book.

Tropical Arctic: Lost Plants, Future Climates, and the Discovery of Ancient Greenland. By Jennifer McElwain, Marlene Hill Donnelly, and Ian Glasspool. 2021. University of Chicago Press. 144 pages and 91 colour plates, 30.00 USD, Cloth, 22.99 USD, PDF or EPUB.

Conservation and Climate Change

The Anthropocene Disruption. By Robert William Sandford. 2019. Rocky Mountain Books. 168 pages, 20.00 CAD, Cloth.

Conservation Science and Advocacy for a Planet in Peril: Speaking Truth to Power. Edited by Dominick DellaSala. 2021. Elsevier. 450 pages, 99.95 USD, Paper.

Is CITES Protecting Wildlife? Assessing Implementation and Compliance. By Tanya Wyatt. 2021. Routledge. 128.00 USD, Cloth, 37.56 USD, Paper, 42.25 USD, E-book.

†**Conservation Technology**. Edited by Serge A. Wich and Alex K. Piel. 2021. Oxford University Press. 328 pages, 49.95 CAD, Cloth. Also available as an E-book.

Conserving the Oceans: The Politics of Large Marine Protected Areas. By Justin Alger. 2021. Oxford University Press. 248 pages, 74.00 CAC, Cloth. Also available as an E-book.

The Empty Sea: The Future of the Blue Economy. By Ilaria Perissi and Ugo Bardi. 2021. Springer International Publishing. 224 pages and 87 black and white illustrations, 39.99 USD, Cloth, 29.99 USD, E-book.

†**The Environmentalist's Dilemma: Promise and Peril in an Age of Climate Crisis**. By Arno Kopecky. 2021. ECW Press. 300 pages, 24.95 CAD, Paper, 16.99 CAD, E-book or PDF.

Handbook of Citizen Science in Ecology and Conservation. Edited by Christopher A. Lepczyk, Owen D. Boyle, and Timothy L.V. Vargo. Foreword by Reed F. Noss. 2020. University of California Press. 336 pages, 85.00 USD, Cloth, 39.95 USD, Paper or E-book.

Strange Natures: Conservation in the Era of Synthetic Biology. By Kent H. Redford and William M. Adams. 2021. Yale University Press. 296 pages, 32.50 USD, Cloth.

Taking a Break from Saving the World: A Conservation Activist's Journey from Burnout to Balance. By Stephen Legault. 2020. Rocky Mountain Books. 168 pages, 20.00 CAD, Paper.

Why Biodiversity Loss Is Not a Disaster. By Bas Haring. 2021. Leiden University Press. Distributed by University of Chicago Press. 88 pages, 17.50 USD, Paper.

Why Nature Conservation Isn't Working: Understanding Wildlife in the Modern World. By A. Spalding. 2021. Siri Scientific Press. 160 pages, 14.99 GBP, Paper.

Ecology

*__Applications for Advancing Animal Ecology__. By Michael L. Morrison, Leonard A. Brennan, Bruce G. Marcot, William M. Block, and Kevin S. McKelvey. 2021. Johns Hopkins University Press. 264 pages, 69.95 USD, Cloth. Also available as an E-book.

†**Beavers: Ecology, Behaviour, Conservation, and Management**. By Frank Rosell and Róisín Campbell-Palmer. 2021. Oxford University Press. 512 pages, 100.00 CAD, Cloth, 49.95 CAD, Paper. Also available as an E-book.

Ecology and Natural History. New Naturalist Series, Volume 143. By David Wilkinson. 2021. William Collins (HarperCollins Imprint). 384 pages, 135.00 CAD, Cloth, 65.00 CAD, Paper, 60.99 CAD, E-book.

Ocean Ecology: Marine Life in the Age of Humans. By J. Emmett Duffy. 2021. Princeton University Press. 464 pages, 80.00 USD, Cloth. Also available as an E-book.

†**Predator Ecology: Evolutionary Ecology of the Functional Response**. By John P. DeLong. 2021. Oxford University Press. 176 pages, 45.95 CAD, Cloth. Also available as an E-book.

†**A Primer of Life Histories: Ecology, Evolution, and Application**. By Jeffrey A. Hutchings. 2021. Oxford University Press. 240 pages and 135 illustrations, 42.95 CAD, Cloth. Also available as an E-book.

Scaling in Ecology with a Model System. Monographs in Population Biology Series. By Aaron M. Ellison and Nicholas J. Gotelli. 2021. Princeton University Press. 336 pages, 110.00 USD, Cloth, 50.00 USD, Paper. Also available as an E-book.

***Wildlife Management and Landscapes: Principles and Applications**. Edited by William F. Porter, Chad J. Parent, Rosemary A. Stewart, and David M. Williams. 2021. Johns Hopkins University Press. 360 pages, 74.95 USD, Cloth or E-book.

ENTOMOLOGY

Ant Architecture: The Wonder, Beauty, and Science of Underground Nests. By Walter R. Tschinkel. 2021. Princeton University Press. 248 pages and 105 colour illustrations, 29.95 USD, Cloth. Also available as an E-book.

Beetles of Western North America. By Arthur V. Evans. 2021. 624 pages, 45.00 USD, Paper. Also available as an E-book.

Common Bees of Eastern North America. Princeton Field Guides. By Olivia Messinger Carril and Joseph S. Wilson. 2021. Princeton University Press. 288 pages, 75.00 USD, Cloth, 27.95 USD, Paper. Also available as an E-book.

Crop Pollination by Bees, Volume 1: Evolution, Ecology, Conservation, and Management. Second Edition. By Keith Delaplane. 2021. CABI. 192 pages, 67.50 USD, Paper or E-book.

Edible Insects: A Global History. By G.L. Hunter. 2021. Reaktion Books. 176 pages and 61 colour illustrations, 11.99 GBP, Cloth.

†The Silken Thread: Five Insects and Their Impacts on Human History. By Robert N. Wiedenmann and J. Ray Fisher. 2021. Oxford University Press. 296 pages and 55 illustrations, 39.95 CAD, Cloth. Also available as a E-book.

A Faunal Review of Aleocharine Beetles in the Rapidly Changing Arctic and Subarctic Regions of North America (Coleoptera, Staphylinidae). By Jan Klimaszewski, Adam J. Brunke, Derek S. Sikes, Mikko Pentinsaari, Benoit Godin, Reginald P. Webster, Anthony Davies, Caroline Bourdon, and Alfred F. Newton. 2021. Springer Nature. 704 pages and 307 colour illustrations, 149.99 GBP, Cloth.

Gardening for Bumblebees: A Practical Guide to Creating a Paradise for Pollinators. By Dave Goulson. 2021. Square Peg. 288 pages, 35.99 CAD, Cloth.

What Insects Do, and Why. By Ross Piper. 2021. Princeton University Press. 224 pages and 150 colour illustrations, 27.95 USD, Cloth. Also available as an E-book.

Observing Evolution: Peppered Moths and the Discovery of Parallel Melanism. By Bruce S. Grant. 2021. Johns Hopkins University Press. 320 pages, 59.95 USD, Cloth or E-book.

Plant Galls of the Western United States. Princeton Field Guides. By Ronald A. Russo. 2021. Princeton University Press. 400 pages, 2.95 USD, Paper.

Silent Earth: Averting the Insect Apocalypse. By Dave Goulson. 2021. Jonathan Cape. 336 pages, 20.00 GBP, Cloth or E-book.

Social Butterflies. Monographs in Population Biology Series. By Henry S. Horn. 2021. Princeton University Press. 288 pages, 120.00 USD, Cloth, 39.95 USD, Paper. Also available as an E-book.

Super Fly: The Unexpected Lives of the World's Most Successful Insects. By Jonathan Balcombe. 2021. PenguinRandomHouse Canada. 352 pages, 24.00 CAD, Paper, 13.99 CAD, E-book.

HERPETOLOGY

Diamonds in the Marsh: A Natural History of the Diamondback Terrapin. New Edition. By Barbara Brennessel with a New Introduction by the author and a Foreword by Bob Prescott. 2021. Brandeis University Press. 256 pages, 27.95 USD, Paper, 22.95 USD, PDF or EPUB.

The Secret Social Lives of Reptiles. By J. Sean Doody, Vladimir Dinets, and Gordon M. Burghardt. 2021. Johns Hopkins University Press. 440 pages, 74.95 USD, Cloth or E-book.

Turtles of the World: A Guide to Every Family. By Jeffrey E. Lovich and Whit Gibbons. 2021. Princeton University Press. 240 pages, 29.95 USD, Cloth. Also available as an E-book.

ORNITHOLOGY

†100 Flying Birds: Photographing the Mechanics of Flight. By Peter Cavanagh. 2021. Firefly Books. 320 pages and 120 colour photographs, 49.95 CAD, Cloth.

†Bird: Exploring the Winged World. By Phaidon Editors. Illustrated by Katrina van Grouw and Jen Lobo. 2021. Phaidon Press. 300 colour images, 79.95 CAD, Cloth.

Bird Talk: An Exploration of Avian Communication. By Barbara Ballentine and Jeremy Hyman. Edited by Mike Webster. 2021. Comstock Publishing Associates. 192 pages, 29.95 USD, Cloth.

Birdpedia: A Brief Compendium of Avian Lore. Pedia Book Series. By Christopher W. Leahy. Illustrated by Abby McBride. 2021. Princeton University Press. 272 pages, 16.95 USD, Cloth. Also available as an E-book.

The Complete Birds of the World: Every Species Illustrated. By Norman Arlott, Ber van Perlo, Jorge R. Rodriguez Mata, Gustavo Carrizo, Aldo A. Chiappe, and Luis Huber. 2021. Princeton University Press. 640 pages and 25 000 colour illustrations, 65.00 USD, Cloth.

How Birds Evolve: What Science Reveals about Their Origin, Lives, and Diversity. By Douglas J. Futuyma. 2021. Princeton University Press. 320 pages, 29.95 USD, Cloth or E-book.

The Hummingbird Handbook: Everything You Need to Know about These Fascinating Birds. By John Shewey. 2021. Timber Press. 240 pages, 24.95 USD, Paper.

†Infectious Disease Ecology of Wild Birds. Edited by Jennifer C. Owen, Dana M. Hawley, and Kathryn P. Huyvaert. 2021. Oxford University Press. 304 pages, 95.00 CAD, Cloth, 49.95 CAD, Paper. Also available as an E-book.

Owls of the Eastern Ice: The Quest to Find and Save the World's Largest Owl. By Jonathan C. Slaght. 2020. Farrar, Strauss and Giroux. 368 pages, 28.00 USD, Cloth, 18.00 USD, Paper, 11.99 USD, E-book.

Peterson Field Guide to North American Bird Nests. By Casey McFarland, Matthew Monjello, and David Moskowitz. 2021. Houghton Mifflin Harcourt. 512 pages, 24.99 USD, Paper, 12.99 USD, E-book.

Swifts and Us: The Life of the Bird that Sleeps in the Sky. By Sarah Gibson. 2021. William Collins (Harper Collins imprint). 304 pages, 29.99 USD, Cloth, 14.99 USD, E-book.

Zoology

Bears of the North: A Year Inside Their Worlds. By Wayne Lynch. 2021. Johns Hopkins University Press. 352 pages and 167 colour photographs, 34.95 USD, Cloth or E-book.

***Bears: The Mighty Grizzlies of the West**. By Julie Argyle. 2021. Gibbs Smith. 224 pages, 50.00 USD, Cloth.

Fathoms: The World in the Whale. By Rebecca Giggs. 2021. Simon & Schuster. 352 pages, 27.00 USD, Cloth, 17.00 USD, Paper, 12.99 USD, E-book.

†Evolution and Phylogeny of Pancrustacea: A Story of Scientific Method. By Frederick R. Schram and Stefan Koenemann. 2021. Oxford University Press. 840 pages, 150.00 CAD, Cloth. Also available as an E-book.

The Handbook of Acoustic Bat Detection. By Volker Runkel, Guido Gerding, and Ulrich Marckmann. 2021. Pelagic Publishing. 216 pages, 69.39 CAD, Paper.

Orca: Shared Waters, Shared Home. By Lynda V. Mapes. 2021. Royal BC Museum. 192 pages, 49.95 CAD, Cloth.

Sharks of the World: A Complete Guide. Wild Nature Press Series. By David A. Ebert and Sarah Fowler. Illustrated by Marc Dando. Foreword by Rima Jabada. 2021. Princeton University Press. 608 pages and 2000+ illustrations, 49.95 USD, Cloth. Also available as an E-book.

Sharks, Skates, Rays and Chimeras of British Columbia. By Gordon McFarlane and Jackie King. 2020. Royal BC Museum. 232 pages, 24.95 CAD, Paper.

***Stories of Predation: 60 Years of Watching Wildlife**. By Dick Decker. 2021. Hancock House Publishers. 240 pages and 40 photos, 24.95 CAD, Paper, Cloth.

Raccoon. By Daniel Heath Justice. 2021. Reaktion Books. 224 pages and 100 illustrations, 19.95 USD, Paper or E-book.

Takaya: Lone Wolf. By Cheryl Alexander. Foreword by Carl Safina. 2020. Rocky Mountain Books. 192 pages, 30.00 CAD, Paper.

Other

Applied Statistics with R: A Practical Guide for the Life Sciences. By Justin C. Touchon. 2021. Oxford University Press. 336 pages, 85.00 CAD, Cloth, 42.95 CAD, Paper. Also available as an E-book.

Biological Control: Global Impacts, Challenges and Future Directions of Pest Management. Edited by Peter Mason. 2021. CRC Press. 644 pages, 128.00 USD, Cloth.

Biological Systematics: Principles and Applications. Third Edition. By Andrew V.Z. Brower and Randall T. Schuh. 2021. Cornell University Press. 456 pages, 61.95 USD, Cloth, 40.99 USD, E-book.

Converging Waters: The Beauty and Challenges of the Broughton Archipelago. Photography by Daniel Hillert. Text by Gwen Curry. 2020. Rocky Mountain Books. 176 pages, 40.00 CAD, Cloth.

The New Statistics with R: An Introduction for Biologists. Second Edition. By Andrew Hector. 2021. Oxford University Press. 288 pages, 95.00 CAD, Cloth, 45.95 CAD, Paper. Also available as an E-book.

Introduction to Fire in California. Second Edition. California Natural History Guides. By David Carle. 2021. University of California Press. 248 pages and 111 colour illustrations, 85.00 USD, Cloth, 24.95 USD, Paper or E-book.

The Pyrocene: How We Created an Age of Fire, and What Happens Next. By Stephen J. Pyne. 2021. University of California Press. 192 pages, 26.95 USD, Cloth or E-book.

The Blue Wonder: Why the Sea Glows, Fish Sing, and Other Astonishing Insights From the Ocean. By Frauke Bagusche. Foreword by Jill Heinerth. Translated by Jamie McIntosh. 2021. Greystone Books. 272 pages and 24-page colour insert, 34.95 CAD, Cloth. Also available as an E-book.

A Country No More: Rediscovering the Landscapes of John James Audubon. By Krista Elrick. 2021. George F. Thompson Publishing. 256 pages and 127 illustrations, 55.00 USD, Cloth.

Crooked Cats: Beastly Encounters in the Anthropocene. By Nayanika Mathur. 2021. University of Chicago Press. 224 pages, 27.50 USD, Paper.

Fuzz: When Nature Breaks the Law. By Mary Roach. 2021. W.W. Norton. 336 pages, 26.95 USD, Cloth.

The Environmentalist's Dilemma: Promise and Peril in an Age of Climate Crisis. By Arno Kopecky. 2021. ECW Press. 24.95 CAD, 264 pages, Paper or EPUB.

The Ghost in the Garden: In Search of Darwin's Lost Garden. By Jude Piesse. 2021. Scribe Publications. 336 pages, 20.00 GBP, Cloth.

Habitats of the World: A Field Guide for Birders, Naturalists, and Ecologists. By Iain Campbell, Ken Behrens, Charley Hesse, and Phil Chaon. 2021. Princeton University Press. 568 pages, 35.00 USD, Paper. Also available as an E-book.

The Heartbeat of Trees: Embracing Our Ancient Bond With Forests and Nature. By Peter Wohlleben. Translated by Jane Billinghurst. 2021. Greystone Books. 264 pages, 32.95 CAD, Cloth. Also available as an E-book.

Holding Back the River: The Struggle Against Nature on America's Waterways. By Tyler J. Kelley. 2021. Simon & Schuster. 256 pages, 27.00 USD, Cloth, 18.00 USD, Paper, 12.99 USD, E-book.

Human, Nature: A Naturalist's Thoughts on Wildlife and Wild Places. By Ian Carter. 2021. Pelagic Publishing. 224 pages, 27.76 CAD, Cloth.

Jungle: How Tropical Forests Shaped the World - and Us. By Patrick Roberts. 2021. Viking Books. 432 pages, 25.00 GBP, Cloth or E-book.

†**Lake Hydrology: An Introduction to Lake Mass Balance**. By William LeRoy Evans III. 2021. Johns Hopkins University Press. 440 pages, 110.00 USD, Cloth. Also available as an E-book.

The Ocean's Whistleblower: The Remarkable Life and Work of Daniel Pauly. By David Grémillet. Translated By Georgia Froman. 2021. Greystone Books. 408 pages, 38.95 CAD, Cloth.

The Ogooué Delta. Edited by Jean P. Vande Weghe and Tariq Stévart. 2021. Missouri Botanical Garden Press. 328 pages and 350 colour plates, 100.00 USD, Paper.

†**Mutation, Randomness, and Evolution**. By Arlin Stoltzfus. 2021. Oxford University Press. 288 pages, 85.00 CAD, Cloth.

Nature Fast and Nature Slow. How Life Works, from Fractions of a Second to Billions of Years. By Nicholas P. Money. 2021. Reaktion Books. Distributed by University of Chicago Press. 224 pages, 22.50 USD, Cloth or EPUB.

Not On My Watch: How a Renegade Whale Biologist Took on Governments and Industry to Save Wild Salmon. By Alexandra Morton. 2021. Royal BC Museum. 384 pages, 35.00 CAD, Cloth.

†**Plastic Legacies: Pollution, Persistence, and Politics**. Edited by Trisia Farrelly, Sy Taffel, and Ian Shaw. 2021. Athabasca University Press. 332 pages, 37.99 CAD, Paper.

Presenting Science Concisely. By Bruce Kirchoff. 2021. CABI. 152 pages, 30.00 USD, Paper or E-book.

The Sound of the Sea: Seashells and the Fate of the Oceans. By Cynthia Barnett. 2021. W.W. Norton. 432 pages, 27.95 USD, Cloth.

Spirits of the Coast: Orcas in Science, Art and His-

tory. Edited by Martha Black, Lorne Hammond, and Gavin Hanke with Nikki Sanchez. 2020. Royal BC Museum. 216 pages, 29.95 CAD, Cloth.

A Year in the Woods: Twelve Small Journeys into Nature. By Torbjørn Ekelund. Translated by Becky L. Crook. 2021. Greystone Books. 256 pages, 32.95 CAD, Cloth.

A Trillion Trees: How We Can Reforest Our World. By Fred Pearce. 2021. Granta. 320 pages, 20.00 GBP, Cloth or E-book, 12.99 GBP, Paper.

The Canadian Field-Naturalist

News and Comment

Compiled by Amanda E. Martin

Upcoming Meetings and Workshops

Student Conference on Conservation Science-New York

The 12th annual Student Conference on Conservation Science-New York to be held as an online meeting 5-8 October 2021. Registration is currently open. More information is available at https://www.amnh.org/research/center-for-biodiversity-conservation/convening-and-connecting/sccs-ny.

Entomology 2021

Entomology 2021, the annual meeting of the Entomological Society of America, to be held as a hybrid event, with an in-person meeting 31 October–3 November 2021 at the Colorado Convention Center, Denver, Colorado and online content available 20 October 2021–3 January 2022. Registration is currently open. More information is available at https://www.entsoc.org/events/annual-meeting.

The Wildlife Society Annual Conference

The 28th annual conference of The Wildlife Society to be held as an online meeting 1–5 November 2021. Registration is currently open. More information is available at https://twsconference.org/.

Entomological Society of Canada and Entomological Society of Ontario's Joint Annual Meeting

The joint annual meeting of the Entomological Society of Canada and Entomological Society of Ontario to be held as an online meeting 15–18 November 2021. The theme of the conference is: 'Strength in Diversity'. Registration is currently open. More information is available at https://www.entsocont.ca/esceso-2021-jam-english.html.

ICCB 2021

The Society for Conservation Biology's 30th International Congress for Conservation Biology to be held as an online meeting, with pre-congress sessions 6–10 December 2021 and the main scientific program 13–17 December 2021. The theme of the conference is: 'The Future is Now: Sustaining Biodiversity for Today and Tomorrow'. Registration is currently open. More information is available at https://conbio.org/mini-sites/iccb-2021/.

In Memoriam: Valerius Geist (2 February 1938–6 July 2021)

University of Calgary Professor Emeritus Valerius Geist died in Port Alberni on Vancouver Island, British Columbia, at age 83 (Vancouver Island Free Daily 2021). He was a pioneer in wildlife ecology focussing on ungulates, wolves, and wildlife population ecology and behaviour. He earned his Ph.D. from the University of British Columbia. A list of selected publications and additional information can be found by searching for his name on the web.

Acknowledgements

Thanks to Carolyn Callaghan for sharing the link to Valerius' obituary.

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D.A.W. LEPITZKI
CFN Editor-in-Chief

In Memoriam: Stuart Houston (26 September 1927–22 July 2021)

Dr. Stuart Houston, a "Golden Anniversary" member of the Ottawa Field-Naturalists' Club (OFNC) since 1943 (Steger 2021), died in Saskatoon, Saskatchewan, at age 93. A medical doctor and radiologist, he was best known in the natural history world as a bird-bander extraordinaire, having banded over 150 000 birds by 2014 (Globe and Mail 2021). One of his most recent publications was *Birds of Saskatchewan* (2019, Nature Saskatchewan), co-edited by Alan R. Smith and J. Frank Roy (Cottam 2019; see Lein 2019 for a full review of the book). More details of his remarkable life are planned for an upcoming issue of *Trail & Landscape*, the regional publication of the OFNC.

Acknowledgements

Thanks to Brenda Lepitzki for sharing the link to Stuart's obituary.

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Globe and Mail. 2021. C. Stuart Houston 1927–2021. 31 July 2021. Accessed 13 September 2021. https://www.legacy.com/obituaries/theglobeandmail/obituary.aspx?pid=199640560.

Lein, M.R. 2019. [Book Review] Birds of Saskatchewan. Canadian Field-Naturalist 133: 277–278. https://doi.org/10.22621/cfn.v133i3.2455

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D.A.W. LEPITZKI
CFN Editor-in-Chief

The Canadian Field-Naturalist

Editors’ Report for Volume 134 (2020)

Mailing dates for the four issues in volume 134 were: 12 August 2020, 16 October 2020, 21 January 2021, and 5 May 2021; online posting dates were 16 July, 21 September, 28 December, and 2 April, respectively. In contrast, the mailing and online posting dates of the four issues in volume 133 ranged from 15 October 2019 through 19 June 2020 and 21 September 2019 through 9 May 2020. Summaries of the distribution of paid subscribers to *The Canadian Field-Naturalist* for 2020 are shown in Table 1, and are compared to volume 133. This list does not include free copies distributed to Honorary Ottawa Field-Naturalists’ Club (OFNC) members or online access, which is included in OFNC membership dues and provided to *Associate Editors*. Institutional subscribers potentially represent many thousands of users. The total number of paid subscribers increased by two.

The number of articles published in volume 134 decreased by nine relative to the number published in volume 133 while the number of notes increased by five, resulting in four fewer manuscripts published in 2020 (*n* = 41; Table 2). Mammals followed by birds were the most popular subjects although there were more manuscripts published on insects and non-insect invertebrates combined than birds (Table 2). Fewer book reviews (*n* = 12) and new titles (42) were published in volume 134 in comparison to volume 133 (Table 3); a new “Books in Brief” type of book review was initiated in volume 134. The total number of pages published increased by seven for volume 134 over volume 133 (Table 4) with fewer pages of articles (*n* = 42) and book reviews and new titles (14) but more pages of notes (24) being published. The largest difference was between the number of pages dedicated to tributes (47 pages in 2020 with tributes to Francis Cook [issue 1], R. Yorke Edwards [3], and Paul-Michael Edwards [4] versus six pages in 2019 with the single tribute to Rudolph (Rudy) Frank Stocek [3]; Table 4); we believe it continues to be important to recognize those who have contributed to the study and communication of Canada’s natural history

Table 2. Number of research articles and notes published in *The Canadian Field-Naturalist*, volume 134 (volume 133), by major field of study.

Subject	Articles	Notes	Total
Mammals	6 (9)	9 (5)	15 (14)
Birds	6 (7)	1 (2)	7 (9)
Amphibians and reptiles	1 (3)	3 (2)	4 (5)
Fishes	2 (3)	0 (0)	2 (3)
Plants	2 (4)	1 (1)	3 (5)
Insects	2 (0)	3 (1)	5 (1)
Non-insect invertebrates	3 (4)	2 (3)	5 (7)
Other	0 (1)	0 (0)	0 (1)
Total	22 (31)	19 (14)	41 (45)

Table 3. Number of reviews and new titles published in the Book Review section of *The Canadian Field-Naturalist*, volume 134 (volume 133), by topic.

	Reviews	New Titles
Zoology	13 (20)	110 (138)
Botany	2 (5)	31 (24)
Miscellaneous	10 (12)	132 (153)
Total	25* (37)	273 (315)

*Not including six “Books in Brief”.

Table 1. The 2020 (2019) circulation of *The Canadian Field-Naturalist*. Compiled by Eleanor Zurbrigg from the subscription list for 134(4). This list does not include copies distributed to Honorary Members or online access which is included in OFNC membership dues.

Subscriber Type	Canada	USA	Other	Total
OFNC Members	47 (39)	2 (2)	0 (0)	49 (41)
Subscriptions:				
Individual	31 (29)	12 (9)	0 (0)	43 (38)
Institutional	61 (66)	82 (88)	11 (11)	154 (165)
Total	139 (134)	96 (99)	11 (11)	246 (244)

TABLE 4. Number of pages per section published in *The Canadian Field-Naturalist*, volume 134 (133), by issue.

	Issue				
	1	2	3	4	Total
Editorials/Editors' Report	0 (0)	4 (0)	0 (3)	0 (0)	4 (3)
Articles	55 (54)	44 (47)	37 (71)	63 (69)	199 (241)
Notes	15 (11)	28 (24)	28 (10)	9 (11)	80 (56)
Thematic Collections	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Tributes	14 (0)	0 (0)	25 (6)	8 (0)	47 (6)
Book Reviews and New Titles	16 (18)	11 (15)	11 (18)	16 (17)	54 (68)
News and Comment*	2 (4)	1 (2)	1 (4)	3 (1)	7 (11)
Reports†	13 (12)	0 (0)	0 (0)	0 (0)	13 (12)
Erratum	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Blank page‡	1 (1)	0 (0)	0 (0)	0 (0)	1 (1)
Index	— (—)	— (—)	— (—)	9 (9)	9 (9)
Total	116 (100)	88 (88)	102 (112)	108 (107)	414 (407)

*Includes the James Fletcher Award for best paper published in the volume.
†Includes Annual Business Meeting Minutes, Annual Committee Reports, and OFNC Awards; Financial Statements are only available online beginning with 132.
‡Necessary to begin each issue with an odd numbered page.

but regret that such recognition often comes after their death. Once again, there were no thematic collections (editor-selected compilations of previously published contributions in both *The Canadian Field-Naturalist* and the regional OFNC publication, *Trail & Landscape*, on a central theme with internet links to each article) nor additional articles on Great Canadian Field-Naturalists, the latter of which were included in News and Comment in volume 131.

Sixteen more manuscripts or enquires about potential submissions were received in 2020 ($n = 63$) than in 2019 (47). Two of the four enquiries resulted in a subsequent submission in 2021 with the other two not being suitable topics for *The Canadian Field-Naturalist*. Similarly, three submitted manuscripts were not sent for formal review because they were not suitable for publication in *The Canadian Field-Naturalist* as determined upon initial examination by the *Editor-in-Chief* and/or *Associate Editors*. Seven were not accepted for publication after a formal review by the assigned *Associate Editor* and/or reviewers. Forty-nine of 61 submissions or enquiries (80%) were accepted or are undergoing revision and review. In 2019, 2018, and 2017, 85%, 83 %, and 90%, respectively, of the submissions were accepted for publication and either published or underwent further revision and review.

Dwayne Lepitzki, *Editor-in-Chief*, initially reviewed the appropriateness of a submission and assigned an *Associate Editor* (AE) after William Halliday, *Online Journal Manager and Webmaster*, determined the completeness of the submission. Dwayne then reviewed the recommendation from the AE and reviewers and decided if and when the revised manuscript was accepted for publication. A *Copy Editor* (Sandra Garland or John Wilmshurst) was then assigned and once their work was reviewed by Dwayne and the authors, the manuscript was sent for layout and typesetting. *Assistant Editor* Amanda Martin edited content, proofread galleys (as did Dwayne), and sent and received author order and transfer of copyright forms; she also prepared the News and Comment. Robert Forsyth typeset galleys, provided corrections for page proofs, and created pdfs for online posting and printing. Barry Cottam, *Book Review Editor*, requested books for review, selected reviewers, edited submitted reviews, and prepared the new titles listings. Ken Young sent page charge invoices to authors and tracked the budget while Eleanor Zurbrigg managed subscriptions and mailed printed copies. William Halliday provided digital content to subscribers, posted tables of contents, abstracts, and pdfs on *The Canadian Field-Naturalist* website, and prepared the Index. Our *Associate Editors* managed manuscripts, provided reviews and recommendations, and guided authors through the revisions process. Dave Seburn, our *Map Editor*, reviewed and provided suggestions for all the maps. The Publication Committee, chaired by Jeff Saarela and consisting of Annie Bélair, Dan Brunton, Carolyn Callaghan, Paul Catling, Barry Cottam, William Halliday, Diane Kitching, Dwayne Lepitzki, Amanda Martin, Karen McLachlan Hamilton, Dave Seburn, Ken Young, and Eleanor Zurbrigg effectively guided the operation of the journal. We are indebted to our very dedicated team.

The following *Associate Editors* managed, assessed, and reviewed manuscripts published in volume 134: R. Brooks, University of Guelph, emeritus, Weymouth NS (2 manuscripts published + 1 not accepted for publication); C. Callaghan, Canadian Wildlife Federation, Ottawa ON (1); P.M. Catling, Agriculture and Agri-Food Canada, retired, Ottawa ON (6 + 2); F. Chapleau, University of Ottawa, Ottawa ON (2 + 1); J. Foote, Algoma University, Sault St. Marie ON (3); G. Forbes, University of New Brunswick, Fredericton NB (2 + 1); W. Halliday, Wildlife Conservation Society Canada, Whitehorse YT and University of Victoria, Victoria BC (7); T. Jung, Yukon Government, Whitehorse YT (4 + 1); D. Lepitzki, Banff AB (1); D.F. McAlpine, New Brunswick Museum, Saint John NB (5); G. Mowat, Government of British Columbia, Nelson BC (3); M. Obbard, Ontario Ministry of Natural Resources and Forestry, retired, Peterborough ON (2); J.M. Saarela, Canadian Museum of Nature, Ottawa ON (1); and J. Skevington, Agriculture and Agri-food Canada, Ottawa ON (2). D. Tozer, Birds Canada, Port Rowan ON (4 expected to be published in 2021 + 1), joined the team in July 2020 as an *Associate Editor* with expertise in birds. As an additional way of recognizing the hard and dedicated work of an *Associate Editor*, their name was added after the received and accepted dates to the manuscripts they handled beginning with 134(2).

As with many other journals, *Associate Editors* are at times having difficulty finding suitable reviewers; without dedicated *Associate Editors* and reviewers there would be no journal. As such, a heart-felt thanks and gratitude is extended to the following who reviewed manuscripts published in volume 134 (number of manuscripts reviewed >1 in parentheses) or submitted in 2020: Jesse Alston, University of Wyoming; Robert Anderson, Canadian Museum of Nature; Lynne Barre, National Oceanic and Atmospheric Administration; Shannon Barber-Meyer, US Geological Survey; Patrice Bouchard, Agriculture and Agri-Food Canada; Jeff Bowman, Ontario Ministry of Natural Resources and Forestry; Ryan Brook, University of Saskatchewan; Joseph Carney, Lakehead University; Pauline Catling, North-South Environmental Inc.; Emily Choy, McGill University; Dean Cluff, Government of Northwest Territories; Stephanie Coates, Boise State University; Hilary Cooke, Wildlife Conservation Society; Rosemary Curley, Stratford PE; Jim Devries, Ducks Unlimited Canada; Tony Diamond, University of New Brunswick; Colin Donihue, Washington University, St. Louis; Christopher Edge, Canadian Forest Service; Mae Elsinger, Agriculture and Agri-food Canada; Marian Fils, University of Life Sciences in Lublin; Graham Forbes, University of New Brunswick; Bruce Ford, University of Manitoba; William Franzin, Laughing Waters Arts & Science, Inc.; Forrest Freund, University of California, Berkeley; Katie Gale, Fisheries and Oceans Canada; Deborah Giles, University of Washington; Lynn Gillespie, Canadian Museum of Nature; Christopher Goguen, Penn State University; Claire Goodwin, University of New Brunswick (2); Patrick Gregory, University of Victoria (2); William Halliday, Wildlife Conservation Society; Doug Heard, University of Northern British Columbia; Christopher Heckscher, Delaware State University; Troy Hegel, Government of Alberta; Tom Herman, Acadia University; Jenny Heron, British Columbia Ministry of Environment and Climate Change Strategy; Geoffrey Holroyd, Environment and Climate Change Canada; Andy Horn, Dalhousie University; Jocelyn Hudon, Royal Museum of Alberta; Deborah Jenkins, Trent University; Ashley Jensen, Algoma University; Michael Jokinen, Alberta Conservation Association; Matt Keevil, Laurentian University; Sarah Kingsbury, Saint Mary's University; Andrea Kortello, Grylloblatta Ecological Consulting; Piia Kukka, Government of Yukon; Karl Larsen, Thompson Rivers University; Randy Lauff, St. Francis Xavier University; Cori Lausen, Thompson Rivers University (2); Rob MacKereth, Ontario Ministry of Natural Resources and Forestry; René Malenfant, University of New Brunswick; Jeff Marks, Montana Bird Advocacy; Carrina Maslovat, Salt Spring Island BC; Shelley Marshall; British Columbia Ministry of Forests, Lands, Natural Resource Operations & Rural Development; Andre Martel, Canadian Museum of Nature; Donald McAlpine, New Brunswick Museum (2); Jenna McCullough, University of New Mexico; Garth Mowat, British Columbia Ministry of Forests, Lands, Natural Resource Operations & Rural Development; Brian McLaren, Lakehead University; Joe Nocera, University of New Brunswick; Erica Nol, Trent University; Rafael Otfinowski, University of Winnipeg; Steve Paiero, University of Guelph; James Paterson, Ducks Unlimited Canada; Michael Peers, University of Alberta; Agnes Pelletier, British Columbia Ministry of Forests, Lands, Natural Resource Operations & Rural Development; Frances Pick, University of Ottawa; George Powell, University of Calgary; Lori Quakenbush, Alaska Department of Fish and Game; Scott Reid, Ontario Ministry of Natural Resources and Forestry (2); Anton Reznicek, University of Michigan; Carl Rothfels, University of California, Berkeley; Linda Routledge, Trent University; Daniel Ruzzante, Dalhousie University; David Seburn, Canadian Wildlife Federation; Fred Schueler, Fragile Inheritance Natural History; Brian Slough, Whitehorse YT; Mary Sollows, New Brunswick Museum (2); Cindy Staicer, Dalhousie University; Bronwyn

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DWAYNE A.W. LEPITZKI, *Editor-in-Chief*

AMANDA E. MARTIN, *Assistant Editor*

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