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COVER: A Grizzly Bear (*Ursus arctos*) family travels near the banks of the Lardeau River in inland British Columbia. The bears are searching for spawning Kokanee Salmon (*Oncorhynchus nerka*), which represent an important dietary subsidy prior to hibernation. See the article by Raymond *et al.* (337–347) that investigated the influence of changing Kokanee abundance on Grizzly Bear observations. Photo: Jim Lawrence.

The Canadian Field-Naturalist

Cases of freeze-dried freshwater turtles at the northern limit of their ranges in southern Ontario

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Abstract

Turtles in northern latitudes are at the limit of their ranges and display various strategies for surviving the winter, including moving under the ice and out of water. Anthropogenic disturbances are often at the root of local habitat changes that can cause turtles to move from underwater refugia onto land, sometimes resulting in freezing and death. Turtles may also leave the water under natural freeze–thaw cycles, with early exits potentially maladaptive and lethal. We document cases of freshwater turtles freezing out of water at all life stages. We give a brief description of the circumstances surrounding the discovery of freeze-dried carcasses and highlight some of the climatic challenges facing overwintering turtles in southern Ontario.

Key words: Brumation; winter; turtle; freeze–thaw cycle; Ontario; wetlands; anthropogenic disturbances

Introduction

Freshwater turtles in Ontario are near or at the northernmost limit of their ranges (Rhodin *et al.* 2021) and face a variety of difficult environmental conditions including shortened active season (Obbard and Brooks 1981) and a prolonged brumation, sometimes more than half their lives (Litzgus *et al.* 1999). All turtles are ectothermic and, therefore, rely on the environment to maintain body temperature. Overwintering turtles face two main threats: freezing and hypoxia, with resulting lactic acidosis (St. Clair and Gregory 1990; Ultsch 2006). Lactic acidosis is brought on by spending time under severely hypoxic conditions and switching to anaerobic metabolism. Turtles can avoid hypoxia and acidosis by selecting overwintering sites that are well oxygenated, by storing lactate in their skeletons (Jackson 2000), and by greatly reducing their metabolism.

Turtles in northern areas lay eggs in early summer, and the eggs hatch later that summer or early fall. Hatchlings of some species leave the nest to overwinter in water while others display delayed emergence, remaining in the nest cavity for their first winter and emerging the following spring. (For a comprehensive review of hatchling overwintering strategies see Costanzo *et al.* 2008.) Hatchlings are the age class most at risk from all types of mortality, with the risk of winter mortality by freezing and desiccation the greatest threat at northern latitudes (Iverson 1991).

Turtles in the northern latitudes use various overwintering strategies to avoid freezing and seek out aquatic hibernacula in water depths where the temperature will remain above 0°C. (See Ultsch 2006 for a comprehensive review of the ecology of overwintering in turtles.) Turtles that survive at these northern limits have behavioural and physiological adaptations, such as seeking near-freezing water to reduce metabolism (Edge *et al.* 2009) and, depending on the species, tolerating potentially severely hypoxic or anoxic water found under ice or in mud. Northern populations of Midland Painted Turtle (*Chrysemys picta marginata*; Reese *et al.* 2000; Jackson 2002) and Snapping Turtle (*Chelydra serpentina*; Reese *et al.* 2002) are the most tolerant of anoxia, more so than their southern conspecifics (Ultsch *et al.* 1985). Spotted Turtle (*Clemmys guttata*; Litzgus *et al.* 1999) and Blanding's Turtle (*Emydoidea blandingii*; Edge *et al.* 2009; Thiel and Wilder 2010) may also be anoxia tolerant while other turtles are less tolerant of anoxia. For example, Northern Map Turtle (*Graptemys geographica*), Eastern Spiny Softshell (*Apalone spinifera spinifera*), and Eastern Musk Turtle (*Sternotherus odoratus*; Reese *et al.* 2001, 2003; Ultsch and Cochran 1994, respectively) cannot survive more than 45 days in anoxic waters at 3°C and must choose well-oxygenated hibernacula. In Ontario, Wood Turtle (*Glyptemys insculpta*) overwinters in well oxygenated shallow rivers where the water temperature is near freezing (Greaves and Litzgus 2007).

It is difficult to estimate how many turtles die annually by winterkill, but large mortality events are not uncommon. Ultsch (2006) reported an incident in Illinois where hundreds of turtles (consisting of Blanding's, Painted, and Snapping Turtles) and thousands of fish died (presumably by suffocation) in a winter when heavy snow and a thick layer of ice covered a wetland. Christiansen and Bickham (1989) reported a winterkill event caused by natural droughts where a shallow lake froze completely, from top to bottom, killing 186 turtles of five species. Bodie and Semlitsch (2000) describe 144 turtles dying over winter in dried wetlands and Seburn *et al.* (2021) report 25 Painted Turtles dying over the course of two winters in an artificial pond with a maximum depth of 1.7 m.

Almost all Ontario turtle species have been reported to be sporadically active under the ice: Snapping Turtle (Brown and Brooks 1994), Painted Turtle (Taylor and Nol 1989), Northern Map Turtle (Graham and Graham 1992), Wood Turtle (Greaves and Litzgus 2007), Blanding's Turtle (Newton and Herman 2009), and Eastern Spiny Softshell (Galois *et al.* 2002). This activity may be related to their seeking air-breathing opportunities in times of ice melt (Meeks and Ultsch 1990), seeking well oxygenated areas of a wetland, or maintaining an optimal water depth (Greaves and Litzgus 2008). Turtles may also relocate if local conditions change. In a study of overwintering Snapping Turtles in a managed wetland in Toronto, Ontario, a sudden drop in the water level for beaver dam management in late November caused turtles that had already entered brumation to reawaken and move to deeper areas (Dupuis-Desormeaux *et al.* 2018).

During the winter, air temperature can increase to well above freezing and then drop back to below zero in the evenings. These freeze–thaw cycles are frequent in southern Ontario (Ho and Gough 2006) and, combined with local micro-habitat features (e.g., hills, large boulders) that can reflect and concentrate the sun's radiation, can cause some areas of a wetland to become temporarily ice-free. These short-term air temperature changes and sunny conditions combined with specific habitat features can create false spring-like weather that might be enough to lure turtles out of water. Snapping Turtles at a study site in Toronto selected overwintering sites that were close to wetland edges (Dupuis-Desormeaux *et al.* 2018), thus giving them early access to any edge thawing. Limitrophe overwintering locations permit short distance forays to the edge of the wetlands for opportunistic air breathing (Meeks and Ultsch 1990; Brown and Brooks 1994). Bolder turtles might even move onto land or the ice to sun themselves. Although this strategy can have some benefits, such as access to more oxygen and increased body temperature from the warmth, it also involves risks, especially if the turtle does not return to safety before the air temperature drops below freezing. Adult freshwater turtles do not tolerate freezing and will die if frozen (Ultsch 2006). The behavioural impetus to exit the water and take advantage of a warm sunny winter day can, therefore, prove maladaptive in northern latitudes and lead to severe injury or death.

As field biologists in southern Ontario, we have come across freeze-dried adult, juvenile, and hatchling turtle carcasses. The intent of this short communication is to document our observations and consider some of the perilous winter conditions experienced by turtles at the northern limits of their ranges.

Methods

The cases presented below are a combination of our personal discoveries and a sample from turtles brought to the Ontario Turtle Conservation Centre, Selwyn, Ontario, home of the Kawartha Turtle Trauma Centre (KTTC). Cases of lethargic or wandering turtles brought in during the winter are rare but not uncommon.

Results and Discussion

During 2016–2020, 17 turtles of various ages (nine adults, two juveniles, five hatchlings, and one undetermined) of three species (Midland Painted, Snapping, and Northern Map) were admitted from various parts of Ontario (including Waterloo, Lindsay, Collingwood, Plympton-Wyoming, Oshawa, and MacTier). Of 4896 admissions at the hospital, these 17 (0.3%) had severe frost injuries or were dead from freezing. Frost injuries and death by freezing was determined by S.J.C., a veterinarian, based on clinical presentation of necrotic tissue. Most of these turtles were found on the snow, on ice, or frozen on beaches or pathways near wetlands. We suspect the small number of admittances probably underestimates the number of turtles that are found frozen and dead because most people would not bother driving a dead turtle to the KTTC.

We present the cases in two broad categories: turtles frozen out of water and hatchlings freezing inside the nest cavity.

Turtles frozen out of water

Case 1—An adult male Snapping Turtle (Figure 1a) was found stuck in the ice near Peterborough,

FIGURE 1. Examples of adult turtles frozen out of water: a. male Snapping Turtle (*Chelydra serpentina*), b. female Red-eared Slider (*Trachemys scripta elegans*), c. female Northern Map Turtle (*Graptemys geographica*), and d. female Snapping Turtle. Photo a: S.J.C. Photo b: I. Drury. Photo c: M.D.D. Photo d: S.G.

Ontario. A passerby alerted the KTTC, and a volunteer went out on the ice to rescue the stranded, live turtle.

Case 2—An adult female Red-eared Slider (*Trachemys scripta elegans*; Figure 1b) was spotted by a photographer on the ice in the middle of Heart Lake in Brampton, Ontario, in January. Firefighters rescued it and sent her to KTTC with signs of necrotic tissue on her extremities. This species is not native to Ontario and is present in many urban wetlands as a result of pet releases (Seburn 2015).

Case 3—A mummified female adult Northern Map turtle (Figure 1c) was discovered desiccated on land in early July on an island in Stony Lake, Douro-Drummond municipality, Ontario, with no signs of predation. The cause of death was not evident, and it is uncertain when the death occurred. Its outstretched neck and hind leg are typical of basking.

Case 4—A freeze-dried adult female Snapping Turtle (Figure 1d) was collected at a southern Ontario wetland near London that is subject to annual winter dewatering. It is uncertain whether the death was a result of the dewatering or poor choice of overwintering site.

Case 5—An adult Spotted Turtle (Figure 2a) was collected after overwintering in a shallow wetland, where water receded quickly during the winter. Bilateral corneal opacity was observed along with necrotic tissue around the eyes, consistent with freeze damage previously observed by S.G. in both captive and wild turtles. In this case, keeping the turtle in a clean, warm enclosure allowed time for the eyes to heal and vision returned. This was a recaptured turtle of a known population with no known health issues the previous season.

Case 6—A subadult Midland Painted Turtle (Figure 2b) was found in southern Ontario in early March, apparently frozen and desiccated. The reservoir along the Thames River where this turtle was found is partly dewatered each fall, reducing the extent of appropriate overwintering habitat.

Case 7—A juvenile male Eastern Spiny Softshell Turtle (Figure 2c) was found in the floodplain of the Thames River, apparently trapped on land after a significant mid-winter flooding event. Water eventually receded leaving multiple fish and this turtle on land to freeze and desiccate.

Case 8—An adult male Eastern Spiny Softshell (Figure 2d) was found in an oxbow lake along the Thames River, likely trapped when river levels swelled and then receded during the winter after a storm event. The oxbow section became isolated from the river, and we assume oxygen levels dropped, eventually leading to a series of events that caused mortality and freezing/desiccation.

Overwintering in nest

Case 9—Snapping Turtle hatchlings typically emerge from the nest to overwinter in water and do not overwinter successfully in the nest (M.D.D. unpubl. data; S.G. pers. obs.). For example, Obbard and Brooks (1981) found only 0.8% (1/129 clutches) successfully overwintered in the nest with 60% (16/27)

FIGURE 2. a. Live adult Spotted Turtle (*Clemmys guttata*) with freeze damage in and around its eye. b. Freeze-dried subadult Midland Painted Turtle (*Chrysemys picta marginata*). c. Freeze-dried juvenile Eastern Spiny Softshell (*Apalone spinifera spinifera*). d. Freeze-dried adult male Eastern Spiny Softshell. Photos: S.G.

of the hatchlings surviving overwinter. A predator-excavated nest containing 25 freeze-dried Snapping Turtle eggs (some close to if not hatched) was discovered at Tommy Thompson Park, Toronto, Ontario, in early August (Figure 3a). The nest was discovered after a predator partly excavated it. We suspect that the substrate above the nest might have become compacted by a vehicle (there were deep tire marks over the nest), thus making emergence after hatching impossible and dooming the eggs and hatchlings to freeze and desiccate over winter in the nest. Dozens of predated turtle nests are discovered at this location annually (M.D.-D. pers. obs.), but this was the only nest found with desiccated eggs and hatchlings.

Cases 10–13—Over a 23-year period along a stretch of the Thames River in southern Ontario, four Snapping Turtle nests were discovered that showed apparent failure because of freezing. Although over 50 successful Snapping Turtle nests were monitored during the same time at the site (S.G. pers. obs.), all of which hatched in late summer and early fall, the four nests in question were discovered in May and early June, approximately a year after the eggs were laid. Two of the nests contained fully developed hatchlings outside the egg (Figure 3b) that had died inside the nest chamber. Two additional nests were found with a small number of living hatchlings, all too weak to emerge and with what appeared to be necrotic tissue on the skin and eyes consistent with freeze damage. The turtles were slowly warmed up and kept in captivity for a short period, but all died soon after discovery.

Case 14—One of dozens of Eastern Spiny Softshell nests found along a stretch of the Thames River in southern Ontario appeared to have been frozen during the winter, with dead/desiccated but fully developed hatchlings (Figure 3c) outside the egg but in the nest chamber. Eastern Spiny Softshell Turtles are not known to survive freezing in the nest chamber (Tornabene *et al.* 2018), and a late clutch of eggs may have resulted in too few days of appropriate heat for hatching and emergence before winter.

Case 15—A Midland Painted Turtle nest found in a backyard garden in London, Ontario, in early April had fully formed dead/desiccated hatchlings, outside the egg (Figure 4a) but still in the nest chamber. Although hatchling Midland Painted Turtles usually successfully overwinter within the nest chamber (Ultsch 2006), these individuals apparently succumbed to the elements.

Cases 16 and 17—Two Northern Map Turtle nests were found along the north shore of Lake Erie in southern Ontario in June with dead hatchlings outside the egg (Figure 4b), but in the nest chamber. The shallow nests were along the edge of an eroded dune, and it is likely that wind erosion reduced the thickness of the substrate layer above the nest the previous year, lessening protection from exceptionally cold temperatures. Although Northern Map Turtle hatchlings can successfully survive freezing in the nest chamber, it is likely that many still succumb to environmental conditions that cause dehydration (Baker *et al.* 2003).

Case 18—A Blanding's Turtle nest was discovered along an eroded dune on the north shore of Lake

FIGURE 3. Evidence of hatchling turtles freezing in the nest over winter: a. Snapping Turtle (*Chelydra serpentina*) hatchlings in their eggs, b. Snapping Turtle hatchlings found in nest cavity, and c. Eastern Spiny Softshell (*Apalone spinifera spinifera*). Photo a: M.D.D. Photos b and c: S.G.

FIGURE 4. Evidence of hatchling turtles freezing in the nest overwinter, including a. Midland Painted Turtle (*Chrysemys picta marginata*), b. Northern Map Turtle (*Graptemys geographica*), and c. Blanding's Turtle (*Emydoidea blandingii*). Photos: S.G.

Erie in early April. All hatchlings were out of the egg, but still in the nest chamber, and were dead/desiccated (see Figure 4c). Blanding's Turtle hatchlings that successfully overwinter on land probably do so in drier terrestrial microhabitat that limits dehydration and permits supercooling (Baker *et al.* 2003).

Conclusions

We present 18 cases of turtles in southern Ontario caught or frozen and desiccated outside water or of eggs and hatchlings frozen/desiccated while overwintering in nests. Some of these deaths could be a result of maladaptive behaviour: erroneous overwintering or nest site selection or seeking mid-winter basking opportunities. However, others could be related to anthropogenic or natural water level fluctuations with or without forced dispersal. It is not possible to relate specific cases to local weather or habitat conditions, given that we do not know exactly when the deaths occurred. The most obvious examples of maladaptive adult behaviour e.g., cases 1 and 2, may be extremely rare and their discoveries were dependent on opportunistic observations.

The population effects of the mortalities are uncertain because it is difficult to quantify the number of mortalities or percentages of nesting failures in relation to the turtle populations or number of nests laid. Winter conditions can be challenging for turtles at the northern end of their ranges, as winter freeze affects eggs, hatchlings, juveniles, and adults. As climate change modifies local freeze-thaw cycles and precipitation levels, it is important to track turtle winterkill events, especially in managed wetlands that undergo annual water level changes, particularly in the winter months when turtles are dormant. We encourage the public to continue to report all discoveries of freeze-dried turtles to KTCC.

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Estimated effects of clear-cuts and burns associated with habitat use by female Newfoundland Caribou (*Rangifer tarandus*)

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Abstract

The decline of Caribou (*Rangifer tarandus*) is mainly attributed to anthropogenic disturbance from resource development (i.e., logging, oil and gas extraction), which causes habitat loss and increased predation risk. Natural landscape disturbance, particularly from fire, can have similar effects, and cumulative effects from disturbance have been associated with lower neonate recruitment. Our objective was to evaluate the potential effects of land cover types on resource selection by females, with an emphasis on clear-cuts and fire, during the calving season (May–June) in three neighbouring herds (Middle Ridge, Gaff Topsails, and Pot Hill) on insular Newfoundland, Canada, and compare results with pre-existing information on calf recruitment. We applied a resource selection framework to analyze location data collected from global positioning system collars between 2007–2010 and estimate relative probability of use for different cover types. Recruitment was lowest in Pot Hill, where ≤10-year old clear-cuts were favoured, whereas recruitment was highest in Middle Ridge and Gaff Topsails, where females favoured burns, suggesting that burns could be more beneficial to Caribou fitness. Further investigation will be needed to more closely examine how anthropogenic versus natural disturbance affects Caribou fitness in Newfoundland and improve our understanding of important habitat for calving females.

Key words: Calving; clear-cuts; disturbance; fire; logging; Newfoundland; radio-collars; resource selection; spatial shifts; Caribou

Introduction

Birthing and rearing sites are an important aspect of reproductive ecology in ungulates because site selection can influence survival and success of neonates (Fox and Krausman 1994; Bangs *et al.* 2005; Gustine *et al.* 2006; Monteith *et al.* 2014) and recruitment may ultimately influence population dynamics in large herbivores (Gaillard *et al.* 1998). For Caribou (*Rangifer tarandus*), calving site locations are typically determined by distance from predators, food availability, hiding cover, and familiarity with the landscape (Bergerud 1996, 2000). Caribou commonly exhibit strong site fidelity to calving grounds (i.e., the geographical area used by most parturient females in a herd; Gunn and Miller 1986; Schaefer *et al.* 2000), although calving grounds may also shift spatially over time (Nagy *et al.* 2011; Gunn *et al.* 2012; Taillon *et al.* 2012). We speculate that such shifts could be a response to resource availability, predation risk, and human use.

Female Caribou on insular Newfoundland, Canada (hereafter Newfoundland) typically move from winter range to calving grounds during March and April and aggregate on calving grounds from May to June during the pre-calving, calving, and post-calving phases of their annual cycle (Bergerud 1974). In the Middle Ridge herd, females demonstrated southward shifts in their seasonal aggregations between 1987 and 1996, whereby the distribution in May–June shifted with increasing distance away from expanding clear-cuts across years (Chubbs *et al.* 1993; Schaefer and Mahoney 2005). By 2009–2010 the calving distribution appeared to be concentrated in an area that burned in 1986 (23–24 years earlier). Calf mortality in the Middle Ridge herd also increased between 1997 and 2003, which was attributed to an increase in predation by American Black Bear (*Ursus americanus;* Mahoney and Weir 2009; Lewis and Mahoney 2014). Clear-cuts are associated with increased predator density (Mahoney and Virgl 2003; Wittmer *et al.* 2007; Brodeur *et al.* 2008; Leblond *et al.* 2016) and predation risk may have increased as clear-cuts expanded, causing shifts in space-use. Logging is also associated with road construction, increased traffic and noise, and surface disturbance, similar to mining operations, and oil and hydroelectric development, to which female Caribou have demonstrated sensitivity and avoidance during calving (Cameron *et al.* 1992; Vistnes and Nellemann 2001; Mahoney and Schaefer 2002; Weir *et al.* 2007).

The decline of Caribou in Canada is attributed mainly to resource development and associated habitat loss and predation risk (COSEWIC 2014). Since 2000, the Boreal population, which occupies mature boreal forest and occurs throughout mainland Canada from the western to eastern seaboards, has been assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2014). An estimated one-third of subpopulations comprising the Boreal population are projected to decline continually as a result of anthropogenic disturbance (COSEWIC 2014). The Boreal population faces increasing predation pressure by Gray Wolf (*Canis lupus*) that use linear features associated with resource extraction (e.g., roads, seismic lines; COSEWIC 2014). Additionally, logging in particular results in habitat conversion from old forest to early seral stands that attract opportunistic predators, such as Black Bear and Coyote (*Canis latrans*; Brodeur *et al.* 2008; Boisjoly *et al.* 2010) and can increase abundance of alternate prey species such as White-tailed Deer (*Odocoileus virginianus*) and Moose (*Alces americanus*), that, in turn, increase predator abundance (Mahoney and Virgl 2003; Wittmer *et al.* 2007). Natural fire disturbance can also contribute to functional habitat loss and higher predation in the same way as logging, and as such may be considered tantamount to human disturbance (Courtois *et al.* 2007; Wittmer *et al.* 2007; Sorensen *et al.* 2008).

The Newfoundland population, which occupies coniferous forest, barrenland, shrubland, and wetland complexes on insular Newfoundland, was assessed as Not at Risk in 2002 by COSEWIC, but the population thereafter declined by approximately 60% and was reassessed as Special Concern in 2014 (COSEWIC 2014). The decline was associated with high population density, harvest, and predation (COSEWIC 2014). Current projections, unlike those for the Boreal population, do not indicate this population is in peril (Randell *et al.* 2012; Weir *et al.* 2014). Caribou on insular Newfoundland are unique from mainland Caribou populations because they do not face predation pressure from wolves, which were extirpated from the island around 1922 (Allen and Barbour 1937). Black Bear and the recently recruited Coyote that colonized the island in 1985 (Mahoney and Schaefer 2002) are major predators (Lewis and Mahoney 2014; Mahoney *et al.* 2015). Moreover, the level of landscape disturbance within Caribou ranges in mainland Canada may be seven times higher, if not more, than that of insular Newfoundland (Sorensen *et al.* 2008; McCarthy *et al.* 2011; Natural Resources Canada 2020).

Recent studies on Caribou on Newfoundland have examined landscape disturbance and calf recruitment (McCarthy *et al.* 2011), predation and neonate survival (Mahoney *et al.* 2015; Rayl *et al.* 2015), effects of vegetation and predation risk (inferred from habitat characteristics) on resource selection by calving females (Bastille-Rousseau *et al.* 2015), and the influence of landscape heterogeneity on neonate mortality risk (Rayl *et al.* 2018). McCarthy *et al.* (2011) detected a negative correlation between calf recruitment and total landscape disturbance (i.e., from anthropogenic and natural factors including clear-cuts and fire) within calving and post-calving ranges. Mahoney *et al.* (2015) reported that predation by Black Bear and Coyote was the leading cause of mortality for Caribou calves from 2003 to 2012, which coincided with the period of population decline after a period of sustained growth between 1979 and 1997. Bastille-Rousseau *et al.* (2015) concluded that calving females selected calving grounds with greater access to forage, while avoiding predation risk in varying degrees across herds. Rayl *et al.* (2018) further revealed that neonate mortality risk from bear predation increased in areas with higher proportions of conifer scrub (i.e., stunted conifer forest) and water, presumably because conifer scrub provides dense cover that enables ambush tactics, and water may limit mobility and escape routes for young calves.

To our knowledge, the effects of fire and clear-cuts associated with resource selection by female Caribou during calving on Newfoundland have not yet been specifically addressed. Given the distribution shifts displayed by calving females in the Middle Ridge herd, we wanted to analyze selection of land cover types with an emphasis on clear-cuts and burns and compare our results with pre-existing information about calf recruitment in selected herds to expand the discussion on habitat selection, landscape disturbance, and calving. Thus, we examined resource selection by females during the calving season between 2007 and 2010 in three neighbouring Caribou herds (i.e., Middle Ridge, Pot Hill, and Gaff Topsails) that used ranges where progressive logging and natural fires occurred. These herds are considered subpopulations and occupy ranges that typically overlap year-round (COSEWIC 2014), although females aggregate by herd affiliation during the calving season and use separate calving grounds. We also visualized spatial shifts in Middle Ridge by comparing mean activity centres during the calving season across years. We hypothesized that negative effects associated with clear-cuts would trigger an avoidance response in calving females and we predicted that females would therefore have a low relative probability of use associated with clear-cuts compared to other available cover types in May and June. Although some studies equate logging to fire disturbance, suggesting burns have similar negative effects on Caribou (Wittmer *et al.* 2007; Sorensen *et al.* 2008; McCarthy *et al.* 2011; Lafontaine *et al.* 2019), researchers have also reported use of burns by calving females (Bergerud 1974; Skatter *et al.* 2017), and Skatter *et al.* (2017) concluded that burns with residuals (i.e., unburned patches) are important calving habitat for the mixture of food-security and safety they may provide. As such, we further hypothesized that burned areas could be variably important for calving females, and we predicted that selection for this cover type might vary across herds. We assumed that selection of land cover types on the calving grounds adequately characterized habitat use by calving females, and considered available cover types within the larger home range traversed by females in May and June to investigate third-order habitat selection (i.e., within the seasonal home range; Johnson 1980) and draw comparisons across herds.

Study Area

The study area was between 49.4570°N and 47.6389°N, and 57.5167°W and 54.2806°W, spanning ~32 000 km^2 of land managed by the Government of Newfoundland and Labrador. This area encompassed ranges used by adult female Caribou during the calving season in the Middle Ridge, Pot Hill, and Gaff Topsails herds, from 1987 to 1996 and from 2007 to 2010. We refer to the calving season as the period 1 May–30 June, when females aggregate on calving grounds (Bergerud 1974).

The study area included the Long Range Barrens (Buchans Plateau subregion), Central Newfoundland Forest, and Maritime Barrens ecoregions characterized by a combination of rocky uplands, coniferous and deciduous forests, heaths, barrens, and bogs (Government of Newfoundland and Labrador 2020; Figure 1). The Long Range Barrens occurred within a portion of the range occupied by the Gaff Topsails herd, and Central Newfoundland Forest and Maritime Barrens occurred in all herd ranges. Elevations ranged from sea level to ~600 m. Common vegetation associated with the ecoregions included Balsam Fir (*Abies balsamea* [L.] Miller), Black Spruce (*Picea mariana* [Miller] Britton, Sterns & Poggenburgh), Tamarack (*Larix laricina* [Du Roi] Koch), birch (*Betula* spp. L.), Mountain Maple (*Acer spicatum* Lamarck), Trembling Aspen (*Populus tremuloides* Michaux), and alder (*Alnus* spp. Miller), commingled with lichen, moss, and Sheep Laurel (*Kalmia angustifolia* L.) dominated dwarf shrub plant communities. Common native mammal species included Black Bear, Canada Lynx (*Lynx canadensis*), Coyote, Red Fox (*Vulpes vulpes*), Northern River Otter (*Lontra canadensis*), Arctic Hare (*Lepus arcticus*), and Caribou. Moose, which are not native to Newfoundland, were also common and were the only other ungulate species present.

In the three ecoregions, summers (July–August) are mild and winters (December–March) are moderate to severe from the coast to inland areas, respectively (Bell 2002). In the Long Range Barrens, mean annual temperature is ~4°C, mean summer temperature is 12°C, and mean winter temperature is −4°C. Mean annual precipitation ranges from 1000 mm to 1400 mm (Bell 2002). In the Central Newfoundland Forest, mean annual temperature is ~4.5°C, mean summer temperature is 12.5°C, and mean winter temperature is −3.5°C. Mean annual precipitation ranges from 1000 mm to 1300 mm (Bell 2002). In the Maritime Barrens, mean annual temperature is ~5.5°C, mean summer temperature is 11.5°C, and mean winter temperature is −1°C. Mean annual precipitation ranges from 1200 mm to over 1600 mm (Bell 2002).

The study area also featured Routes 1 and 360, and the urban communities of Buchans and Badger, which occurred in the Gaff Topsails range. Towns close to the Pot Hill and Middle Ridge ranges included Howley, Grand Falls-Windsor, and Gander. Land-use consisted of logging, hunting, and recreation. In 2007, the Pot Hill and Gaff Topsails Caribou herds had an estimated 3066 and 2182 individuals, respectively, whereas the Middle Ridge herd had an estimated 8814 individuals in 2010, and the island wide population was estimated to be 38 241 individuals in 2008 (Randell 2019). Based on autumn herd composition surveys, average yearly calf recruitment ratios (calves:females) were ~7:100 for Pot Hill and ~19:100 for Gaff Topsails in 2005–2008 (McCarthy *et al.* 2011), and an estimated 18:100 for Middle Ridge in 2009–2010 (Ellington *et al.* 2020).

We note that between 1960 and 1966, herds occupied calving grounds that were different from each

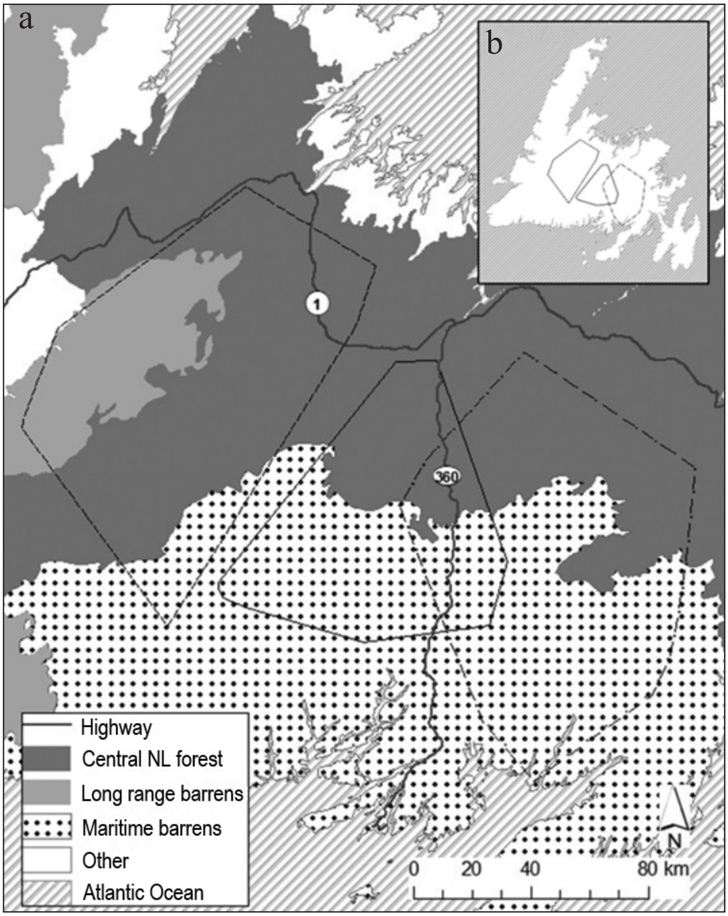

FIGURE 1. a. Delineations of the Gaff Topsails (dashed), Pot Hill (solid, black), and Middle Ridge (dash-dot) Caribou (*Rangifer tarandus*) herd ranges used from 1 May to 30 June in Newfoundland, Canada. Ranges were estimated with 100% minimum convex polygons using location data collected from adult females in 2007–2009 (Gaff Topsails and Pot Hill), and 1987–1996 and 2009–2010 (Middle Ridge). Ecoregions associated with herd ranges are also shown. b. Island of Newfoundland, Canada.

other in terms of cover characteristics (Bergerud 1974), and we therefore expected to find some variation in resource selection patterns across herds during our study. Bergerud (1974) reported that females in the Middle Ridge herd previously occupied areas with large marshes dominated by sedge (*Carex* spp. L.) during the calving season, whereas females in the Pot Hill herd occupied a bog complex with islands of closed-canopy spruce forest and females in the Buchans Plateau occupied open terrain consisting of sedge marshes and dry uplands that had burned 40 years prior.

Methods

Telemetry data

We used location data collected from adult female Caribou during the calving season in 2007–2010 to delineate calving grounds for each herd, which we identified as the area where the highest concentration of locations occurred in those years. We used additional May–June location data collected in 1987–1996 and 1993–1996, respectively, from adult females and calves in Middle Ridge to estimate earlier calving distributions. Adult female Caribou were net-gunned or darted from helicopter and collared on wintering grounds by the Newfoundland and Labrador Department of Environment and Conservation. Darted animals were chemically immobilized using a combination of Telazol (Zoetis, Parsippany-Troy Hills, New Jersey, USA) and xylazine (LGM Pharmaceuticals, Boca Raton, Florida, USA; 1.5 mg/kg Telazol + 0.75 mg/kg xylazine), etorphine hydrochloride (0.06 mg/kg), or Carfentanil (0.03 mg/kg;

Glenmark Pharmaceuticals, Mumbai, India). Calves were located by helicopter and captured at <5 days old without use of net-guns or chemical restraints. In Middle Ridge, females were fit with very high frequency (VHF) radio-collars (Lotek Engineering, Aurora, Ontario, Canada; Telonics, Mesa, Arizona, USA) monitored from 1987 to 1996. Calves were fit with expandable VHF radio-collars (Lotek Engineering; Telonics) in 1993–1996. Between 2007 and 2010, adult females from the three herds were fit with global positioning system (GPS) satellite-collars (Lotek Wireless, Newmarket, Ontario, Canada). Locations from VHF collars were obtained at altitude via fixed-wing aircraft approximately every 1–2 weeks. Location data from GPS collars were downloaded through an ultra-high frequency (Schwartz and Arthur 1999) modem or received through the Iridium satellite system (Iridium Communications, McLean, Virginia, USA). Locations from GPS-collars were recorded at varying intervals and we resampled data to achieve a standard frequency of five locations/day spaced 4–5 h apart for resource selection models.

Land cover covariates

We obtained spatial land cover data from the North American Land Change Monitoring System (NALCMS; https://www.mrlc.gov/data/north-american-land-change-monitoring-system, accessed 6 June 2020). The data were based on Landsat 7 satellite imagery with 30 m resolution collected in 2010 (Latifovic *et al.* 2017; CEC 2020). Land cover classifications were specified by NALCMS (Table 1; CEC 2020). We included four additional land cover classes: ≤ and >10-year clear-cut, 10-year burn, and 20-year burn. Twenty-year burns were the oldest burns in the available dataset while the oldest clear-cut was 37 years (see below). We differentiated between clear-cuts ≤ and >10 years old based on research in boreal forest ecosystems showing that vegetation trends in regenerating stands shift after 10 years following clear-cut logging (Archambault *et al.* 1998). Spatial clear-cut data were provided by the Newfoundland and Labrador Department of Natural Resources. We used the National Burned Area Composite from the Canadian Wildland Fire Information System (https://cwfis.cfs.nrcan.gc.ca/datamart, accessed 6 June 2020) to map historical burns retrospective to 1980.

Clear-cuts >10 years old had a median age of 24 years in Middle Ridge (range 11–37 yr), 17.5 years in Pot Hill (range 11–24 yr), and 18 years in Gaff Topsails (range 11–25 yr), whereas clear-cuts ≤10 years old in all ranges had a median age of 5.5 years (range

TABLE 1. Land cover types classified in the North American Land Change Monitoring System spatial data layer, which we used to analyze habitat use by adult female Caribou (*Rangifer tarandus*) during the calving season (1 May to 30 June) in Newfoundland, Canada, 2007–2010.

Land cover type	Description
Barrenland	Areas characterized by bare rock, gravel, sand, silt, clay, or other earthen material, and vegetation generally accounts for less than 10% of total cover
Lichen–moss barren	Areas dominated by a mixture of bare areas with lichen and moss that typically account for at least 20% of total vegetation cover
Lichen–moss grassland	Areas dominated by grassland with lichen and moss typically accounting for at least 20% of total vegetation cover
Lichen–moss shrubland	Areas dominated by dwarf shrubs with lichen and moss typically accounting for at least 20% of total vegetation cover
Mixed forest	Generally taller than 3 m and more than 20% of total vegetation cover, neither needleleaf nor broadleaf tree species occupy more than 75% of total tree cover, but are co-dominant
Subpolar broadleaf deciduous forest	Generally taller than 3 m and more than 20% of total vegetation cover, greater than 75% of tree crown cover represented by deciduous species
Subpolar grassland	Areas dominated by graminoid or herbaceous vegetation, generally accounting for greater than 80% of total vegetation cover
Subpolar needleleaf forest	Generally taller than 3 m and more than 20% of total vegetation cover, tree crown cover contains at least 75% of needle-leaved species
Subpolar shrubland	Areas dominated by woody perennial plants with persistent woody stems less than 3 m tall and typically greater than 20% of total vegetation
Urban	Areas that contain at least 30% or more of urban constructed materials for human activities (cities, towns, roads)
Water	Areas of open water, generally with less than 25% cover of non-water cover types and consistently covered by water
Wetland	Areas dominated by perennial herbaceous and woody wetland vegetation with the water table at or near surface over extensive periods of time (includes marshes, swamps, bogs)

1–10 yr). We removed used and available locations associated with clear-cuts that overlapped both age classes during the study. Burns were classified as 10 years and 20 years old (10-year and 20-year burn were ~ages whereby 10-year represented burns 8–12 years old and 20-year represented burns 18–24 years old, 24 years being the oldest burn for which there were data). We modified the NALMCS land cover layer to accommodate clear-cut and burn polygons using ArcGIS 10.5 (Esri 2016), such that clear-cut and burn classifications replaced other cover types identified by NALCMS in those areas.

Visualizing distribution shifts in Middle Ridge

To examine apparent shifts in calving distributions in Middle Ridge, we applied the kernel density tool in ArcGIS 10.5 (Esri 2016) to all May–June location data collected from VHF collars in 1987–1996 and from GPS collars in 2009–2010. We used a 98% contour to delineate the area where most use occurred for each year, based on fixed kernels with reference bandwidth (Worton 1995; Seaman and Powell 1996; Börger *et al.* 2006). We then visualized distribution shifts using locations within the 98% contours to calculate weighted centroids representing mean centres of activity for each year. (Note: we used a 98% contour to conservatively estimate calving ground boundaries, such that a single area with the highest concentration of use was defined, and outlier locations were excluded. The location data captured using a 95% versus 98% contour were essentially the same, but the 98% contour allowed for a continuous boundary around the entire area, whereas the 95% contour resulted in several smaller areas containing the same location data.)

Evaluating resource selection

We used a resource selection framework to evaluate habitat selection, whereby we compared sampling proportions of used and available units to analyze relative use (Manly *et al.* 2002). We used a logistic regression model with a *logit link* function following the *log-linear resource selection* function (RSF) for fixed-effects as defined by Manly *et al.* (2002: 100):

$$\hat{w}(x) = \exp(\hat{\beta}_1 x_1 + \hat{\beta}_2 x_2 + \cdots + \hat{\beta}_n x_n) \quad \text{(Equation 1)}$$

where $\hat{w}(x)$ is the predicted relative probability of use and $\hat{\beta}_1,\ldots,\hat{\beta}_n$ are coefficients for covariates $x_1,\ldots, x_n$. To account for individual variation and unequal sampling among individuals, we added a random intercept (γ_0) to equation 1 for each individual and included the intercept β_0 as per Gillies *et al.* (2006), whereby the individual animal is specified as the sample unit, yielding the following mixed effects model:

$$\hat{g}(x) = \exp(\hat{\beta}_0 + \hat{\beta}_1 x_{1ij} + \hat{\beta}_2 x_{2ij} + \cdots + \hat{\beta}_n x_{nij} + \gamma_{0j}) \quad \text{(Equation 2)}$$

which estimates the relative probability of use, $\hat{g}(x)$, at location i for animal j.

To obtain samples of available units, we applied 100% minimum convex polygons to all (i.e., non-resampled) May–June location data for each herd (we included VHF collar locations for Middle Ridge) and generated random points within polygons using ArcGIS 10.5 (Esri 2016). We assumed that a 100% minimum convex polygon encompassing all May–June locations from adult females within a given herd provided an accurate estimate of the area and resources available to those females during this period and represented the spatial extent of the herd home range traversed by females in May–June. For used units, we pooled all May–June GPS locations for each herd and study period and estimated calving ground boundaries using 98% fixed kernels with reference bandwidth (Silverman 1986). We assumed GPS locations outside of kernel boundaries were not representative of space-use by calving females at the herd level, and consequently identified them as potential outliers and removed those observations from the analysis.

To reduce location error, we excluded all GPS locations with 2D fix dimensions (i.e., if fewer than four satellites were used to obtain the fix) or dilution of precision >10, presumably yielding locations with low mean error (<30 m; Lewis *et al.* 2007; Ironside *et al.* 2017). We resampled locations such that individuals had five used units/day (unless data were missing because of location error or failed fixes), and we used a 1:5 ratio for used:available units to achieve large samples of available units (i.e., >10 000 locations) and ensure adequate sampling of land cover availability and convergence of coefficient estimates (Northrup *et al.* 2013). Finally, we projected used and available locations onto the land cover layer and extracted land cover types for all used and available locations using ArcGIS 10.5 (Esri 2016). We did not combine categorical levels of land cover types because we felt doing so would result in a loss of important information regarding use and could possibly bias results.

We evaluated relative use of all available cover types for each herd in separate analyses using the "lme4" package (version 1.1-23; Bates *et al.* 2020) in R version 3.6.3 (R Development Core Team 2020). We coded cover types as categorical variables (i.e., ≤ and >10-year clear-cut, 10-year burn, 20-year burn, and cover types identified in Table 1) and assigned water as the reference category because availability was similar across ranges; parameter estimates for cover types therefore represented apparent effects on relative use compared to the effect associated with water (i.e., fixed intercept). Each observation (i.e., data point) was mutually exclusive in terms of cover type. We removed cover types from the models if estimates did not converge because of too few or no used locations associated with them. Our final models estimated parameters successfully, and because the number of used observations was >800 times the number of parameters (9–12) in each model, theoretically the number of parameters we evaluated should not interfere with model performance. To examine multicollinearity among land cover covariates, we used the variance inflation factor (VIF) and interpreted VIF values <5 as indicative of low correlation between a given covariate and alternate covariates, values between 5–10 as indicative of moderate correlation, and values >10 indicative of high correlation (Wooldridge 2012; Vanhove 2019; Lüdecke 2020). We calculated VIFs using the "performance" package (Lüdecke 2020) in R (R Development Core Team 2020).

We compared relative odds of use for particular cover types compared to water to make inferences about selection strength and assessed general avoidance and selection of cover types based on proportional use versus proportional availability of samples (i.e., [number of used points associated with a particular cover type]/[total number of used points] versus [number of available points associated with a particular cover type]/[total number of available points]) for each herd. We concluded that animals were selecting a particular cover type if proportional use > proportional availability, and that animals were avoiding a particular cover type if proportional use < proportional availability (Johnson 1980). Lastly, we interpreted differences in selection of clear-cut and burn classes across herds by comparing relative odds of use if availability of a particular class was comparable across herd home ranges (i.e., <5% difference).

As a final step to verify and compare the importance of burns and clear-cuts on resource selection with respect to other cover types, we developed model sets containing other cover types with and without burn and clear-cut variables analyzed for each herd. We ranked models using AICc (Akaike 1973; Hurvich and Tsai 1989) with the "AICcmodavg" package in R (Mazerolle 2019; R Development Core Team 2020). We assessed the importance of the burn and clear-cut variables in our models for each herd by comparing their individual relative variable importance (sum of Akaike weights across all models in the set where variable *j* occurs; Burnham and Anderson 2010) to the grouped relative variable importance of the remaining covariates representing undisturbed land cover. We considered variables with values closer to one as most important (Burnham and Anderson 2010; Symonds and Moussalli 2011).

Model testing

Equation 2 assumes random effects were normally distributed with a mean of zero and unknown variance components (Breslow and Clayton 1993). We tested normality of random effects using normal quantile plots generated with the *qqnorm* function in R (R Development Core Team 2020). To evaluate goodness of fit we used the theoretical coefficient of determination (r^2) for binomial generalized linear mixed effects models as defined by Nakagawa *et al.* (2017), which we calculated using the "MuMIn" package (Barton 2020) in R (R Development Core Team 2020).

Results

Estimation of herd home ranges and calving grounds

To generate 100% minimum convex polygons for estimation of herd home range boundaries, and 98% kernels for estimation of calving ground boundaries, we used 19 080 GPS-collar locations from 24 adult females in Middle Ridge in May–June 2009 and 2010 (Tables S1 and S2) and 1145 locations from VHF collars on 52 females and 75 calves in May–June 1987 through 1996. For Pot Hill, we used 28 268 GPS-collar locations from 14 adult females in May–June 2007 through 2009 (Tables S1 and S2). For Gaff Topsails, we used 31 193 GPS-collar locations from 20 adult females in May–June 2007 through 2009 (Tables S1 and S2). Kernel density estimates captured >79% of GPS-collar locations for each herd (Figure 2).

Distribution shifts in Middle Ridge

We used 1034 locations from VHF collars on 46 females and 75 calves in May–June 1987 through 1996 (range 36–159 locations/year; median 121 locations/year) and 7416 resampled GPS-collar locations from 21 females in May–June 2009 and 2010 (4206 locations from 2009; 3210 locations from 2010) to calculate centroids for each year. Centroids indicated that yearly activity shifted southward away from clear-cuts between 1987 and 1996 (Figure 3). In May–June 2009 and 2010, females were clustered in a 20-year burn (Figure 3).

There were no documented range shifts from the other two herds. And, we do not have earlier collar data from these two herds.

Relative use, selection, and avoidance

Availability of some land cover types differed appreciably across herd ranges (Table 2, Figure S1). We analyzed resource selection by females on calving grounds based on 7416 locations from 21 females in Middle Ridge, 9274 locations from 13 females in Pot Hill, and 12 037 locations from 20 females in Gaff Topsails. Selection of land cover types varied among herds (Table S3, Figure S1), whereas individual variation was not appreciably different within each herd as indicated by low to no random intercept variance

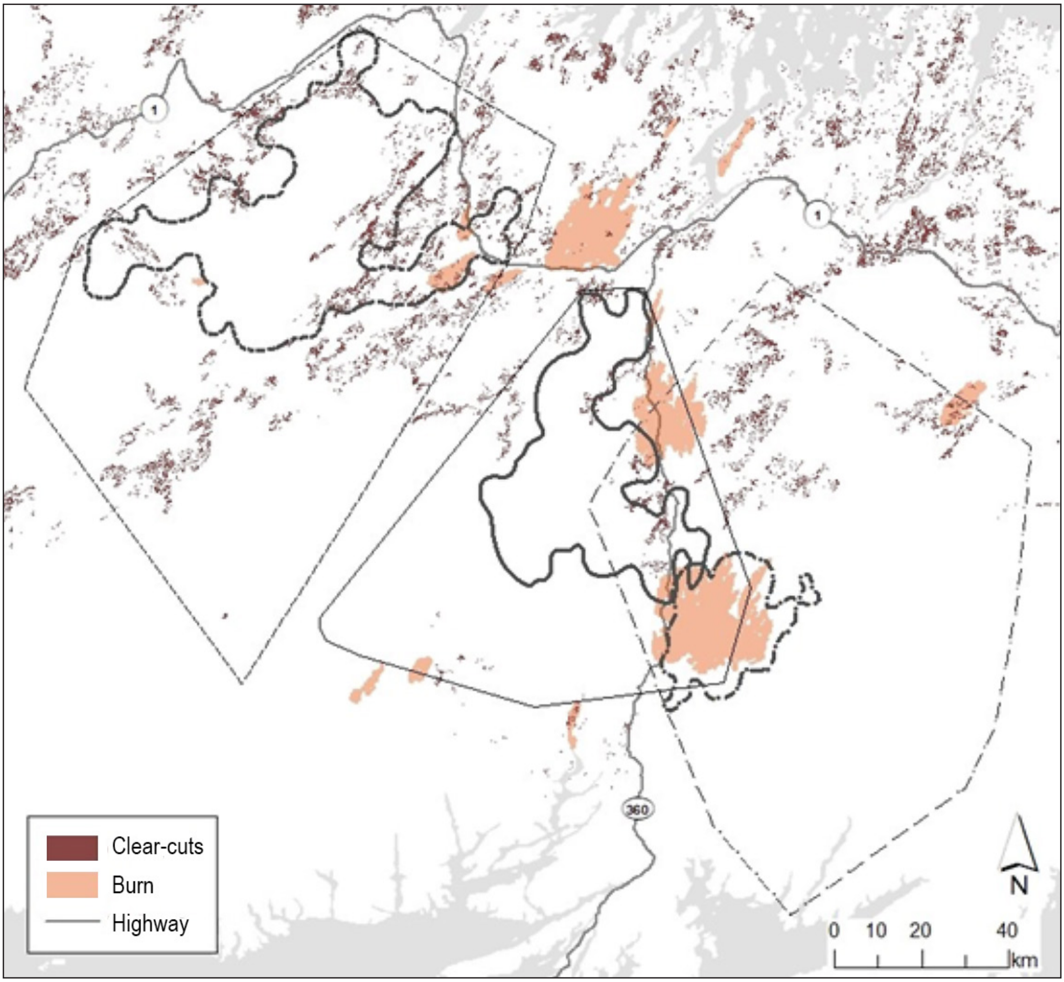

FIGURE 2. Delineations of the Gaff Topsails (dashed), Pot Hill (solid), and Middle Ridge (dash-dot) Caribou (*Rangifer tarandus*) herd ranges (black) and calving grounds (grey) based on location data collected from adult females from 1 May to 30 June in Newfoundland, Canada. Herd ranges were estimated with 100% minimum convex polygons applied to data collected in 2007–2009 (Gaff Topsails and Pot Hill), and 1987–1996 and 2009–2010 (Middle Ridge). We estimated calving ground boundaries using kernel density estimators with 98% contours to identify areas where the highest concentration of locations occurred in 2007–2009 (Gaff Topsails and Pot Hill), and in 2009–2010 (Middle Ridge).

(Middle Ridge: $\sigma^2_u = 0.016$; Pot Hill: $\sigma^2_u = 0.00$; Gaff Topsails: $\sigma^2_u = 3.25 \times 10^{-17}$). In Middle Ridge, 20-year burn was selected for and had the highest relative probability of use ($\beta = 4.83$, SE 0.09), while all other cover types were avoided (Table S3, Figures 4 and S1); clear-cuts and 10-year burn were not included in this analysis because these cover types did not occur within the calving grounds and therefore could not be evaluated. In Pot Hill, females selected for ≤10-year clear-cut, which had the highest relative probability of use ($\beta = 2.98$, SE 0.11). In Gaff Topsails, 10-year burn was more strongly selected ($\beta = 2.89$, SE 0.16) than >10-year clear-cut ($\beta = 2.53$, SE 0.12) and ≤10-year clear-cut ($\beta = 2.35$, SE 0.10).

In Middle Ridge, moderate collinearity was associated with 20-year burn. In Pot Hill there was high collinearity associated with needleleaf forest and moderate collinearity associated with subpolar shrubland. In Gaff Topsails, there was high collinearity associated with needleleaf forest and subpolar shrubland, and moderate collinearity associated with broadleaf deciduous forest and wetland.

Availability of ≤ and >10-year clear-cut was similar in all ranges. In Middle Ridge, ≤ and >10-year clear-cuts were not used at the herd level (i.e., these cover types did not occur on calving grounds

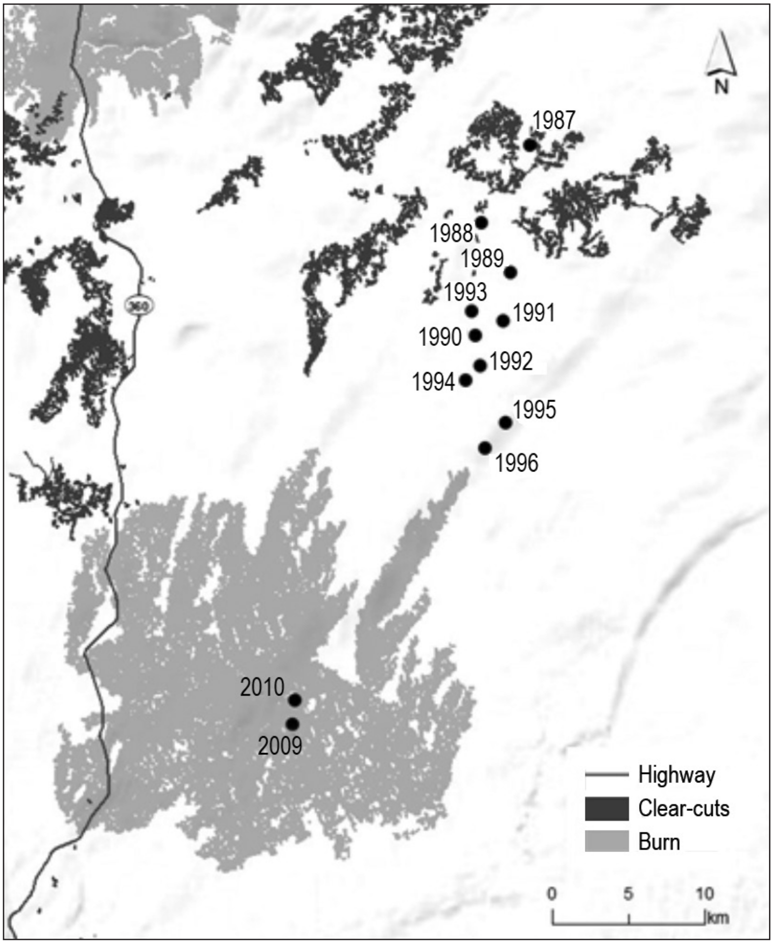

FIGURE 3. Weighted centroids representing yearly mean centres of activity based on calving distributions of adult female Caribou (*Rangifer tarandus*) in the Middle Ridge herd. Centroids were calculated from location data collected during the calving season (1 May to 30 June) in Newfoundland, Canada between 1987–1996 and 2009–2010.

and therefore could not be included in our analysis), whereas Pot Hill females selected for ≤10-year clear-cut, relative use being 19.60 (95% CI 15.96–24.29; Figures 4 and S1) times more likely based on relative odds compared to water, and appeared to avoid >10-year clear-cut as much as water (i.e., 95% CI overlapped 1; odds ratio = 0.60 , 95% CI 0.19–1.92). In Gaff Topsails, females selected for ≤ and >10-year clear-cut, with relative use 10.53 (95% CI 8.67–12.81) and 12.60 (95% CI 10.07–15.80) times more likely compared to water, respectively (Figures 4 and S1).

Availability of 10-year burn was comparable in Middle Ridge (0.2%) and Gaff Topsails (0.3%), and availability of 20-year burn was comparable in Middle Ridge (4.8%) and Pot Hill (7.5%). In Middle Ridge, 10-year burn was not used at the herd level, whereas in Gaff Topsails 10-year burn was selected for and females were 18.08 (95% CI 13.20–24.78) times more likely to use 10-year burn than water based on relative odds (Figures 4 and S1). In Middle Ridge, 20-year burn was selected for and females were 125.29 (95% CI 104.58–149.90) times more likely to use 20-year burn than water, whereas in Pot Hill, 20-year burn appeared to be avoided as much as water (odds ratio = 0.99, 95% CI 0.77–1.26; Figures 4 and S1).

In Middle Ridge, the relative variable importance for 20-year burn was 1 and equalled the grouped relative variable importance of remaining available cover types. (Table S4). In Pot Hill, the relative importance of ≤10-year clear-cut, which had the highest selection, was 1 and equalled the grouped importance of remaining available cover types barring >10-year

TABLE 2. Proportions of used and available cover types estimated from female Caribou (*Rangifer tarandus*) and random locations in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada, 2007–2010.

Land cover type	Middle Ridge		Pot Hill		Gaff Topsails	
	Used (%)	Available (%)	Used (%)	Available (%)	Used (%)	Available (%)
Barrenland	0.00	0.27	0.03	0.02	0.05	0.30
10-year burn	0.00	0.23	—	—	0.59	0.33
20-year burn	79.17	4.81	1.07	7.50	0.05	0.16
≤10-year clear-cut	0.00	1.13	2.91	1.03	3.25	3.13
>10-year clear-cut	0.00	1.00	0.03	0.37	1.62	1.30
Lichen–moss barren	0.04	0.17	0.00	0.03	0.02	0.08
Lichen–moss grassland	0.23	2.78	0.66	0.78	5.16	3.69
Lichen–moss shrubland	—	—	—	—	0.02	0.01
Mixed forest	0.69	10.12	5.26	7.61	2.99	12.69
Subpolar broadleaf deciduous forest	2.47	8.98	4.41	4.78	9.55	9.34
Subpolar grassland	0.01	0.09	0.08	0.03	0.22	0.34
Subpolar needleleaf forest	3.83	23.24	53.13	37.20	29.97	32.43
Subpolar shrubland	7.42	26.82	21.64	19.31	35.32	19.65
Urban	0.00	0.04	0.00	0.09	0.02	0.24
Water	1.74	10.29	1.94	13.32	1.01	10.57
Wetland	4.41	10.04	8.84	7.93	10.18	5.75

clear-cut and 20-year burn, which had low relative variable importance (0.36 and 0.27, respectively). In Gaff Topsails, the relative importance of ≤ and >10-year clear-cut and 10-year burn was one and equalled the grouped importance of remaining available cover types barring 20-year burn, which had slightly lower relative variable importance (0.82).

Clear-cuts and burns were mostly good predictors of use across herds, although their estimated influence on selection varied. In Middle Ridge, females appeared to select most strongly for 20-year burn compared to other cover types evaluated. In Pot Hill, females appeared to select most strongly for ≤10-year clear-cuts compared to other cover types, including burn and older age clear-cuts. In Gaff Topsails, females appeared to select more strongly for 10-year burn compared to both classes of clear-cuts and 20-year burn.

Residual normality and model fit

Quantile plots indicated that the assumption of normality for the random intercept had been met in the Middle Ridge and Gaff Topsails analyses. The individual intercepts in the Pot Hill model were all equal such that the residuals were zero. The Middle Ridge model had the best fit ($r^2 = 0.48$), followed by Gaff Topsails ($r^2 = 0.20$) and Pot Hill models ($r^2 = 0.18$).

Discussion

The selection of clear-cuts and burns by females during the calving season varied across Caribou herds. In Middle Ridge, where females had shifted away from clear-cuts prior to our study, use of clear-cuts appeared nonexistent, while females appeared to select exclusively for a 20-year burn (clear-cuts and 10-year burn were not evaluated in our models because these cover types did not occur on the calving grounds although they occurred within the seasonal range). In Pot Hill, ≤10-year clear-cuts had the strongest selection compared to other cover types and >10-year clear-cuts were avoided along with 20-year burn. Females in Gaff Topsails appeared to select for both clear-cut classes and females showed even stronger selection for 10-year burn, which was not used in Middle Ridge although availability was comparable. We caution that a direct comparison of selection coefficients for all available cover types across herds can be misleading given differences in availability, which largely influence estimated effects with respect to relative use and can lead to changes in habitat use that reflect a direct or indirect functional response (Mysterud and Ims 1998; Holbrook *et al.* 2019).

Clear-cuts and burns are associated with increased predation risk because early succession growth provides quality forage that attracts omnivores, herbivorous prey species, and consequently specialist predators (Mahoney and Virgl 2003; Wittmer *et al.* 2007; Brodeur *et al.* 2008; Lafontaine *et al.* 2019). We hypothesized that negative effects associated with clear-cuts, including higher predation, would cause females to avoid them, which was not supported by

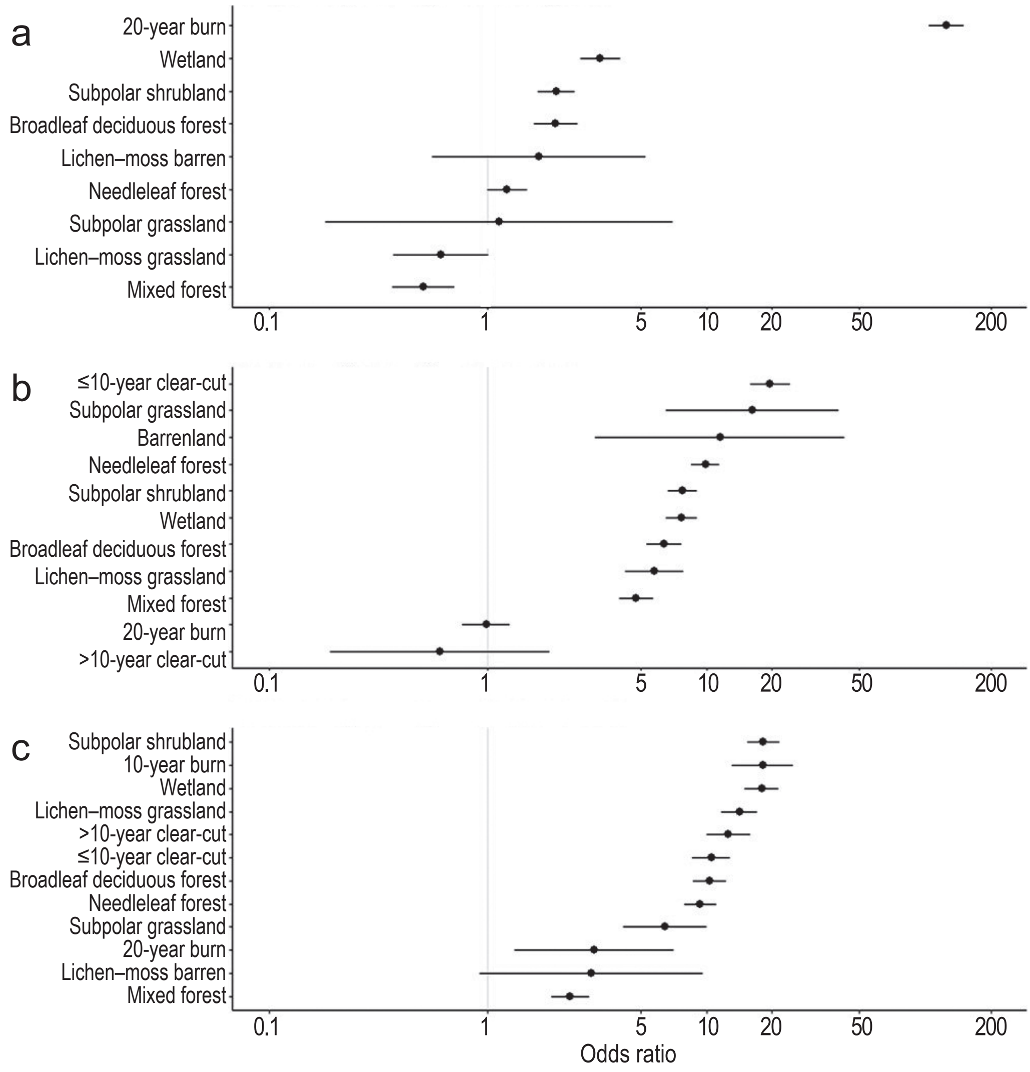

FIGURE 4. Relative odds ratios for use of cover types compared to water based on third-order resource selection by female Caribou (*Rangifer tarandus*) during the calving season (1 May to 30 June) in Newfoundland, Canada between 2007 and 2010. a. Middle Ridge herd; b. Pot Hill herd; c. Gaff Topsails herd. Relative odds of use were estimated using resource selection functions. A value of one indicates no effect (i.e., relative odds of use are equal to water).

our findings. We recognize that females may also trade off risk with foraging opportunities to meet nutritional demands (Barten *et al.* 2001; Gustine *et al.* 2006; Bastille-Rousseau *et al.* 2015), a strategy that could have contributed to differences in selection of clear-cuts and burns across herds. Our results provided support for our second hypothesis that burns could be important to calving female Caribou.

Clear-cut use by Caribou has been documented by other researchers and Caribou have demonstrated differing responses with respect to age of clear-cuts, associated predation risk, wildfire history, and availability (Courbin *et al.* 2009; Dussault *et al.* 2012; Leblond *et al.* 2016; Lafontaine *et al.* 2019). Courbin *et al.* (2009) indicated that female Caribou in the Boreal population (Côte-Nord region of Quebec, Canada) avoided recent (5 years) and later stage (5–10 years) clear-cuts in areas where wolf presence was strong and bear density was low, whereas Dussault *et al.* (2012) reported that female Caribou north of Québec City (Quebec, Canada) selected both classes during calving, with predation by bears being the main mortality factor for neonates in clear-cuts 5–20 years old, and no predation by wolves or bears detected in <5-year clear-cuts. Perhaps the absence of wolves in Newfoundland may partially explain the use of clear-cuts by female Caribou in the Pot Hill and Gaff Topsails Caribou herds, although predation by Black Bears was a major source of calf mortality during the study (Mahoney *et al.* 2015).

More recently, Lafontaine *et al.* (2019) reported that female Boreal Caribou historically exposed to frequent wildfires in regions across Quebec were more likely to avoid clear-cuts than Caribou that had less evolutionary experience with fire disturbance, likely because of their heightened awareness to predation risk in regenerating habitat. They also reported that Caribou avoided older burn areas (6–20 years old), regardless of evolutionary experience with fire, and Caribou with more historical fire exposure avoided recent burns (0–5 years old), whereas naïve Caribou displayed selection for recent burns. In contrast, Skatter *et al.* (2017) reported that burned areas were important Caribou calving habitat in northern Saskatchewan and that females preferred residual unburned patches within burns. Skatter *et al.* (2017) concluded that residuals may act as island refuges and, given that residual unburned habitat patches can account for up to one-third of the area within a fire perimeter (DeLong and Kessler 2000; Kachmar and Sanchez-Azofeifa 2006), burns may provide a variety of resources that allow for safety and food-security. We suspect that patchiness in burns may have also influenced selection for burns among females in Newfoundland. We could not measure historical fire exposure prior to 1980 or the influence of fire on selection from an evolutionary perspective, but Chubbs *et al.* (1993) reported that female Caribou in Newfoundland avoided <5-year burns and Bergerud *et al.* (1974) observed females in Newfoundland using 8-year and 40-year burns during the calving season.

Differences in response to clear-cuts and burns across herds in our study may have contributed to differences in calving success. In Pot Hill, where selection for ≤10-year clear-cuts by calving females was strongest, average yearly recruitment was lowest compared to Gaff Topsails and Middle Ridge, where 10-year and 20-year burn were strongly selected for, respectively. Bastille-Rousseau *et al.* (2015) detected differences in the level of predation risk calving females were exposed to while selecting for habitat across herds in Newfoundland. Their study did not specifically evaluate clear-cuts and burns, but they noted that females in Pot Hill differed from all other herds by favouring open-canopy coniferous forest (we presume likely included ≤10-year clear-cuts), and in so doing were exposed to higher levels of predation risk compared to other herds. Evidently, vegetation density in regenerating boreal forest increases in the first 10 years after logging, subsequently decreasing (Archambault *et al.* 1998), and higher neonate mortality risk from bear predation is associated with dense vegetation that likely enables ambush tactics (Rayl *et al.* 2018). We speculate that recruitment may have been higher in herds where females favoured regenerating burns over clear-cuts (assuming vegetation density of regrowth was somewhat similar) because residual patchiness, likely absent from logging tracts, can potentially offset predation risk (Skatter *et al.* 2017), and burns may also lack the road networks of logging operations that potentially facilitate predator access (James and Stuart-Smith 2000).

Differences in selection of clear-cuts and burns across herds in our study, and in other studies, suggest that there may be situational factors influencing use of these cover types. The Caribou population in Newfoundland underwent a period of population growth (1979–1997) followed by a period of decline (2003–2012), which has been attributed to density-dependent food competition that resulted in lower adult and calf nutrition and ultimately higher rates of neonate mortality (Mahoney *et al.* 2015). If regenerating clear-cuts and burns offer good quality foraging opportunities, perhaps female Caribou in Newfoundland were more likely to select these cover types during the phase of population decline, when our study occurred. Furthermore, differences in selection of burns and clear-cuts across herds in our study may have been influenced by relative availability of those cover types. For example, the higher proportion of 20-year burn to 10-year burn in Middle Ridge, compared to Gaff Topsails, may have led to stronger selection for 20-year burn in Middle Ridge, even though availability of each class was comparable across ranges. We also acknowledge that social cues may have influenced selection. For example, the herd home range in Pot Hill encompassed much of the 20-year burn in Middle Ridge, and females in Pot Hill may have displayed a negative response to 20-year burn partially because they were distancing themselves from conspecifics in another herd (Bergerud 1992).

The amount of variance explained by models for each herd differed, and we suspect that other habitat components we could not control for (e.g., insect harassment, predation pressure, human presence; Bergerud 1974; James and Stuart-Smith 2000; Vistnes and Nelleman 2001; Courbin *et al.* 2009; Leblond *et al.* 2016) may have contributed to the differences. Accounting for these variables might have improved model fit but would not likely change our conclusions. The low variance associated with random intercepts in our models indicated that there was little variance among individuals within herds, which is what we would expect among females in the same herd, given the social nature of the species. Additionally, we note that strong correlations between covariates generally indicate a lack of independence but, for indicator variables with more than three categories, higher multicollinearity can result from a smaller proportion of observations in the reference category compared to other categories. In such cases, collinearity increases variance estimates but does not affect mean parameter estimates and can be safely ignored (Allison 2012; Vanhove 2019).

Caribou population decline is mainly attributed to anthropogenic disturbance (COSEWIC 2014), although anthropogenic and natural landscape disturbance are both associated with habitat loss and increased predation risk (Courtois *et al.* 2007; Wittmer *et al.* 2007), and cumulative effects of disturbance have been associated with lower neonate recruitment (Sorensen *et al.* 2008; McCarthy *et al.* 2011). Our study indicated that calving female Caribou on insular Newfoundland responded differently to two disturbance features, clear-cuts and burns, whereby two herds showed strong selection for different aged burn classes, apparently favouring them over clear-cuts, and another herd favoured clear-cuts over burns. Recruitment was higher in herds that favoured burns, suggesting that this land cover type could be more beneficial to calving females in terms of food-security and safety. We recognize that other cover types can influence calving success as well, and may have also contributed to observed differences in recruitment. McCarthy *et al.* (2011), for example, detected a negative correlation between calf recruitment and total landscape disturbance (i.e., from anthropogenic and natural factors including clear-cuts and fire) within calving and post-calving ranges, but also detected a negative relationship with total area of mixed forest. We further acknowledge that our study occurred during a population decline (associated with density-dependent regulation), when recruitment rates were low in general (Weir *et al.* 2014; Mahoney *et al.* 2015). We submit that differences in recruitment across herds may be less apparent during years when the population is less constrained by density-dependent processes.

Nevertheless, the distribution shifts away from clear-cuts and into a 20-year burn in Middle Ridge suggest that females may have perceived the burn as better habitat and begs the question of whether burns are beneficial to Caribou in terms of fitness, or if both disturbance features may ultimately act as ecological traps (Hale and Swearer 2016). Current projections indicate that the island-wide Caribou population in Newfoundland, unlike the Boreal population, is not endangered (Randell *et al.* 2012; Weir *et al.* 2014), presumably because of lower total landscape disturbance within Caribou ranges on the island. But we submit that negative effects associated with landscape disturbance may still have consequences for local herds. We suspect that spatial shifts, as demonstrated by females in Middle Ridge, reflect a dynamic process in an ever-changing landscape in which animals must make choices that ultimately influence their survival. As such, we conclude that protecting areas to ensure adequate resource options for Caribou over space and time may be important for the future success of the population, but further investigation will also be needed to more closely examine how anthropogenic versus natural disturbance affects Caribou fitness. Information from such studies can guide future management policy on sustainable levels of resource development in the context of Caribou conservation in Newfoundland, and potentially improve our understanding of important habitat for calving female Caribou.

Author Contributions

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

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SUPPLEMENTARY MATERIALS:

TABLE S1. Radio-collar sample sizes and associated location data from Caribou (*Rangifer tarandus*) in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada, 1987–1996 and 2007–2010.

TABLE S2. Yearly location data from global positioning system-collars on adult female Caribou (*Rangifer tarandus*) in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada, 1987–1996 and 2007–2010, used for resource selection modelling.

TABLE S3. Parameter estimates from mixed effects resource selection models analyzing relative use of cover types by adult female Caribou (*Rangifer tarandus*) in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada, 2007–2010.

TABLE S4. Resource selection model sets evaluating relative use of land cover types by adult female Caribou (*Rangifer tarandus*) in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada between 2007–2010.

FIGURE S1. Proportions of used and available cover types estimated from actual and random locations used to analyze habitat use by adult female Caribou (*Rangifer tarandus*) in three herds (i.e., Middle Ridge, Pot Hill, Gaff Topsails) during the calving season (1 May to 30 June) in Newfoundland, Canada between 2007–2010.

TABLE S5. Resampled raw data used for resource selection analysis evaluating relative use of land cover types by adult female Caribou (*Rangifer tarandus*) in the Middle Ridge herd during the calving season (1 May to 30 June) in Newfoundland, Canada between 2009–2010.

TABLE S6. Resampled raw data used for resource selection analysis evaluating relative use of land cover types by adult female Caribou (*Rangifer tarandus*) in the Pot Hill herd during the calving season (1 May to 30 June) in Newfoundland, Canada between 2007–2009.

TABLE S7. Resampled raw data used for resource selection analysis evaluating relative use of land cover types by adult female Caribou (*Rangifer tarandus*) in the Gaff Topsails herd during the calving season (1 May to 30 June) in Newfoundland, Canada between 2007–2009.

The Canadian Field-Naturalist

Note

Malocclusion in an Arctic Wolf (*Canis lupus arctos*) from northeast Greenland

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Abstract

I document the first case of malocclusion in an Arctic Wolf (*Canis lupus arctos*) from Greenland. All canine teeth of a wolf found dead on the tundra of northeast Greenland showed evidence of heavy anterior wear resulting from occlusion with the opposite teeth. Additional heavy wear on the incisors indicated a level bite. No cases of malocclusion were found in the largest museum collection of Arctic Wolf skulls (n = 11) from Greenland. However, the collection consisted exclusively of specimens from a northeast Greenland wolf population extirpated ca. 1939; thus, it provided no information on the incidence of malocclusion in more contemporary wolves. A finding of malocclusion in the more recent wolf population could be important because the condition is genetically based and the trait is expressed more frequently with increased inbreeding. The small, geographically isolated wolf population that this wolf was a part of disappeared for reasons unknown after 2002 and genetic conditions cannot be excluded as a contributing factor. Future study of the prevalence and severity of this abnormality in Arctic Wolves from Greenland will be problematic because of the difficulty of acquiring comparative material, but could be conducted on other populations of Arctic Wolves.

Key words: *Canis lupus arctos*; Arctic Wolf; malocclusion; Greenland; Canada; Ellesmere Island

Malocclusion occurs when opposing teeth contact each other in an abnormal way as the jaw is closed. The condition has been documented to various degrees in wolves and other canids. In Scandinavia, 13.7% of 131 Gray Wolf (*Canis lupus*) specimens in the Swedish Museum of Natural History with sufficient material to assess dental anomalies exhibited malocclusion, likely as a result of inbreeding or genetic deterioration (Räikkönen *et al.* 2013). In the Netherlands, a 16.7% incidence of malocclusion in Red Fox (*Vulpes vulpes*) was related to a founder effect (Bouwmeester *et al.* 1989). In other geographic areas, factors associated with the condition have been less certain. Wolves from the former Soviet Union exhibited malocclusion at a rate of at least 3%, but affected individuals did not originate from isolated segments of the population (Vilà *et al.* 1993). In Portugal, where inbreeding was considered low, 4.6% of wolves showed malocclusion (Pires *et al.* 2020). In the Middle East, 15% of wolves exhibited the condition, but the authors did not associate their finding with any factor (Janssens *et al.* 2016). In Alaskan wolves, 17.9% exhibited malocclusion, but less severely than in the sample from Sweden; again, no associated factors were identified (Döring *et al.* 2018).

Little is known about malocclusion in Arctic Wolf (*Canis lupus arctos*), a subspecies that inhabits parts of the Canadian Arctic Archipelago and north Greenland. Range-wide in Canada, Arctic Wolf has long been the least studied subspecies of Gray Wolf (Hayes and Gunson 1995) because of the inaccessibility of its habitat. Only a single case of malocclusion involving a wild Arctic Wolf has been reported: a skull collected in 1986 on Ellesmere Island, Nunavut, showed malocclusion so extreme that it may have caused the animal to starve to death (Clutton-Brock *et al.* 1994). A study on captive-bred Arctic Wolf suggested that malocclusion may be genetically based and that the trait is expressed more frequently with increasing levels of inbreeding (Federoff 1996).

Malocclusion has not been documented in Arctic Wolf in Greenland, where this subspecies has an interesting history. Arctic Wolf was present in northeast Greenland when Europeans arrived in 1899, but commercial hunters exterminated the population by

1939 (Marquard-Petersen 2012). In 1979, wolves from north Greenland re-colonized their former range (Marquard-Petersen 2011). During the following decades, the new population grew but remained small and likely never exceeded about 23 individuals distributed in three packs (Marquard-Petersen 2009). Because of its small size, the population was at continual risk from stochastic variation and other detrimental factors; it eventually declined in the late 1990s and disappeared after 2002 (Marquard-Petersen 2021). The cause of the disappearance has not been investigated. Arctic Wolf can still be found in north Greenland, but that population is also small and likely does not exceed 30–40 individuals during favourable years (Marquard-Petersen 2022). This note reports the first case of malocclusion in the Greenland Arctic Wolf population, thereby adding to the scarce information on this condition in the wolves that inhabit the northern-most parts of the world.

In August 1995, the carcass of an Arctic Wolf was found on the tundra of northeast Greenland in Ole Rømer Land near the lake Krumme Langsø (74.079°N, 23.873°W). Only the skull was collected and then deposited in the Natural History Museum of Denmark (catalogue number M10575); additional details on its genomics have been published (Sinding *et al.* 2018). I also examined all wolf skulls ($n = 11$) from Greenland in the Zoological Museum in Copenhagen, the principal repository of Greenland wolf hides and skeletal material since 1869, to see if any showed malocclusion similar to that of the Krumme Langsø wolf.

The Krumme Langsø skull represented a young wolf of undetermined sex and age. The cranium had not been cleaned, and remaining tissue was desiccated and hardened, giving the skull a mummified appearance (Figure 1a), probably as a result of freeze-drying in the polar, semi-desert environment. That

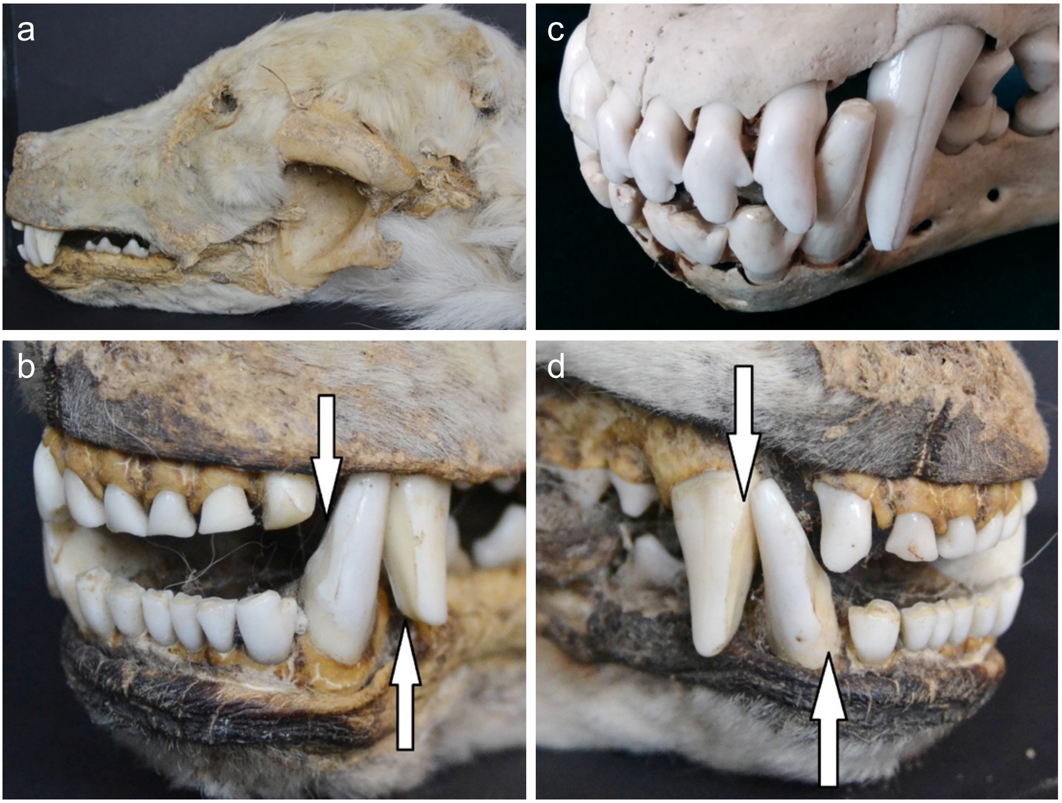

FIGURE 1. a. Lateral view of an Arctic Wolf (*Canis lupus arctos*) skull from northeast Greenland with malocclusion. b. Close-up view of the left anterior side showing broken third maxillary incisor, broken maxillary canine, and heavy occlusal wear on both canines (arrows). Notice also that the maxillary incisors show evidence of premature wear from excessive attrition indicative of a level bite. c. Normal bite in a Gray Wolf (*Canis lupus occidentalis*) legally harvested in interior Alaska. Notice the absence of wear on the incisors compared with the condition of the teeth of the Arctic Wolf from Greenland. d. Close-up view of the right anterior side of the Arctic Wolf skull, showing occlusal wear on both canines (arrows). Photos: U. Marquard-Petersen.

condition made a closer inspection of several relevant features unrealistic, including the extent of closure of the canine apical foramen and possible misalignment of the maxillary third premolars (see Clutton-Brock *et al.* 1994; Federoff 1996). Premolars that were readily observable showed little normal wear, indicating young age. On the left side of the maxilla, however, tips of the third incisor and the canine were broken. The latter exhibited abnormal, heavy lateral wear, resulting from occlusion with the mandibular canine that indicated contact with the maxillary third incisor (Figure 1b; Figure 1c shows normal wolf occlusion and tooth wear). Similar abnormal wear was observed on both right canines, but those teeth and the maxillary third incisor were intact (Figure 1d). Both mandibular canines appeared to have grown into a tilted position, thereby producing the abnormal wear on the maxillary canines. Additional heavy wear on the incisors was suggestive of a specific type of dental malocclusion termed a “level bite” (see Figure 3b in Döring *et al.* 2018), where the tips of the upper and lower incisors contact each other in contrast to a normal incisor scissor bite, where the upper incisors precisely overlap the lower ones.

The Zoological Museum in Copenhagen has 11 Arctic Wolf skulls from northeast Greenland collected during 1908–1935, thus representing the early 20th century wolf population extirpated ca. 1939. I found no evidence of malocclusion similar to that observed in the Krumme Langsø wolf, but several skulls showed tooth damage consistent with each animal’s documented history of being trapped in steel, foot-hold traps. The collection did not contain specimens from the late 20th century population and little insight could be gained into the incidence of malocclusion in that population.

This is the first case of malocclusion in the Greenland Arctic Wolf population. Based on the amount of tissue left on the skull and its general condition, showing limited evidence of scavenging, it is likely that the carcass had been on the tundra for weeks or a few months and that the wolf probably died the year it was found. The degree of malocclusion was much less severe than that of the skull from Ellesmere Island reported in Clutton-Brock *et al.* (1994), but the mummified condition of the Greenland skull did not permit a complete study, and interpreting overall differences between the two skulls was difficult.

A level bite has also been reported in other wolf populations and was the most commonly reported form of malocclusion in Alaskan wolves (Janssens *et al.* 2016; Döring *et al.* 2018). The condition causes premature attrition of the incisors from tooth-to-tooth contact and might have made it more difficult for the Krumme Langsø wolf to grasp and hold prey. Wolves commonly break at least one tooth during their lifetime, with higher rates of breakage in populations that rely more heavily on scavenging, when large ungulate prey is scarce (Van Valkenburgh *et al.* 2019). Canines are the most frequently broken teeth in large predatory mammals (Van Valkenburgh 1988). The overall effect of the minor malocclusion might have been a decrease in fitness.

It is particularly relevant that founder effect and inbreeding have been implicated in malocclusion in canids, because the wolf population in northeast Greenland was likely founded by three or four wolves and was geographically isolated (Marquard-Petersen 2011). The much larger Scandinavian wolf population, consisting of hundreds of wolves, was also founded by a few individuals; it has become highly inbred and has shown an increase in the incidence of congenital vertebral and dental anomalies (Räikkönen *et al.* 2013). Therefore, the potential involvement of inbreeding and founder effect in the malocclusion in northeast Greenland wolves, and in the disappearance of the late 20th century population, warrants future consideration.

Another potentially important factor in producing the observed malocclusion, where both incisors and canines were affected, could involve nutritional deficiency in a severe habitat. Food stress resulting in undernutrition during early life could have resulted in a rostrum that did not reach full length, thereby producing the heavy, abnormal wear observed on the lower canines from contact with the maxillary third incisors. Evidence to support nutritional deficiency as a cause is largely from laboratory studies (e.g., Tonge and McCance 1973; Pucciarelli *et al.* 1990; Miller and German 1999), but should be considered because wolf range in Greenland may constitute the most impoverished wolf habitat in North America (Marquard-Petersen 2009).

There was little comparative material other than the skull from Ellesmere Island, and that constraint is not likely to change in the near future. In northeast Greenland, finding the carcass of a wolf with a skull suitable for examination is an exceptionally rare occurrence because of the extremely low wolf density. Skulls of wolves killed nowadays in Greenland have traditionally been destroyed after testing for rabies as part of a surveillance program. Additional insight into the prevalence and severity of dental anomalies in this subspecies is, therefore, likely to come from the Canadian part of Arctic Wolf’s range.

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Observations of Grizzly Bear (*Ursus arctos*) associated with abundance of spawning Kokanee (*Oncorhynchus nerka*) at an inland river, British Columbia, Canada

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Abstract

Salmon (*Oncorhynchus* spp.) are an important food source for Grizzly Bear (*Ursus arctos*), but many salmon populations are declining. While most research on Grizzly Bear–salmon interactions occurs in coastal ecosystems, declining salmon may also affect Grizzly Bears in inland ecosystems where salmon are also an important part of their diet. We document changes in the number and distribution of observations of Grizzly Bears and changing Kokanee (i.e., landlocked Sockeye Salmon, *Oncorhynchus nerka*) abundance at an inland river. We hypothesized that reduced abundance of Kokanee would limit the number of Grizzly Bear observations at the river. We compared Kokanee abundance and Grizzly Bear observations ($n = 535$) between 2012 and 2019 at the Lardeau River, British Columbia, Canada. We used a generalized linear mixed model to test if the number of bear observations changed as a function of Kokanee abundance among four river reaches during eight consecutive years of study. Kokanee abundance was a strong statistical predictor of Grizzly Bear observations ($\beta = 0.52$, $P = 0.001$, CI = 0.12–0.87), and Kokanee abundance and reach explained 73% of the variance. Our results suggest that reduced Kokanee abundance also reduces Grizzly Bear presence, likely because bears seek out other, more available food sources, away from Kokanee spawning habitat. This pattern could limit ecosystem services provided by Grizzly Bears adjacent to spawning areas and it could have implications for bear management and conservation.

Key words: Grizzly Bear; *Ursus arctos*; Kokanee; *Oncorhynchus nerka*; community science; animal behaviour; dietary plasticity; optimal foraging theory

Introduction

Pacific salmon (*Oncorhynchus* spp.) represent an important food source for some subpopulations of Grizzly Bear (*Ursus arctos*; e.g., Hilderbrand *et al.* 1999; Mowat and Heard 2006). Grizzly Bears that access salmon are larger and occur at higher densities (Hilderbrand *et al.* 2018). Dietary salmon also increases litter size (Hilderband *et al.* 1999), decreases cortisol levels (Bryan *et al.* 2013), and is important for individual and population fitness (Mowat and Heard 2006; Bryan *et al.* 2013). Unfortunately, many Pacific salmon stocks are declining (Irvine and Fukuwaka 2011), with some runs becoming extinct (Gustafson *et al.* 2007). A major contributor to salmon declines is ongoing climate change (e.g., Irvine and Fukuwaka 2011; Isaak *et al.* 2011; Ward *et al.* 2015; Schoen *et al.* 2017; Crozier *et al.* 2021) via increased water temperature (e.g., Martins *et al.* 2012; Atlas *et al.* 2021) and low water levels associated with limited rainfall (e.g., Tillotson and Quinn 2017). Low salmon density may affect the distribution of salmon within spawning areas, for example, via decreased intraspecific competition for spawning sites (Adkison *et al.* 2014; Falcy 2015). Changes in abundance or distribution of salmon in spawning areas may affect the presence and distribution of Grizzly Bears that use them as food (e.g., Quinn *et al.* 2003, 2016; Deacy *et al.* 2016, 2019).

Grizzly Bears exhibit considerable dietary plasticity (e.g., Cristecu *et al.* 2015). Diverse diets that rely on seasonally available foods require Grizzly Bears to travel among habitats (Hamer and Herrero 1987; MacHutchon and Wellwood 2003; Mowat and Heard 2006; Fortin *et al.* 2013). For example, in Banff National Park, Alberta, Canada, seasonal changes in habitat use were related to changes in the phenology

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of forage species, with more use of higher elevations and slopes with a northern aspect as the growing season progressed and snow receded (Hamer and Herrero 1987). They may also change their diet and location annually in response to changing food availability (Schwartz *et al.* 2013; Costello *et al.* 2014). Schwartz *et al.* (2013) found that autumn fat levels in Grizzly Bears did not depend on the quality of Whitebark Pine (*Pinus albicaulis* Englemann) seed production because bears accessed more meat in years when seed crops were poor. Grizzly Bears also respond to temporal changes in food availability. For example, bears follow resource waves by relocating to areas with abundant spawning salmon, even though the phenology of salmon runs changes among years (Deacy *et al.* 2016, 2019). Selectivity extends even to individual prey items, with Grizzly Bears consuming a larger proportion of each fish captured and targetting the most energy-rich fish in years with limited salmon abundance. By contrast, in years when salmon are abundant, they consume only the most energy-rich parts of the fish (e.g., eggs, brains; Gende *et al.* 2001). Dietary changes reflect optimal foraging, which predicts foraging that maximizes energetic intake by selecting foods that provide the greatest energetic reward relative to energy invested (MacArthur and Pianka 1966; Charnov and Orians 1973); this strategy has been observed in Grizzly Bears (e.g., Hamilton and Bunnell 1987; Edwards *et al.* 2011). For Grizzly Bears, the optimal food may change depending on its abundance and accessibility. For example, when salmon abundance is low, the energetic expenditure of finding and catching fish increases (e.g., Cunningham *et al.* 2013) and may exceed the energetic benefit of its consumption. The theory of ideal despotic distribution, which postulates that more competitive individuals occupy high-quality habitat with denser resources (Calsbeek and Sinervo 2002), could also affect Grizzly Bear presence in spawning areas. Dominant males would be expected to occupy river sections with abundant and accessible salmon (i.e., high-quality habitat), which could encourage more vulnerable demographics (e.g., mothers with cubs) to seek other food sources (e.g., Nevin and Gilbert 2005). Finally, bears may select mixed diets because consumption of a variety of different foods is nutritionally beneficial (Rode and Robbins 2000; Erlenbach *et al.* 2014), even if a single food item is most energetically efficient.

While most studies of Grizzly Bear and salmon interactions have occurred in coastal areas, salmon are also an important food source for interior bear populations. Belant *et al.* (2006) found that salmon comprised a large proportion of Grizzly Bear diet and was important for body condition at a site in southcentral Alaska, over 200 km from the coast. Salmon is also an important food source for interior, montane Grizzly Bears in the low Arctic (Sorum *et al.* 2019; Mangipane *et al.* 2020). In central British Columbia (BC), landlocked Sockeye Salmon (*Oncorhynchus nerka*), known as Kokanee, represent an important food source for Grizzly Bears (Mowat and Heard 2006; Herbison 2008). In the Kootenay Lake system of BC, Kokanee have spawned in the Lardeau River since the end of the last ice age (Gayton 2002). Spawning Kokanee in the Lardeau River have been counted annually since 1979 (excepting 1985; Bassett *et al.* 2018). The number of spawning Kokanee declined dramatically from ~500 000 in 2012 (Neufeld 2012) to ~6000 in 2017 (Neufeld 2017). The decline was attributed to increased abundance of piscivorous salmonid predators (Redfish Consulting Ltd. 2016; Bassett *et al.* 2018), but the impacts of the decline on Grizzly Bear presence and distribution has not been explored.

Our aim was to examine changes in the number and distribution of Grizzly Bear observations in response to changing abundance of Kokanee at an inland river. We hypothesized that reduced Kokanee abundance would decrease the attractiveness of this food source for Grizzly Bears and predicted a positive relationship between the number of Kokanee and the number of Grizzly Bear observations. Understanding density dependent changes in salmon distribution and how Grizzly Bears respond to these changes could be valuable for management, conservation, and bear-viewing operations, especially as climate change progresses and salmon populations decline.

Methods

The Lardeau Valley (50.457°N, 117.194°W) is a sparsely human-populated valley in the Selkirk Mountains of southeastern BC (Figure 1). The Lardeau River spans roughly 46 km from the outlet of Trout Lake to the confluence with the Duncan River at the north end of Kootenay Lake. Because the Lardeau River has no flow control structures or dams, its width and depth vary considerably along its length and its numerous side channels and logjams represent excellent spawning habitat (Slaney and Andusak 2003). Along with the Meadow Creek spawning channel, located 6.5 km south of reach 1, the Lardeau River is one of the primary spawning locations for Kootenay Lake Kokanee (Redfish Consulting Ltd. 2016). Riverside ecosystems are classified as the Interior-Cedar-Hemlock biogeoclimatic zone (Herbison 2008). Our study area overlaps the boundaries of both the North Purcells and Central Selkirk Grizzly Bear population units, both of which have been assigned a conservation ranking of ‘moderate’ by the

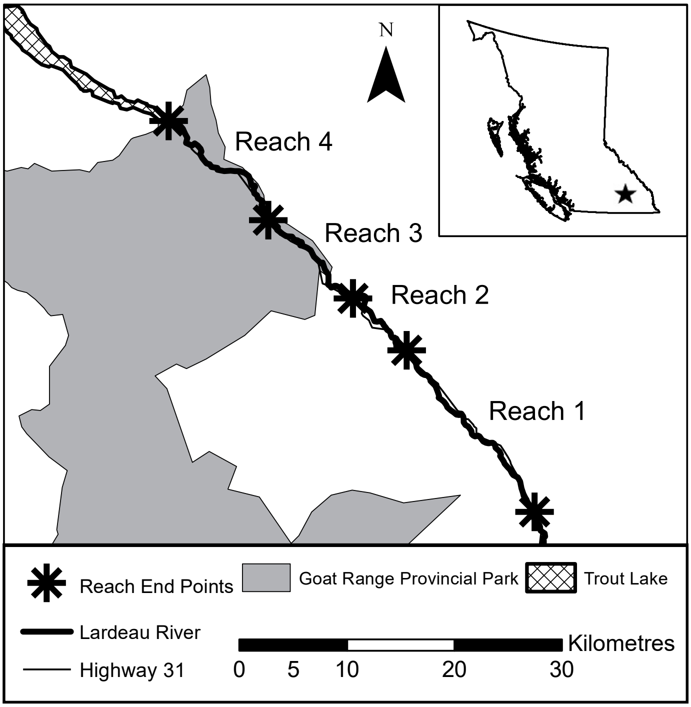

FIGURE 1. The study area in the Selkirk Mountains of southeastern British Columbia, Canada. The Lardeau River was divided into four reaches that were used for analysis. Reaches 1 and 4 are the furthest downstream and upstream reaches, respectively. The Meadow Creek spawning channel is located 6.5 km south of reach 1.

province (Environmental Reporting BC 2020). In the study area, Grizzly Bears typically consume vegetation and Yellow Glacier Lily (*Erythronium grandiflorum* Pursh) bulbs upon emerging from hibernation, followed by Mountain Huckleberry (*Vaccinium membranaceum* Douglas ex Torrey) in the subalpine during the summer, moving to valley bottoms to feed on Kokanee prior to hibernating (Mowat and Heard 2006; Herbison 2008).

Salmon abundance

We retrieved spawning Kokanee count data from the BC Ministry of Environment's Ecological Reports Catalogue (https://a100.gov.bc.ca/pub/acat/public/welcome.do). Briefly, from 2012 through 2014, Kokanee were counted once, with a single overland flight resulting in a peak count (Neufeld 2012, 2014a,b). In 2015 (Neufeld 2016a) and 2017 (Neufeld 2017), three counts occurred, and in 2016 (Neufeld 2016b), 2018 (Neufeld 2018), and 2019 (Bassett 2019) fish were counted twice. Flight dates were selected to represent peak Kokanee activity based on observations at the Meadow Creek spawning channel (Bassett *et al.* 2018). Provincial government personnel counted all fish between the Duncan River's outflow into Kootenay Lake and the headwaters of the Lardeau River at Gerrard, BC. They counted fish in six discrete reaches, four of which we used in our study (Figure 1). Reaches were unequal in length and we used ArcGIS Version 10.7 to determine the length of each reach. Counts were not meant to represent absolute abundance of Kokanee, but they provided an index of abundance that allowed comparison among years and locations (Bassett *et al.* 2018). For brevity, we use the term abundance in our study. Although the number of flights and the complement and number of surveyors varied and may have affected abundance accuracy among years, we used the maximum Kokanee abundance provided in government reports for analysis. Government reports included inflation factors meant to adjust Kokanee counts for factors that affected count accuracy (e.g., shading, water surface conditions, height/speed of aircraft, etc.). We applied this correction factor equally across counts in all reaches.

Bear observations

We compiled records of bear observations from Wild Bear Lodge, a commercial bear viewing company that operates tours along the Lardeau River when Grizzly Bears congregate along the river to consume spawning Kokanee (J.S. unpubl. data). As part of their operational program and to comply with

Provincial Park Permits, lodge employees, i.e., 'surveyors', recorded bear observations, including location, time, date, the number of bears, the platform from which the observation occurred (i.e., foot, raft, vehicle), and the bear's response to viewing. We collected records that occurred between 2012 and 2019 during the Kokanee spawning period, which we defined as 1 September to 31 October. Start dates for data collection ranged from 1 to 4 September and end dates ranged from 25 to 31 October. We excluded observations of Black Bear (*Ursus americanus*), observations that occurred >500 m from the Lardeau River's banks, and any records lacking clear location information, or when bear species was unknown. Overall, we omitted 42 observations, 35 of which occurred in 2012. We omitted between zero and three observations from all other years. We considered family groups (i.e., mother with offspring) as single observations. If surveyors lost sight of a bear and then detected a bear within half an hour and 1 km of where the first bear had been located, we considered it a single observation. Given a lodge policy to leave an area if a bear entered cover or appeared disturbed, such occurrences were rare (n = 11). Surveyors recorded bear locations based on familiar landmarks and kilometre markers along the highway. To facilitate analysis, we reclassified the location of each observation as occurring in one of the four reaches used for Kokanee abundance estimation (Figure 1). If a bear moved among reaches during a viewing, we recorded it as a single observation occurring in the reach where it was originally detected, which rarely occurred (n = 4). We used work logs to calculate daily effort spent searching for bears annually, defining a day of effort as one surveyor spending all daylight hours searching for bears, with or without commercial guests. Surveyors all received the same training and used similar search methods, which involved walking or sitting in high-quality habitat, scanning riverbanks with binoculars, and rafting down the Lardeau River, but some search time was spent in vehicles (typically in transit to a trailhead). Although search methods varied, they were approximately consistent among years and reaches. Surveyors spent time approximately equally along the river's length, however private property adjacent to reaches 1 and 2 somewhat reduced effort in these sections.

Analyses

We used Chi-square goodness-of-fit tests to compare Kokanee abundance among years (assuming equal counts annually) and to compare Kokanee distribution among reaches within years (assuming distribution was proportional to reach length). We also used Chi-square goodness-of-fit tests to compare the number of bear observations among years (with expected values based on effort) and within years but among reaches (assuming observations would be proportional to reach length).

To determine the predictive capacity of Kokanee abundance on bear observations, we used a generalized linear mixed effects model (GLMM) to test the number of bear observations in each reach during each year of the study (n = 32) in relation to annual local Kokanee abundance divided by reach length. Human presence (Gibeau *et al.* 2002; Schwartz *et al.* 2010a), spawning habitat (Adkison *et al.* 2014), and high-quality fishing locations (Luque and Stokes 1976; Gende and Quinn 2004) can affect bear presence and varied along the river's length, so we included reach as a covariate in the model. To address inter-annual variation, we included year as a random effect and included an offset term for the number of days of search effort. We used a negative binomial distribution to accommodate overdispersion in the data (Coxe *et al.* 2009). We scaled (by 1 SD) and mean-centred Kokanee abundance prior to modelling. To assess model fit and the value of including Kokanee abundance as a covariate, we used AIC weights adjusted for small sample sizes (AICc) and likelihood ratio tests. We assessed the amount of variance explained by the model using an adjusted r^2 metric suitable for GLMMs following negative binomial distributions (Nakagawa *et al.* 2017). Lastly, we confirmed the absence of collinearity among variables using variance inflation factors. We completed all statistical analyses using R Studio Version 4.2.2. We report averages as mean ± SD and use a significance level of $P = 0.05$.

Results

The mean annual abundance of Kokanee summed across the four reaches was 95 634 ± 144 239 and ranged between 399 929 in 2012 and 5210 in 2017 (Table S1). Abundance varied significantly among years (χ^2_7 = 1 522 878, P <0.001). In each year, the distribution among the four reaches differed significantly from what would be expected based on distribution proportional to reach length (χ^2_3 ranging from 4906 to 118 925, P <0.001 for all years). Over time, Kokanee abundance in reaches 1 and 2 was relatively constant (Figure 2a). With the exceptions of 2012 and 2019, when the proportion of Kokanee was similar in reaches 3 and 4, most fish were in reach 4 until 2014, after which the greatest proportion of fish was found in reach 3.

There were 535 bear observations that occurred during 487 days of search effort with sufficient information to include in our analysis (Table S2). The number of Grizzly Bear observations/day ranged

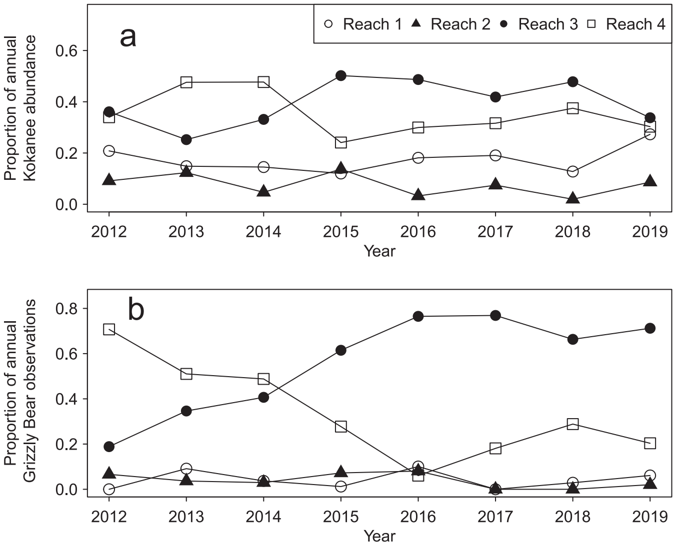

FIGURE 2. Distribution of spawning Kokanee (*Oncorhynchus nerka*) and Grizzly Bear (*Ursus arctos*) observations among four reaches of the Lardeau River, British Columbia, 2012–2019.

from 0.33 in 2017 to 3.03 in 2012. Compared to what would be expected based on survey effort, the number of observations varied significantly among years (χ^2_7 = 208, *P* <0.001), and distribution of observations among reaches differed significantly from what would be expected based on distribution proportional to reach length for each year (χ^2_3, range 40–143, *P* <0.001 for each test). The proportion of observations in reaches 1 and 2 was relatively stable over the study period, and most bear observations occurred in reach 4 until 2014, after which most observations occurred in reach 3 (Figure 2b).

The mean rate of Grizzly Bear observations (i.e., number corrected by effort) roughly paralleled annual Kokanee abundance (Figure 3). Model results indicated that local fish abundance was a significant predictor of the number of bear observations (β = 0.52, *P* = 0.001, CI = 0.12–0.87). To confirm that Kokanee abundance was an important predictor of bear observations, we conducted a likelihood ratio test between models including and excluding Kokanee abundance as a predictor; the model including Kokanee abundance fit the data significantly better (*P* = 0.02). Fixed effects (i.e., Kokanee abundance and reach) accounted for 72.7% of the variance in bear observations, while random terms (i.e., year) accounted for only 0.9 % of variance. The ΔAICc between the null model and our top model was 27.3 AICc points, and likelihood ratio testing indicated the final model had significantly better fit (*P* <0.001). Variance inflation factors confirmed the absence of collinearity among variables (VIF ≤ 1.18).

Discussion

Consistent with our predictions, Grizzly Bear observations were strongly predicted by Kokanee abundance, suggesting that bears modified their distribution based on food availability, potentially seeking other food sources when Kokanee were limited. Distribution of Kokanee within the Lardeau River appeared to change over time, which is consistent with observations of density-dependent changes in salmon distribution in spawning areas elsewhere (Adkison *et al.* 2014; Falcy 2015). The observed shift towards reaches further downstream (i.e., from reach 4 to reach 3) in years of low abundance could relate to reduced competition for spawning sites during years with few fish (Adkison *et al.* 2014; Falcy 2015), with individuals conserving energy by occupying the first suitable site they encounter (Adkison *et al.* 2014).

The frequency of Grizzly Bear observations was temporally (i.e., among years) and spatially (i.e., among reaches) predicted by Kokanee abundance. This observation is consistent with findings that suggest Grizzly Bears shift their distribution to accommodate the geographic location of food sources (Hamer and Herrero 1987; MacHutchon and Wellwood 2003; Mowat and Heard 2006; Fortin *et al.* 2013). For example, in the Greater Yellowstone Ecosystem, Grizzly Bears moved into Whitebark Pine habitat as seed crops became available (Costello *et al.* 2014), and Grizzly Bears followed resource waves of spawning salmon (Deacy *et al.* 2016, 2019). The predictive capacity of Kokanee abundance on bear observations was also consistent with the work of others who have

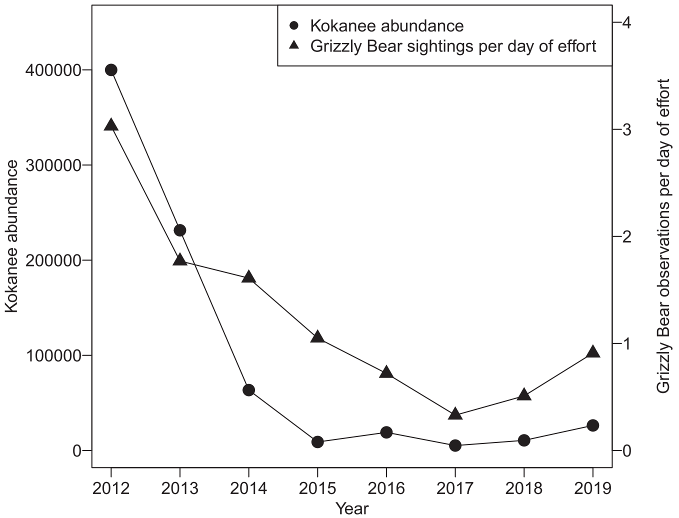

FIGURE 3. Kokanee (*Oncorhynchus nerka*) abundance and Grizzly Bear (*Ursus arctos*) observations/day of effort at the Lardeau River, British Columbia, 2012–2019.

found that salmon predation by bears increases with increasing salmon density (Quinn *et al.* 2003, 2016).

Besides reduced bear presence, an explanation for fewer observations in years of Kokanee scarcity could be that reduced Kokanee density promotes behaviour that affected bear detectability. When fish are scarce, bears may become more selective when fishing to compensate for the high energetic cost of locating fish. For example, Cunningham *et al.* (2013) found that Grizzly Bears selectively caught large fish when salmon density was low and Gende *et al.* (2001) observed selection of the most energy-rich fish when salmon were scarce. Because fishing success is higher at night (e.g., Klinka and Reimchen 2002), bears may have selectively fished at night during years of salmon scarcity, reducing detections during daytime surveys.

Lastly, when resources are sparse, individual animals may occupy and defend larger areas to meet resource requirements (Calsbeek and Sinervo 2002). If the most dominant male bears, which are largely nocturnal, occupied larger areas of the river corridor in years of Kokanee scarcity, they may have limited the presence of more vulnerable demographics, such as mothers with cubs, which are more diurnal and therefore easier to detect using our methods (Nevin and Gilbert 2005). In other systems, intraspecific competition and risk of infanticide have been proposed as reasons some Grizzly Bears fail to consume salmon despite its availability in their home ranges (Gende *et al.* 2001; Deacy *et al.* 2016), and this effect could increase in years when resources are limited, and competition therefore increases.

When Kokanee were scarce and Grizzly Bears were largely absent from the Lardeau River, individuals may have switched to other food sources, which has occurred following declines of historically available foods in other ecosystems (e.g., Schwartz *et al.* 2013; Costello *et al.* 2014; Cristecu *et al.* 2015). Although we did not attempt to test if a dietary change occurred, Wild Bear Lodge staff anecdotally observed bears using the subalpine and scats containing Mountain Huckleberry later than average in years of Kokanee scarcity (J.S. unpubl. data). At low fish densities, the energetic cost of fishing may exceed the energetic rewards (Quinn *et al.* 2003, 2016), even when bears become more selective about the individual salmon they target (Gende *et al.* 2001; Cunningham *et al.* 2013). Optimal foraging theory (MacArthur and Pianka 1966; Charnov and Orians 1973) would predict selection of other food sources. In our study area, the primary alternate food source in years of Kokanee scarcity may have been Mountain Huckleberry in the subalpine (e.g., Mowat and Heard 2006), which, given favourable weather, can persist well into the autumn (Minore and Smart 1978). Finding, handling, and consuming berries represents an energetic investment, and the energetic benefits of berry consumption decline if berry density or size is low, or if berry bushes are sparse (Welch *et al.* 1997). The attractiveness of huckleberries compared to Kokanee could therefore vary among years depending on the quality of the berry crop. Compared to Kokanee, berries are high in carbohydrates and low in protein and lipids (Rode and Robbins 2000; Erlenbach *et al.* 2014), and the latter may be especially important in the fall prior to hibernation (Erlenbach *et al.* 2014). Nutritionally, the optimal Grizzly Bear diet would be mixed (Erlenbach *et al.* 2014), which would likely mean consumption of both Kokanee and huckleberries. In our study area, the distance and elevation change between the Lardeau River where Kokanee spawn and the subalpine where huckleberries can be found in autumn is considerable, and the energetic investment of travelling between these ecosystems could influence food selection. An important next step in this system could be to better understand the role of Kokanee in the diets of bears and what foods bears use when Kokanee are limited.

Various factors limited the strength of our findings. Multi-year studies can be affected by inter-annual variation. We controlled for such variation in our models by including year as a random effect; however, inter-annual changes may have affected our results, and we did not study the sources of this variation (e.g., quality of berry crop). We failed to account for the myriad factors besides Kokanee abundance that may have affected Grizzly Bear distribution, such as land cover (e.g., Milakovic *et al.* 2012) and human presence (e.g., Gibeau *et al.* 2002; Schwartz *et al.* 2010a). These factors varied among reaches. For example, reach 4 occurred primarily within Goat Range Provincial Park, where human presence was lower. Spawning habitat (Adkison *et al.* 2014) and good fishing sites (Luque and Stokes 1976; Gende and Quinn 2004) likely varied among reaches and affected bear presence. We accounted for these factors in our modelling approach by using reach as a covariate. Additionally, we used the number of Grizzly Bear observations as a metric for bear presence, but we did not survey at night, and Grizzly Bears increase nocturnality in response to human presence (Olson 1998; Rode *et al.* 2006; Ordiz *et al.* 2011, 2014). Finally, there were several limitations associated with using community science data. Inconsistent data collection in 2012 resulted in the omission of many ($n = 35$) observations from analysis, but this omission would not have changed the direction of the effects we observed. Surveyors were different among years, and, although they received the same training, their abilities to detect bears could have differed. Upon observing a bear, surveyors typically stopped searching for additional bears, so bears in other reaches may have gone unnoticed. This effect is likely small because most bear observations lasted less than an hour. Although individual bears tolerate human viewers to different extents (e.g., Olson *et al.* 1998; Nevin and Gilbert 2005), surveyors could not reliably distinguish among individual bears, which may have affected results. For example, the presence of a habituated individual in some years but not others could have inflated viewing rate in some years. Similarly, Kokanee abundance accuracy may have varied among years given variation in the number of flights and the number and complement of surveyors.

Despite these sources of error, our data provide valuable information about the Kokanee–Grizzly Bear dynamics of a system for which there was no existing monitoring, and we made use of publicly available and community-sourced data, which increases efficiencies, democratizes science, and promotes valuable conservation and research outcomes (De Sherbinin *et al.* 2021).

Conclusions

Community science data provided considerable support that changes in Kokanee abundance and distribution was linked to changes in Grizzly Bear observations adjacent to an inland, salmon-bearing river in southeastern British Columbia. These findings are consistent with research from coastal ecosystems, but these principles had not previously been examined in a system with landlocked salmon. The dietary flexibility exhibited by Grizzly Bears may promote resilience as climate change and other factors alter seasonally available foods (e.g., Schwartz *et al.* 2013; Costello *et al.* 2014; Cristecu *et al.* 2015), and this flexibility may be especially valuable given widespread salmon declines (Gustafson *et al.* 2007; Irvine and Fukuwaka 2011). However, the amount of dietary salmon is functionally related to fitness (Mowat and Heard 2006) and, in coastal systems, bear–salmon interactions culminate in complex and beneficial ecosystem services (Levi *et al.* 2020). Declines in food sources may promote increased human–bear conflict; for example, in years of Whitebark Pine seed scarcity, Grizzly Bears in the Greater Yellowstone Ecosystem increased use of low-elevation habitat (Mattson *et al.* 1992), where risk of human-associated mortality increases (Schwartz *et al.* 2010b). It follows that declines in Kokanee abundance may limit bear fitness and provision of ecosystem services, and could increase human–bear conflict. Lastly, ecotourism businesses that centre operations around salmon-bearing streams (e.g., Rode *et al.* 2006) may encounter financial difficulties as salmon populations decline and bear distributions change, which could limit the conservation outcomes of wildlife viewing (e.g., Tisdell and Wilson 2001). We recommend future research on how salmon declines affect Grizzly Bear populations, especially as climate change progresses, as well as better understanding the role of Kokanee in the diets of Grizzly Bears.

Author Contributions

Writing – Original Draft: S.R.; Writing – Review & Editing: N.F. and S.R.; Conceptualization: J.S. and

S.R.; Investigation: S.R.; Methodology: S.R.; Formal Analysis: S.R.; Funding Acquisition: N.F. and S.R.

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SUPPLEMENTARY MATERIALS:

TABLE S1. Spawning Kokanee (*Oncorhynchus nerka*) abundance observed by British Columbia provincial government personnel in the Lardeau River, British Columbia, 2012–2019.

TABLE S2. Number of Grizzly Bear (*Ursus arctos*) observations adjacent to four river reaches, effort spent searching for bears, and observations/day of effort at the Lardeau River, British Columbia, 2012–2019.

The Canadian Field-Naturalist

Combining current and historical biodiversity surveys reveals order of magnitude greater richness in a British Columbia marine protected area

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Abstract

The value of biodiversity and of documented biodiversity surveys is well established. Extracting historical biodiversity data and synthesizing them with current data can provide a more comprehensive estimate of total diversity and guide future monitoring. We demonstrate the utility of compiling historical and recent biodiversity data to better characterize taxon richness and composition. Our focus is an otherwise unmonitored habitat in an unmonitored British Columbia provincial park, in a heavily impacted region of the Salish Sea that was designated a United Nation Biosphere Reserve in 2021. We conducted surveys and compiled historical records that together spanned three intertidal habitats and 43 years. From these combined data we report a total of 99 taxa, an order of magnitude increase over the number listed in the park's Master Plan. These include seven non-native species, of which four are newly reported here. Rarefaction, extrapolation, and multivariate dissimilarity analyses revealed the roles of methods and habitat types in contributing to differences in taxon richness and composition among surveys. This data compilation illustrates many of the challenges and opportunities in aligning and assembling independent space-time snapshots of alpha (i.e., local) diversity to better understand the gamma (i.e., regional) diversity of a marine protected area and provides the foundational data needed to design effective future monitoring at molecular to ecosystem scales.

Key words: Biodiversity monitoring; British Columbia; cobble beach; historical data; invasive species; marine protected area; Porteau Cove Provincial Park; riprap; UN Biosphere Region

Introduction

The benefits of assembling biodiversity inventories and monitoring changes in species composition are well established (e.g., Lindenmayer *et al.* 2012). Nevertheless, the amount of consistent, widely available diversity-monitoring data remains limited (Lindenmayer and Likens 2010; Hortal *et al.* 2015; Pendleton *et al.* 2019), and in marine systems new taxa continue to be discovered (Costello *et al.* 2010; Bucklin *et al.* 2016; Chenuil *et al.* 2019). While future data collection will continue to add to our knowledge of diversity, compiling historical data can also contribute to current estimates and inform future planning (Bates *et al.* 2009; Sloan and Bartier 2009; Stevens *et al.* 2014; Mannino *et al.* 2020). However, unless such data are part of a stringent long-term study, historical data from a given location typically consist of an assemblage of alpha (local) diversity snapshots reflecting different times, sites, and methods. The challenge is to glean from such data whatever knowledge one can of the gamma (regional) diversity of an area (Mushet *et al.* 2019).

The goal of our study is to demonstrate the utility of combining historical and recent biodiversity data to characterize the intertidal biodiversity of a provincial park in British Columbia (BC). British Columbia has the greatest reported biodiversity of Canada's provinces and territories (Austin *et al.* 2008), but a provincial audit revealed major gaps in biodiversity knowledge (OAG 2013). British Columbia Parks is North America's largest regional park system, smaller only than Parks Canada and the United States National Parks Service (BC Parks 2017). Its long-term ecological monitoring (LTEM) program established in 2011 spans five biomes, including the intertidal zone (Wright and Stevens 2012).

Within the BC Parks system, Porteau Cove Provincial Park (PCPP; Figure 1) is ripe for an intertidal

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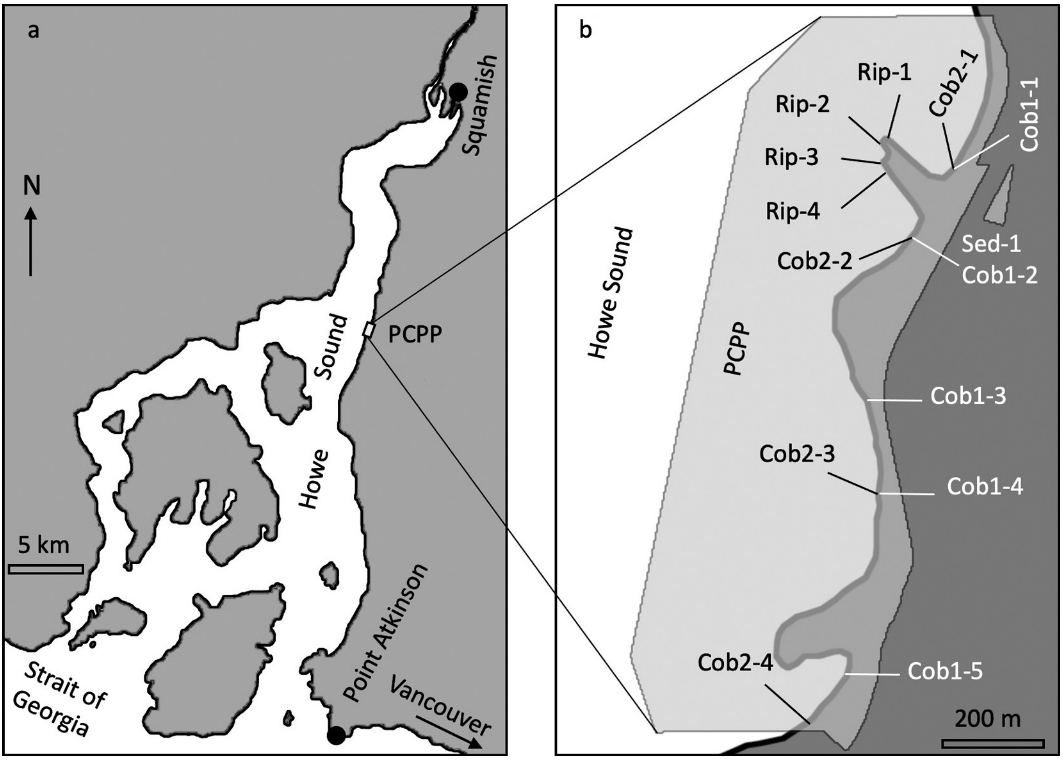

FIGURE 1. a. Porteau Cove Provincial Park (PCPP) in Howe Sound, British Columbia, Canada. b. Location of four intertidal biodiversity surveys: Sed, sediment survey from Levings and McDaniel (1976); Cob1-x, cobble-beach survey from Birch *et al.* (1990); Cob2-x, cobble-beach survey and Rip-x, riprap survey from our study.

biodiversity assessment. Neither the park nor its intertidal habitat types are currently included in BC Parks' LTEM program (BC Parks 2015). The park is situated in a region with an extensive history of industrial contamination and commercial exploitation (Bard 1998; Bright *et al.* 1999; Levings *et al.* 2004; Zis *et al.* 2004; Wilson *et al.* 2005), with myriad active and proposed conservation and development initiatives (Marliave and Challenger 2009; Ocean Wise Research Institute 2020; DFO 2022), and with a 2021 designation as the Átl'ka7tsem/Howe Sound United Nations Biosphere Reserve (UNESCO 2021). As the park contains one of the few accessible beaches in this Biosphere Reserve, its biotic inventory can help inform the region's management plan development. Further, while the park's Master Plan lists only eight intertidal species (BC Parks 1990), our personal observations indicated there were more.

Methods

Study area

Porteau Cove Provincial Park (49°33′N, 123°14′W) is located in southern coastal BC, Canada (Figure 1a). It is on the eastern side of Howe Sound, an estuarine fjord of the northern Salish Sea ~43 km long, with mid-sound surface salinities of ~15 ppt and a tidal amplitude averaging 3.2 m in a mixed semi-diurnal regime (Thomson 1981). Established in 1981, PCPP consists of a ~1.5 km strip of coastline with 4 ha of terrestrial forest and 56 ha of marine habitat. The shoreline is a gently sloping cobble-gravel-sand beach extending out ~100 m at low tide (4–20% grade; Birch *et al.* 1990; Figure S1). A tidal level of 1.0 m or lower (relative to the tidal datum of Lower Low Water Large Tide, LLWLT) provides access to the majority of its intertidal area (see Figure 2 for interannual variation in lower low tide levels). The park receives over 0.6 million day and overnight visitors annually (BC Parks 2018); anchoring, fishing, harvesting, and collecting are prohibited.

Our methods and taxonomy

We conducted two intertidal biodiversity surveys in PCPP: one on shallow-sloping cobble-gravel-sand beach that constitutes most of the park's intertidal habitat (hereafter: cobble) and one on the steep boulder riprap that surrounds the decommissioned ferry pier

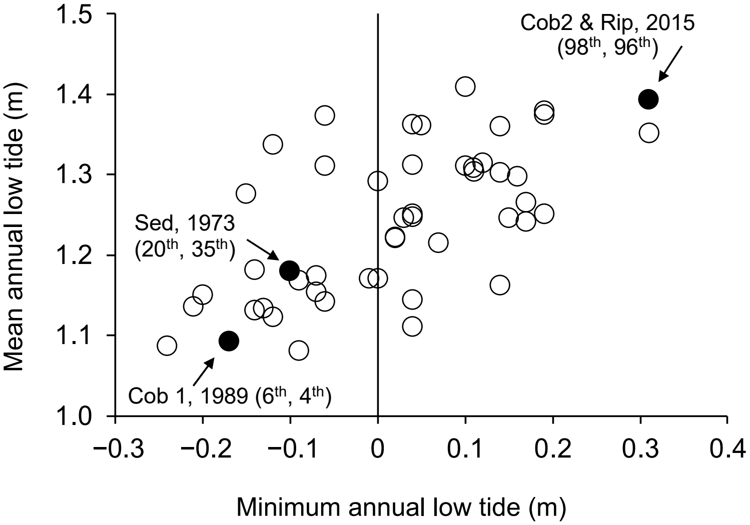

Figure 2. Annual minimum and annual mean daily lower low tides (m > LLWLT [Lower Low Water Large Tide]) recorded from 1970 to 2018 near Porteau Cove Provincial Park (PCPP), British Columbia, Canada. Solid points indicate the three years in which four intertidal biodiversity surveys were conducted at PCPP. Values in parentheses are percentile values for the (minimum, mean) low tides that year, out of the *n* = 49 years shown. Vertical line indicates chart datum, LLWLT. Data retrieved from Fisheries and Oceans Canada Tidal Inventory Data Station at Point Atkinson, the nearest station to PCPP (station no. 7795; 49.34°N, 123.25°W; DFO 2015).

(Figure S1a,b), during low tides in June–July 2015. For each survey, we selected four similar sites separated by at least 100 m (cobble [Cob]) or 10 m (riprap [Rip]; Figure 1b). Tidal elevations are reported as metres above chart datum, LLWLT, with reference to the nearest Fisheries and Oceans Canada Tidal Inventory Data Station (Point Atkinson, station no. 7795; 49.34°N, 123.25°W; DFO 2015). (Tide heights average 2.3 cm higher in Squamish than at Point Atkinson [± 1 SD = 2.4, *n* = 2027, based on three months in 2006 when data were recorded at both stations]; PCPP is located between the two [Figure 1a].)

At each site, we established six transect lines parallel to shore evenly spaced between the upper biotic limit (barnacles on cobble; algae on riprap) and the waterline at low tide (Table 1). Along each transect, we placed a 25×25 cm quadrat randomly in each 1/10th transect block, with a minimum distance between quadrats (cobble 0.5 m; riprap 0.25 m). Of the six cobble transects at each site, we pooled and designated the upper two as high, the middle two as mid, and the lower two as low, giving each of these three intertidal zones 20 quadrats per site. The three riprap transects at each site were designated high, mid, and low, each with 10 quadrats. In each quadrat, we recorded all epifauna and epiflora visible to the naked eye on the surface, and from underneath the uppermost layer (cobble) or under rocks that could easily be lifted with one hand (riprap).

The cobble beach was tightly compacted and not amenable to digging for infaunal sampling. However, after noting abundant empty shells of the non-native Purple Mahogany or Purple Varnish Clam (*Nuttallia obscurata* (Reeve, 1857)) near site Cob2-1 (Figure 1b), we sampled the more loosely-packed sandy beach immediately to the north (Figure S1c) for live clams by digging two to three holes, each 30×25 cm and 30 cm deep, at 10 m intervals along a 70 m transect line running down the shore from the high-water mark.

We identified organisms in the field to the lowest taxonomic level possible (Cox *et al.* 2017; Gerwing *et al.* 2020). Taxa that can reliably be identified only using genetic techniques were identified to morphospecies (Bay Mussel as *Mytilus* "*trossulus*", per Wonham [2004]; Sitka and Checkered Periwinkle as *Littorina* "*sitkana*" and *Littorina* "*scutulata*", per Hohenlohe [2004]) or genus (e.g., the dominant red alga *Mastocarpus* spp., per Le Gall and Saunders [2010]; very small limpets [<0.5 cm long], *Lottia* spp.). The majority of barnacles were Acorn Barnacle (*Balanus glandula* Darwin, 1854); subsequent analysis of collected specimens revealed that Crenate Barnacle (*Balanus crenatus* Bruguière, 1789) was present at lower tidal elevations but as these were not distinguished in the field, counts refer to *Balanus* spp.

Larger invertebrates were identified following Kozloff (1996) and Carlton (2007). Specimens were

TABLE 1. Quantitative methods for four intertidal biodiversity surveys at Porteau Cove Provincial Park, British Columbia, Canada: Sed (Levings and McDaniel 1976); Cob1 (Birch *et al.* 1990); Cob2 and Rip (our study). Taxa consisted of invertebrates, fishes, macroalgae, and vascular plants. Low tides, minimum tidal elevations during sampling are as archived at Point Atkinson tidal station. For Cob1, the predicted low tides of 0.1–0.2 m that informed the sampling design were 10–20 cm above the observed lows on the sampling days, i.e., lowest samples were likely collected even lower than the report indicated. Upper and Lower quadrats give mean elevations ±1 SD for *n* sites in m > LLWLT (tidal datum, Lower Low Water Large Tide). Quadrat min–max gives minimum and maximum quadrat elevations across entire survey. Transect orientation is vertical (perpendicular to shore) or horizontal (parallel to shore). *n* gives number of sites per survey / transects per site / quadrats per transect. Quadrats in Sed were dug 2 cm deep.

Source	Historical		Current	
Survey	Sed (sediment)	Cob1 (cobble)	Cob2 (cobble)	Rip (riprap)
Sampling dates	May 1973	Nov–Dec 1989	Jun–Jul 2015	Jun–Jul 2015
Time of day	Day	Night	Day	Day
Taxa	Invertebrates	All	All	All
Tidal elevations				
Low tides	0.9	−0.1–0.3	0.7–0.9	0.7–0.9
Upper quadrats	4.4	4.26 ± 0.29	3.6 ± 0.7	4.2 ± 0.1
Lower quadrats	1.0	0.49 ± 0.25	1.5 ± 0.5	1.7 ± 0.3
Quadrat min–max	1.0–4.4	0.1–4.7	1.1–3.9	1.4–4.4
Design				
Transect length (m)	~85	45–95	30	10
Transect orientation	Vertical	Vertical	Horizontal	Horizontal
n sites/transects/quadrats	1/1/8	5/1/7–9	4/6/10	4/3/10
Total quadrats	8	40	240	120
Quadrat size	25 × 25 cm	5 × 5 m	25 × 25 cm	25 × 25 cm
Total sampling area (m^2)	0.5	1000	15	7.5

collected for smaller invertebrates that could not readily be identified in the field (amphipods, isopods, polychaetes, small shrimp); these were returned to the lab, euthanized in 77% $MgCl_2$ for 1–4 h, fixed in 4% buffered formalin for 1–8 h, rinsed and stained with 0.5% Rose Bengal for 2–8 h, preserved in 80% ethanol, and identified by Biologica Environmental Services, Ltd. (Victoria, BC). The specimens were not archived. Gunnel and prickleback fishes (Pholidae and Stichaeidae) were enumerated in the field but were not identified further because we did not have a vertebrate research permit. Macroalgae were identified using Gabrielson *et al.* (2006).

Nomenclatures follow the online databases WoRMS (https://www.marinespecies.org/) for animals, AlgaeBase (https://www.algaebase.org) for macroalgae, and The Plant List (http://www.theplantlist.org/) for vascular plants, as of January 2021. Our surveys were conducted in 2015 as part of an unpublished undergraduate thesis (Gerstle 2016); however, we report the definitive methods and results here.

Historical surveys

To assemble a more comprehensive picture of the total intertidal biodiversity at PCPP, we compiled our two surveys with two historical surveys. The historical surveys are designated "Sed" (1973 sediment survey; Levings and McDaniel 1976) and "Cob1" (1989 cobble beach survey; Birch *et al.* 1990). Our two current surveys are designated "Cob2" (2015 cobble beach survey), and "Rip" (2015 riprap survey; Figure 1, Table 1). The Sed data were extracted from a government report that included PCPP as part of a larger Howe Sound survey. The Cob1 data were extracted from a consulting report that was unknown to PCPP staff or to us and surfaced only after our current study had been completed. The vertical extent of sampling differed across surveys because of the substantial interannual variation in low tide levels (Table 1, Figure 2). No specimens were vouchered from either historical survey.

We obtained additional qualitative records from Willems (2004) and by searching the GBIF (Global Biodiversity Information Facility) database for the latitude and longitude coordinates of PCPP (GBIF 2023). The GBIF search revealed only a few species that could be confirmed as having been found in the intertidal, and that had not already been reported in the four quantitative surveys above (see Table S1). A search of the online collection records at the Beaty Biodiversity Museum, the Royal British Columbia

Museum, and the Canadian Museum of Nature for the location keyword "Porteau" returned no additional records.

Data analysis

To summarize total taxon richness, we compiled a list of all quantitative and qualitative records across all four surveys, plus the additional sources (99 taxa; Tables 2, S1).

For quantitative analysis, we used only the quadrat data from the four quantitative surveys and counted only the distinctly identified taxa (84 taxa; Table S2); for example, unidentified limpets *Lottia* spp. were not counted as an additional taxon beyond the identified *Lottia* species.

To assess richness versus sampling effort in each survey, we used rarefaction and extrapolation analysis of frequency data using iNEXT version 2.0.17 in R version 3.3.3 for OSX (Gotelli and Colwell 2011; Chao *et al.* 2014; Hsieh *et al.* 2016). To examine the effects of smaller versus larger quadrats, we compared observed and estimated richness for a subset of Cob1 and Cob2 quadrats with matched taxonomic resolution and tidal elevation range, and with taxon accumulation data rescaled to the number of taxon occurrences rather than number of quadrats (see Gotelli and Colwell 2011). For this analysis we assigned the quadrats in Cob1 to the High, Mid, and Low elevation zones defined in Cob2, adding the zones Very High and Very Low for the Cob1 quadrats that fell above or below the Cob2 range.

To explore patterns in taxon composition, we followed Clarke (1993). Between-quadrat similarities were calculated using the Bray Curtis similarity index, on untransformed presence–absence data. Patterns of similarity were visualized using non-metric multidimensional scaling (nMDS) plots, and differences between surveys were evaluated using Analysis of Similarities (ANOSIM) routines. All multivariate analyses were performed in PRIMER (version 6, Primer-E).

Because the number of sites, transects, and quadrats, the size of quadrats, and the vertical intertidal elevation differed among surveys, it is not possible to meaningfully analyze differences in diversity over time. Instead, we report the magnitude of differences between surveys where they are notable, make selected methods-based comparisons where possible, and focus primarily on descriptive summary statistics calculated within each set of survey data.

Results

Taxon richness

In our two surveys we found 54 taxa, including 19 taxa newly reported from PCPP (Table 2). Combining these with the two historical surveys, we report a total of 99 distinctly identified intertidal taxa in the park (Tables 2, S1). In each survey, the estimated taxon richness was greater than the observed taxon richness, substantially so for Sed (154%), moderately so for Cob2 (15%) and Rip (13%), and only slightly for Cob1 (6%; Figure 3a,b, Table 3). Only in Cob1 was the sampling effort sufficient to sample an estimated ≥99% of taxa; the other three surveys were undersampled (Table 3).

Of the two cobble beach surveys, Cob1 reported a 63% greater observed richness and a 48% greater estimated richness than Cob2 (Table 3). To further explore this difference in richness, we examined the three main methodological differences between the two surveys. First, Cob1 extended one vertical metre lower into the intertidal than Cob2. Richness per quadrat increased nearly 4.5-fold from high to low elevation in Cob1 but did not vary over the narrower elevation range sampled in Cob2 (Figure 4a,b). This richness increase in Cob1 was due largely to the greater number of taxa found uniquely in the quadrats

TABLE 2. Number of taxa for each broad taxonomic grouping, total number of taxa, and number of non-native taxa reported from the intertidal zone at Porteau Cove Provincial Park (PCPP), British Columbia, Canada. The two historical surveys (Sed, Cob1) and our two surveys (Cob2, Rip) are characterized in Table 1. The number of Total and New taxa are given for our two surveys combined. "Other records" are qualitative reports of additional taxa from sources listed in Table S1. PCPP total is the number of distinct taxon records across all sources.

Taxa	Surveys						Other records	PCPP total
	Historical		Our study					
	Sed	Cob1	Cob2	Rip	Total	New		
Invertebrates	36	34	36	24	44	16	3	75
Fishes	0	5	1	0	1	0	1	6
Macroalgae	0	11	8	7	8	3	1	15
Vascular plants	1	3	1	0	1	0	0	3
Total	37	53	46	31	54	19	4	99
Non-native	1	2	3	2	4	4	0	7

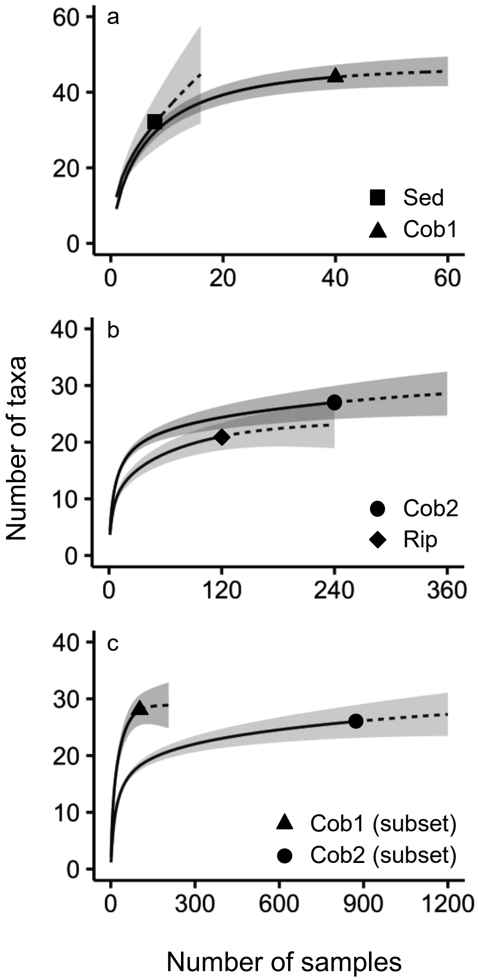

FIGURE 3. Observed intertidal taxon richness (points) with rarefaction (solid lines) and extrapolation (dashed lines) analyses showing estimated richness at Porteau Cove Provincial Park, British Columbia, Canada. a. Quadrat-based sampling in two historical surveys (Sediment [Sed] and Cobble 1 [Cob1]). b. Quadrat-based sampling in our survey of two habitats (Cobble 2 [Cob2] and Riprap [Rip]). c. Number of taxon occurrences for a matched subset of data from Cob1 and Cob2 with the same taxonomic resolution and tidal elevation range. Grey shading shows 95% CIs.

that fell below the range of Cob2 (Figure 4c versus d). Second, Cob1 used quadrats 16× larger than Cob2, sampling a total area 67× greater than Cob2. In the subset of data standardized for quadrat size, taxonomic resolution, and intertidal elevation however, the observed and estimated richness were similar between the two surveys, although observed richness saturated much faster in Cob1 than in Cob2 (Table 3, Figure 3c). Third, Cob1 sampled one site more than Cob2, but the additional site (Cob1-3; Figure 1) contributed only one taxon unique to that survey.

Taxon composition

For each survey, the similarity in taxon composition among quadrats was lowest for cobble beach (average Bray-Curtis similarity for Cob1 36.4%; Cob2 44.5%), moderate for Rip (54.4%), and highest for Sed (56.9%; Figure 5). In pairwise comparisons between surveys, taxon composition differed significantly for each survey pair: Rip and Sed were the least similar, whereas Rip and Cob2 were the most similar (Figure 5, Table 4). In all pairs except Rip and Cob2, the majority of taxa were not shared between surveys (Table 4).

The two dominant taxa in sediment were dipterans and oligochaetes, whereas those in cobble and riprap were barnacles and mussels (Figure S2). In the cobble surveys, greater numbers of lower intertidal taxa were found in Cob1 (sponge, anemone, flatworm, chiton, oyster, shrimp, nudibranch, seastar, kelp) than in Cob2 (Table S1, Figure S2). Of the eight species reported in the PCPP Master Plan (BC Parks 1990), six were found in one or more of the four surveys (Table S1). The other two, California Mussel (*Mytilus californianus* (Conrad, 1837)) and the orange nemertean *Tubulanus polymorphus* (Renier, 1804) (no common name), were not reported in any of the four surveys. The mussel would not be expected to be found in this habitat, and at small sizes could be mistaken for "*M. trossulus*". We have not seen it in 12 years of taking intertidal class field trips to this site (M.W. and C.B. pers. obs.) and exclude it from the list of reported species at PCPP (Table S1). The nemertean can be found in low-energy beach habitats (Kozloff 1983) and although we have not seen it here, it is so conspicuous that it would be impossible to mistake for anything else. We therefore leave this species in the inventory (Table S1).

Four non-native species newly reported from PCPP are Purple Mahogany Clam, Softshell Clam (*Mya arenaria* L., 1758), and amphipods *Ampithoe valida* (Smith, 1873) and *Monocorophium acherusicum* (Costa, 1853) (no common names). Including the previously reported Pacific Oyster (*Magallana* (= *Crassostrea*) *gigas* (Thunberg, 1793)), tanaid *Sinelobus* (= *Tanais*) *stanfordi* (Richardson, 1901) (no common name), and Japanese Wireweed (*Sargassum muticum* (Yendo) Fensholt), a total of seven non-native intertidal species are reported from the park (Tables 2, S1). Purple Mahogany Clam constituted 98.5% of the 451 clams collected from the sandy beach north of site Cob1-1, with a mean estimated density of 172/m^2 (± 1 SD 230, n = 8 intertidal elevations) and a maximum of 2147/m^2 in one upper intertidal sample.

TABLE 3. Observed and estimated taxon richness based on rarefaction and extrapolation analysis from four intertidal biodiversity surveys at Porteau Cove Provincial Park, British Columbia, Canada. Survey names as in Table 1. First four data columns show results for all taxa from all quadrats, with quadrat as sampling unit. Last two columns show results for subset of data adjusted to the same taxonomic resolution and tidal elevation range, with sampling unit rescaled to number of taxon occurrences. Estimated Samples, number of samples (quadrats or taxon occurrences) predicted to be required to sample 90%, 95%, or 99% of the estimated richness in each study; >2*n* indicates analysis was truncated at twice the number of original samples.

Survey	Historical		Current		Matched data subset	
	Sed	Cob1	Cob2	Rip	Cob1	Cob2
Sampling unit	Quadrat	Quadrat	Quadrat	Quadrat	Occurrence	Occurrence
Observed						
Taxon richness	32	44	27	21	28	26
Total quadrats	8	40	240	120	28	240
Mean taxa/quadrat	12.3	9.1	4.9	3.7	3.7	3.6
Taxon occurrences					103	871
Estimated						
Taxon richness	81	46	31	24	29	30
SE	43.7	2.9	5.3	3.5	1.5	5.3
Samples for 90%	>2*n*	28	302	130	67	1122
Samples for 95%	>2*n*	41	461	187	87	1727
Samples for 99%	>2*n*	75	>2*n*	>2*n*	138	>2*n*

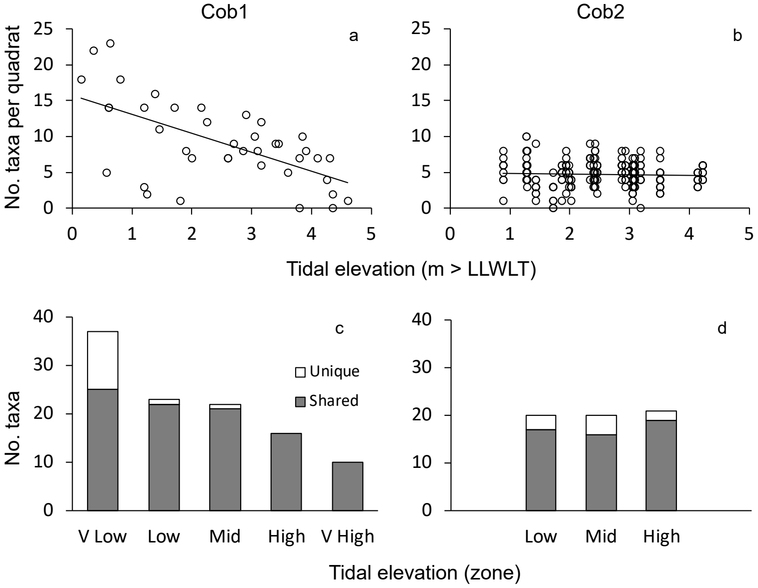

FIGURE 4. Intertidal taxon richness reported for Porteau Cove Provincial Park, British Columbia, Canada in cobble beach surveys Cob1 (a,c) and Cob2 (b,d). Number of taxa per quadrat versus intertidal elevation in m > LLWLT (Lower Low Water Large Tide) in a. $y = -2.6x + 15.7$, $r^2 = 0.38$ and b. $y = -0.10x + 5.0$; $r^2 < 0.01$). Total number of taxa per zone in c and d, distinguishing those taxa found uniquely in each zone (open) from those shared by two or more zones (shaded), within each survey.

Discussion

What is the intertidal diversity of PCPP?

Our compiled inventory of 99 intertidal taxa constitutes an over 12-fold increase above the eight taxa listed in the 30-year old PCPP Master Plan (BC Parks 1990) and provides the most complete picture of intertidal diversity from any location in Howe Sound to date.

This apparent increase in richness results primarily from the Master Plan not having included all the

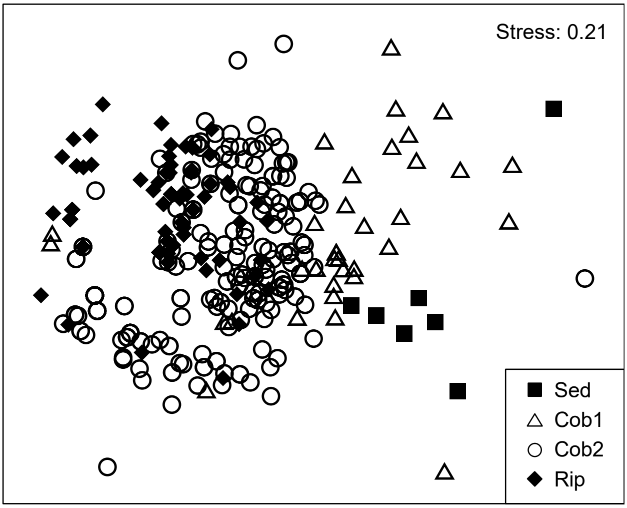

FIGURE 5. Non-metric multidimensional scaling ordination representing between-quadrat Bray-Curtis similarity based on per-sample taxon frequencies for four intertidal surveys at Porteau Cove Provincial Park, British Columbia, Canada.

TABLE 4. Multivariate taxon composition analyses for four intertidal biodiversity surveys at Porteau Cove Provincial Park, British Columbia, Canada. ANOSIM, Analysis of Similarities; % Dissimilarity, average percent dissimilarity between surveys, based on pairwise quadrat comparisons.

	ANOSIM		Number of taxa		% Dissimilarity
	R	*P*	Shared	Not shared	
Global comparison	0.28	<0.001			
Pairwise comparisons					
Rip-Sed	0.93	<0.001	6	41	83.1
Cob2-Sed	0.71	<0.001	6	47	81.5
Sed-Cob1	0.32	0.016	8	60	78.4
Rip-Cob1	0.72	<0.001	9	47	75.2
Cob2-Cob1	0.48	<0.001	14	43	73.6
Cob2-Rip	0.10	<0.001	16	16	57.2

taxa listed in the two historical surveys, and from the additional taxa we found in our surveys. It should not be construed necessarily as an increase in diversity over time, although it may reflect some species recolonization as the Sound continues to recover from historical contamination (Ocean Wise Research Institute 2020), and it includes new site records for four non-native species that are otherwise known from the region (Wonham and Carlton 2005). The most conspicuous of these, Purple Mahogany Clam, was readily visible as empty shells on the north side of the ferry pier. Its mean live density in the sandy beach to the north was similar to the mid-range of densities reported from other Salish Sea sites (Byers 2002; Dudas *et al.* 2007; Gordon *et al.* 2018). This is the one species we consider most likely to be a genuinely new colonizer in PCPP because the two historical surveys did not report it, and its large purple-interior shells make it difficult to miss. Overall, however, the data compiled here are too much of a habitat-and-methods mosaic to be read as a diversity timeline.

Our taxon inventory was compiled from quadrat-based surveys that, compared to other standard intertidal survey methods, are likely to sample the most taxon richness (Cox *et al.* 2017). Although our compilation represents an order of magnitude increase in known taxa at PCPP, it nevertheless underestimates the park's total intertidal richness. Particularly in sediment, rarefaction and extrapolation suggest that saturated sampling using the same methods would return over twice as many infaunal taxa. Even for more conspicuous taxa the records gleaned from iNaturalist via GBIF (Table S1) are testament to the additional species that can be reported by large numbers of natural historians who contribute observations outside the coverage of quantitative surveys. In addition, not all identifications were made to species level, and finer taxonomic resolution of cryptic taxa would likely reveal more species (e.g., Chenuil *et al.* 2019). Finally, additional richness would be recorded if the transient terrestrial and subtidal predators that frequent the intertidal at low or high tide were included (e.g., Northwestern Crow [*Corvus caurinus* Brehm, 1822] and Common Raccoon [*Procyon lotor* (L., 1758)]; Sunflower Sea Star [*Pycnopodia helianthoides* (Brandt, 1835)] and Pacific Octopus [*Enteroctopus dofleini* (Wülker, 1910)]; BC Parks 1990; Birch *et al.* 1990). (Sunflower Sea Star mortality from wasting syndrome has triggered a trophic cascade in Howe Sound [Schultz *et al.* 2016], and the species was recently assessed as Critically Endangered globally by the International Union for the Conservation of Nature due to population and range declines [Gravem *et al.* 2021].) Our inventory is, at the same time, slightly inflated by a few terrestrial insects and spiders that were visiting the intertidal from their supra-littoral habitat (e.g., Romanuk and Levings 2003).

The biotic composition and zonation observed at PCPP are consistent with those of a typical sheltered estuarine cobble shore in the Salish Sea (Kozloff 1983; Dethier and Schoch 2006). In Puget Sound, Washington, Dethier and Schoch (2006) reported 166 taxa from 45 sites with similar gravel/cobble habitat. The PCPP taxon count, which extended across a greater tidal elevation range, was 51% greater than that of the richest individual Puget Sound site but contained only 56% of the total richness of all Puget Sound sites. The number of reported non-native species at PCPP (n = 7) is less than 10% of the number reported from the Salish Sea region (Wonham and Carlton 2005). Although the surface salinity at PCPP is lower than full ocean salinity (Thomson 1981) and therefore less hospitable to some marine species, we expect that future sampling at PCPP and similar intertidal habitats in the region will reveal yet more native and non-native taxa in Howe Sound.

What is the value of compiling diversity studies?

Despite the long history of human impact in Howe Sound, primarily from acid mine drainage (Levings *et al.* 2004; Zis *et al.* 2004; Wilson *et al.* 2005), pulp and paper processing (Bard 1998; Bright *et al.* 1999), and fisheries and habitat modification (Marliave and Challenger 2009; Ocean Wise Research Institute 2020), there is a paucity of published intertidal diversity data from this region. Assembling historical taxonomic records can help us better understand current and future diversity patterns (Bates *et al.* 2009; Sloan and Bartier 2009; Stevens *et al.* 2014; Mannino *et al.* 2020) and inform future surveys at molecular, organismal, and ecosystem scales (e.g., Bucklin *et al.* 2016; Castelin *et al.* 2016; PISCO 2016).

Compiling these four intertidal surveys gives us insight into methodological and habitat effects on estimates of richness and composition at PCPP. Of the three habitats, cobble beach had the highest reported taxonomic richness and riprap the lowest (compared with Gittman *et al.* 2016). However, rarefaction and extrapolation estimates suggest that riprap richness might be similar to, and sediment richness might even exceed, that of cobble. Despite its small overall area within PCPP, riprap contributed four unique taxa to the overall richness.

Of the two cobble beach surveys, Cob1 reported more taxa than Cob2. It also sampled lower in the intertidal, used larger quadrats, and sampled one additional site. All three of these factors are well known to increase sample richness (Stephenson and Stephenson 1949; Gotelli and Colwell 2011; Chao *et al.* 2014). In this instance, it was the lower elevation that likely contributed the most to higher observed richness. Interannual variation in tidal amplitudes (Denny and Paine 1998) was such that unusually low tides exposed much more habitat in 1989 for Cob1, whereas unusually high low tides exposed much less in 2015 for Cob2. The Cob1 quadrats that fell below the reach of Cob2 contained the most unique taxa, and the majority of the total richness reported in Cob1. In contrast, larger quadrats in Cob1 appear to have had a lesser effect when quadrat size, taxonomic resolution, and intertidal elevation range were accounted for, and the additional site in Cob1 contributed only one additional taxon.

Finally, differing taxonomic expertise contributed to the composition differences among surveys, with a plethora of polychaetes in Sed, fish in Cob1, and amphipods (our study) identified based on available expertise. Overall, these composition differences illustrate the value of compiling alpha-diversity snapshots from multiple intertidal habitats to move toward a more comprehensive picture of the gamma diversity (Mushet *et al.* 2019) of a location, providing the organismal level ground-truthing required to design and implement future diversity monitoring (e.g., Castelin *et al.* 2016; Lobo *et al.* 2017).

This data compilation illustrates general challenges and opportunities in assembling historical data (e.g., Lindenmayer and Likens 2010; Hortal *et al.* 2015; Pendleton *et al.* 2019). All four PCPP surveys had limited original dissemination: Levings and McDaniel (1976) is a technical government report, Birch *et al.* (1990) is an unpublished consulting report, and the two surveys from our study were originally collected for an unpublished undergraduate thesis (Gerstle 2016). Neither of the historical studies was referenced in the PCPP Master Plan (BC Parks 1990), and the Birch *et al.* (1990) report was brought to our attention by parks staff only after our study was completed. A fifth survey conducted by Bard (1998) at multiple intertidal Howe Sound sites including Porteau Cove reported taxon numbers but not identities; one species from that study has since been identified in an unpublished thesis (Willems 2004).

A second major difficulty in such a data compilation is that voucher specimens were not archived by any of the four studies, including ours. This limitation can arise from lack of funding or institutional capacity or both, and hampers future confirmation of identifications. Digital vouchers in the form of photographs on iNaturalist (via GBIF) allowed us to confirm the identifications of several large and conspicuous species that added to the overall taxon list. The growing capacity to store and search digitized collection records will continue to make both physical and photographic vouchers easier to search and share (e.g., Pendleton *et al.* 2019; Hedrick *et al.* 2022), facilitating future biodiversity compilations.

Our compilation of current and historical surveys demonstrates the value of doing the detective work to obtain and analyze such hidden and scattered data: it makes available historical information, it substantially updates our diversity knowledge of a provincial park, it reports on a habitat otherwise uncatalogued in a provincial monitoring program, and it provides the foundational data needed to inform future monitoring at multiple ecological scales.

Author Contributions

Conceptualization: C.G. and M.W.; Methodology: C.G.; Investigation: C.G.; Supervision: M.W.; Data Curation: M.W.; Formal Analysis: M.W. and C.B.; Visualization: M.W. and C.B.; Writing – Original Draft: M.W., C.B., and C.G.; Writing – Review & Editing: M.W., C.B., and C.G.

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SUPPLEMENTARY MATERIALS:

FIGURE S1. Intertidal survey habitats at Porteau Cove Provincial Park, British Columbia.

FIGURE S2. Rank-order frequency curves for taxa found in four intertidal biodiversity surveys at Porteau Cove Provincial Park, British Columbia.

TABLE S1. Intertidal taxa found in four quantitative surveys or reported as qualitative text records in Porteau Cove Provincial Park, British Columbia.

TABLE S2. Compiled quadrat records of intertidal taxa from four quantitative intertidal surveys at Porteau Cove Provincial Park, British Columbia.

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Note

American Marten (*Martes americana*) and Northern Goshawk (*Accipiter gentilis*) simultaneously attack Gray Squirrel (*Sciurus carolinensis*)

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Abstract

A Northern Goshawk (*Accipiter gentilis*) was observed following an American Marten (*Martes americana*). The marten's attempts to capture a Gray Squirrel (*Sciurus carolinensis*) forced the squirrel into the open where the goshawk repeatedly attempted to capture it as the marten chased it through the trees. Attacks on prey flushed by heterospecific predators have been reported for a few other raptors, but this type of interaction has not been reported previously for either goshawks or martens.

Key words: Northern Goshawk; *Accipiter gentilis*; American Marten; *Martes americana*; Gray Squirrel; *Sciurus carolinensis*; predation

Several species of raptors have been reported to exhibit a form of noncooperative hunting in which one species flushes potential prey into the open where another species of predator can attack it. For raptors, Ellis *et al.* (1993) summarized reports of a Peregrine Falcon (*Falco peregrinus*) following a Raven (*Corvus corax*), a White Hawk (*Leucopternis albicollis*) following a troop of monkeys (species not indicated), and a Golden Eagle (*Haliaeetus leucocephalus*) following an American Badger (*Taxidea taxus*). Brockman and Barnard (1979), Kozma (2016), and McConnell (2011) report Merlins (*Falco columbarius*) using the hunting activity of other raptors to expose prey to capture. Kozma (2016) also saw American Kestrels (*Falco sparverius*) exhibiting similar behaviour. Bandy and Bandy (1978) report Marsh Hawks (*Circus hudsonius*) following Red Fox (*Vulpes vulpes*), and Graves (2004) observed a Red-shouldered Hawk (*Buteo lineatus*) using Wild Turkeys (*Meleagris gallopavo*) to flush insect prey. Such intraguild competition for shared food resources may include kleptoparasitism (stealing food that has already been captured by another animal), and either species may attempt to exploit resources made more easily available by the other (Jung *et al.* 2009; Jung 2021). We report observations of similar interactions between a Northern Goshawk (*Accipiter gentilis*) and an American Marten (*Martes americana*).

These observations were made between ~0920 and 0925 on 6 January 2022. The temperature was −11.1°C, wind speed was ~14.5 kph, and snow depth was ~39.4 cm in the area. A storm over the previous two days had produced ~30 cm of fluffy new snow. B.M.G. and S.M.P. were inside a house in Marquette Township, Michigan (46.560885°N, 087.472622°W), that was adjacent to large areas of relatively natural woodlands. A bird feeder in the yard commonly attracted Red Squirrel (*Tamiasciurus hudsonicus*) and Eastern Gray Squirrel (*Sciurus carolinensis*).

A marten was observed within 10 m of the bird feeder. It was travelling through the snow toward an Ironwood (*Ostrya virginiana* (Miller) K. Koch) tree where an Eastern Gray Squirrel was located. While we watched the marten, we saw a goshawk in the trees above it. The marten chased the squirrel up a large Sugar Maple (*Acer saccharum* Marshall) tree. The goshawk attempted to ambush the squirrel while the squirrel attempted to escape the marten. Both the goshawk and marten made numerous attempts to capture the squirrel and were within <1 m of each other several times. The squirrel jumped to another tree, but the marten did not leap after it. The marten descended part way to the ground, then leapt from the tree from a height of 5–10 m, landing in the fluffy snow. This happened twice as the marten moved between trees. The marten crossed the open yard to follow the squirrel to a clump of Black Spruce (*Picea mariana* (Miller) Britton, Sterns & Poggenburgh) ~40 m to the northeast. It did not get close to the squirrel again, and the squirrel escaped through the tree tops further to the northeast. The goshawk stayed in the maple tree and watched. The marten left the spruce and was last seen travelling on the ground ~100 m to the south of the spruce. The goshawk followed it until both were out of sight over a hill.

Direct competitive interactions for food resources can take several forms, dependent on costs, benefits, and opportunities. First and simplest with regard to evolution, learning, and cognition is that a predator may opportunistically detect a prey item that happens to have been made more vulnerable because of pursuit by another predator. This entails no modification of normal hunting behaviour; a predator simply detects prey and attacks.

A second situation would involve kleptoparasitism. This behaviour is adaptive if the cost of taking prey from another predator is less than the cost of catching that prey by oneself. We saw no evidence of this; the marten did not capture the squirrel, and the goshawk attacked the squirrel, rather than the marten. Furthermore, kleptoparasitism in this situation could be costly. Allowing the marten to capture the squirrel and then stealing that meal would save the goshawk the cost of capturing the squirrel. However, a marten may be a formidable adversary, as martens are capable of killing and eating goshawks (Paragi and Wholecheese 1994).

A third situation would involve an evolutionary or cognitive association between the activity of an intraguild predator and the availability of prey. The predator might reduce its foraging costs and increase encounter rate by letting the intraguild competitor expose prey (to act as a "beater"; Rand 1954). Thus, it would pay to follow the competitor. This is a simpler behavioural modification than kleptoparasitism, because the following predator must simply learn to associate the beater with the likely presence of prey and then respond as normal to cues from prey. Indeed, Brockman and Barnard (1979) suggest that kleptoparasitism could evolve from the use of beaters.

Is there any evidence to indicate whether this was a chance encounter of goshawk and marten, followed by an opportunistic response by the goshawk to normal prey-associated stimuli, or whether the goshawk was using a more complex foraging strategy in which it associated the marten with prey availability? Although parsimony would argue for the former, all else being equal, we suggest that several pieces of evidence support the latter possibility.

We do not know whether the goshawk had been following the marten before we saw them, but it did follow the marten after both had been unsuccessful in capturing the squirrel until they were out of visual range. Furthermore, the goshawk did not attack the squirrel when the marten was travelling on the ground between trees, but instead sat in a tree watching. Finally, while Red Squirrel is a common component of goshawk diets in the western Great Lakes region, Eastern Gray Squirrel is not (Boal *et al.* 2006). Eastern Gray Squirrels in southeastern Minnesota average 600.4 g (Thoma and Marshall 1960), while Red Squirrels in the Upper Peninsula of Michigan average 163.4 g (Kramm *et al.* 1975). Thus, because gray squirrels are almost four times the body mass of Red Squirrels, adult gray squirrels may be difficult for goshawks to capture, and this kind of interspecific interaction could facilitate success. These actions support our interpretation that the goshawk was using the marten as a beater and that this was not a chance encounter of two predators attracted to the same prey. Of course, this is a single observation; verification of such behaviour will require more data.

Although goshawk foraging ecology has been relatively well studied (e.g., Penteriani *et al.* 2013; Miller 2017; Kusal and Kajtoch 2020; Squires *et al.* 2020), use of another foraging animal to flush prey has not been reported previously for this species, nor has any raptor been reported to use a marten in this manner. Ellis *et al.* (1993) suggested that use by raptors of other species to flush prey might be much more common than the few anecdotes they cited would suggest, especially among forest species whose foraging behaviour is difficult to observe. Our observation broadens the distribution of this foraging strategy to another taxon of raptor and another mammalian carnivore species used to flush prey.

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Impact of anthropogenic disturbance on nesting Chimney Swift (*Chaetura pelagica*) including best practices for conservation

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Abstract

The effect of anthropogenic disturbance on nesting Chimney Swift (*Chaetura pelagica*) is poorly described. We review five case studies of anthropogenic disturbance around Chimney Swift nest sites caused by building construction, demolition, and maintenance activities in St. Adolphe, Manitoba. Chimney Swift behaviour and nest site activity did not appear to be overtly influenced by building demolition and construction conducted on adjacent buildings or lots within 13–30 m of nest chimneys. In contrast, Chimney Swift behaviour and breeding success appeared to be negatively affected by loud interior renovations and rooftop work conducted in or on the same building as the nest chimneys. The presence of humans on the roof of the nest building prevented Chimney Swifts from entering the nest site and reduced the overall rate of feeding young. Based on these observations, we provide conservation best practices for building construction and maintenance projects conducted within or on the same building as nest chimneys to help ensure protection of Chimney Swifts and their nesting habitat during the breeding season.

Key words: Chimney Swift; disturbance; behaviour; Manitoba; habitat avoidance; breeding success; nest site; conservation

Introduction

Many animals perceive disturbances caused by the presence and activities of humans in a way similar to predation risk (Frid and Dill 2002). Anthropogenic disturbances, therefore, can cause physiological or behavioural responses in animals that often mimic responses to predators (Storch 2013; Van de Voorde *et al.* 2015). These responses can divert individuals from key activities, including feeding and caring for their young (Frid and Dill 2002). In birds, behavioural responses include avoidance of disturbed areas, temporary and permanent abandonment of nests, and reduced feeding; physiologically, stress hormones may also increase (Møller 2008; Strasser and Heath 2013; Moss *et al.* 2014; Samia *et al.* 2015). These disturbances are recognized for their insidious and cumulative impacts on wildlife and are often considered a primary conservation concern (Gill 2007; Price 2008). Consequently, many jurisdictions have legislation to protect vulnerable species from anthropogenic disturbance.

Chimney Swift (*Chaetura pelagica*), a bird that forages on aerial insects, is listed as a Threatened species under federal (*Species at Risk Act* [SARA]; S.C. 2002, c. 29; SARA Registry 2021) and provincial (*The Endangered Species and Ecosystems Act* [ESEA]; C.C.S.M. c. E111; 1990; Province of Manitoba 2016) legislation. It is also protected under the *Migratory Birds Convention Act* (MBCA; S.C. 1994, c. 22). The *Species at Risk Act* and its ensuing regulations include prohibitions against collecting, possessing, killing, harming, or harassing migratory birds (birds or eggs) listed as Extirpated, Endangered, or Threatened as well as against damaging or destroying their residences, i.e., nests, anywhere in Canada. Critical Habitat identified for listed migratory birds must be legally protected on federal lands and effectively protected on all other lands in Canada (SARA 2002). *The Endangered Species and Ecosystems Act* (ESEA 1990) makes it an offence to disturb or interfere with a member of an Endangered or Threatened species. Furthermore, ESEA (1990) provides the same level of protection to the habitat and the natural resources on which the species depends as it does to the individuals of such species.

Despite this legislated protection, three factors can reduce its effective application in Manitoba. First, Chimney Swifts are often unwittingly subject to disturbances as building owners and managers are unaware of the presence of the species on their property. Most external building maintenance and construction projects in Canada, especially in the Prairie Provinces, occur during the spring, summer, and early fall, due to the prolonged periods of sub-zero temperatures in winter. This creates a risk of conflict between construction and maintenance of buildings and the protection of the species. Second, and most significantly, there is a lack of specificity in the Acts on what constitutes disturbance, which limits the ability of authorities to enforce protection for the species, most notably at their breeding sites. The proposed federal recovery strategy describes actions that prevent access to the chimney as examples of activities likely to result in destruction of those sites which meet the criteria for designation as Critical Habitat (ECCC 2022a). Third, there are no known published studies documenting the impacts of anthropogenic activity on Chimney Swifts. We address this last factor.

The Manitoba Chimney Swift Initiative (MCSI) is a collaborative partnership of environmental non-governmental organizations (NGOs), independent researchers, and biologists from provincial and federal governments that has provided a focus for monitoring, stewardship, outreach, and research of Chimney Swifts in Manitoba since 2007 (Stewart *et al.* 2017). The MCSI began an ongoing long-term study of five nest site chimneys in 2007 in St. Adolphe (49.672°N, 97.111°W), a town in the Red River Valley south of Winnipeg (Stewart and Stewart 2010, 2013). This is the longest known nest site study documenting annual phenology and breeding success in Canada. During four separate breeding seasons at these sites in St. Adolphe there were opportunities to observe the behaviour of breeding adult Chimney Swifts associated with potential anthropogenic disturbances. The disturbances were building construction, building demolition, interior renovation, and rooftop repairs. Here we report and evaluate the impacts of these activities on Chimney Swifts by comparing behaviour at the time of disturbance to expected behaviour at various stages of nesting (Stewart and Stewart 2010, 2013). We then suggest best practices for nest site management to support the application of protection measures currently afforded under primary legislation in Canada.

Methods

Five nest site chimneys on four historical buildings in St. Adolphe (Figure 1) were monitored for 15 Chimney Swift breeding seasons (2007–2021 inclusive; Stewart and Stewart 2010, 2013; B.E.S. unpubl. data). Single chimneys were located at a private residence (known as Main St.), the Paroisse St. Adolphe Church (Church), and Brodeur Bros./St. Adolphe Childcare Centre (known as Brodeur Bros.). The Brodeur Bros. building is no longer known under this name, but we have retained the name first applied (Stewart and Stewart 2010, 2013) to it to avoid confusion. Two chimneys were located at Club Amical (NE Club Amical, SE Club Amical). Breeding success was confirmed by behavioural observations of fledglings and physical evidence observed in the cleanout traps of the Brodeur Bros. and Main St. sites. Estimates of fledging at the Church and Club Amical were limited to behavioural observations due to inaccessible cleanouts.

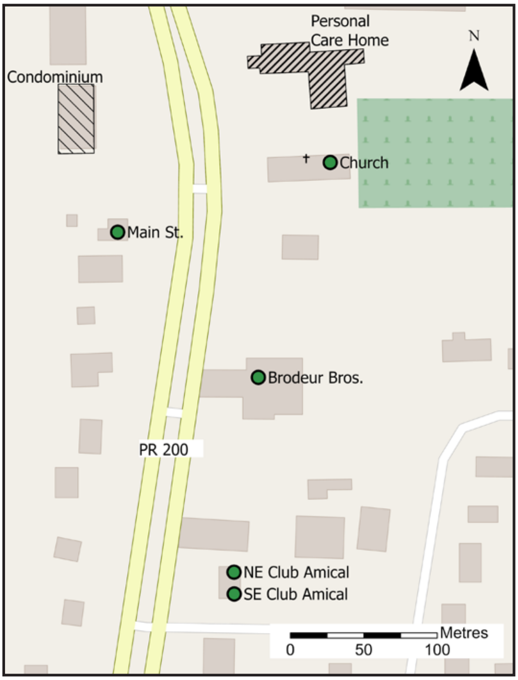

FIGURE 1. Plan of St. Adolphe, Manitoba, showing locations of all chimneys (circles), the site of the condominium construction and the site of the personal care home that was demolished in 2017. Map data copyrighted OpenStreetMap contributors and available from https://www.openstreetmap.org (https://wiki.openstreetmap.org/wiki/Researcher_Information).

Monitoring protocols remained constant across observation years. Monitoring involved watching a chimney top during the roosting hour (0.5 h before to 0.5 h after local sunset) or during the day (0.5 h before sunrise to 0.5 hour before sunset) and recording entries and exits of Chimney Swifts to the nearest second. Information about approaches and departures of Chimney Swifts (speed, direction, vocalizations, etc.) was also documented. Most observation sessions lasted 60–90 min, but ranged from 10 to 150 min. The frequency and sequence of entry and exit events were used to identify the various stages of nesting (Stewart and Stewart 2010, 2013). We used the phenology derived from these studies to identify typical or expected behaviour (Table 1), deviations from which might be indicative of disturbance.

Monitoring effort varied among years, but a consistent effort was made to document dates for the onset of each stage of nesting. Incubation starts with the second last egg laid with clutch size varying from two to seven eggs (Steeves *et al.* 2020). It is difficult to establish the exact onset of incubation by behavioural observation, but it is possible to recognize incubation as it becomes established. Stewart and Stewart (2013) and B.E.S. (unpubl. data) have noted in St. Adolphe that as full-time incubation progresses, adult swifts increase attendance to ≥50% of the time and partner exchanges between incubating adults inside the chimney become shorter (from ≤10 min to 0.5–2 min) and less frequent (Table 1). Dates for hatching and the transition from feeding brooded to feeding non-brooded juveniles were established by observing increases in activity at the nest sites (Table 1). Daily monitoring was required to note these transitions.

Behaviourally, nest failure was indicated by waning of entry/exit rates over several days or an abrupt lack of attendance. These were confirmed by a lack of daytime entries or exits in three independent observation periods, each between 60–90 min duration, over at least two days.

As nesting progressed, observations of Chimney Swift behaviour were made during building construction, building demolition, interior building renovation, and while rooftop activity occurred. There were five instances of four types of possible disturbance: building construction near Main St., building demolition near the Church, major interior renovation in Brodeur Bros., and rooftop repair on Club Amical and Brodeur Bros. Controls used were: contiguous observations at the same site after the work had stopped, monitoring data from other local sites at the same stage of nesting on any given day, and published information (Table 1).

All observations were made by an experienced observer, B.E.S., who positioned herself to view the two chimneys at Club Amical simultaneously. Distances from the focal chimney to the construction and demolition sites were determined using Google Earth. For the construction of the condominium, the lot line marked the nearest site edge. For the demolition of the personal care home, churned earth marked the demolition area.

The observer was unaware of daily human activity until she arrived at the sites so data were obtained opportunistically, resulting in small sample sizes and “controls” that may not be ideal. Obtaining larger sample sizes, or a more robust experimental design, was not possible. Thus, there were too few data to warrant statistical tests.

We used data for entries because, unless there was excessive noise outside the chimney, Chimney Swifts may have been unaware of what was occurring in the vicinity when exiting the chimney (e.g., machinery or people nearby). On approach, the birds could make

TABLE 1. Typical or expected behaviour and activity for a pair of breeding Chimney Swift (*Chaetura pelagica*) at a nest site, based on 15 years of data from St. Adolphe, Manitoba, Canada (2007–2021; Stewart and Stewart 2010, 2013; B.E.S. unpubl. data). The roosting hour is defined as 0.5 h before to 0.5 h after sunset. All other observations are daytime records. Nest building continues through incubation until hatching. Note that attendance can vary in a given session due to weather and food availability.

Stage	Behaviour	Activity
Spring arrival	No daytime use of nest site	Two roosting entries; exits occur the following morning
Nest building (+ egg laying)	Daytime entries by a single Chimney Swift or pair together; egg laying cannot be estimated	1–2 entries and exits/h during the day; variable duration-in/turnaround times
Incubation (+ nest building until hatching)	Characterized by ≥50% attendance during observation session, ≤10 min duration in/turnaround time, and/or 1 entry followed by exit within 0.5–2 min	One entry and one exit/h; one adult usually in chimney but short unattended periods
Feeding brooded young	Hatching = day 1 of feeding/brooding; young are brooded for 6–7 days	Two entries and two exits/h; short turnaround times for partner exchanges
Feeding non-brooded young	Periods with both parents absent; consecutive entries or exits indicate young are unattended	Four entries and four exits/h; longer duration-in intervals while parents feed young before exit
Fledging	Juveniles’ first flights outside the nest site at 28–30 days of age	Highly variable daytime site use by young and adults; waning daytime use for ~7 days as juveniles’ flight competency increases

a full assessment of activity in the area. Conversely, it is not possible to observe birds inside the chimney that abort an exit. There was, however, one exit of note. On 9 July when roofers were first observed on the Brodeur Bros. rooftop at 9:58:19, a bird exited at 9:58:42. Without knowing when the roofers arrived, we cannot say that the exiting bird had not entered when there were people on the roof.

Results

Building construction—Main St., 2012

Construction of a three-storey condominium on a previously vacant lot located ~30 m north of the Main St. nest site was at the framing stage when Chimney Swifts ($n = 4$) were first observed flying in town on 10 May. Equipment and activity were typical of a building site with truck traffic, power and pneumatic tools, generators, ladders, and platform lifts, which were used to position heavy materials on upper levels. Construction continued through the entire Chimney Swift nesting season.

Observations totalled 32 h 26 min spread across 30 days from 14 May to 20 August. Most observations (23 h 26 min) were made during the daytime. The first observed use of this chimney was on 16 May, when three birds roosted overnight. On 24 May, there were no entries during the day, but there was one on 31 May, indicating nest building. Thereafter, the breeding attempt proceeded as expected with hatching on 9 July. Young fledged on 5 August when both adults and juveniles were observed feeding above the new condominium building. On 8 August, a crane was lifting material to the roof of the new condominium building and there were no Chimney Swift entries in 1 h. On 9 August, while workers in an elevated bucket installed windows, there was one Chimney Swift entry. Day-use is highly variable at this stage of nesting (Table 1) and the observed use on 8 and 9 August was consistent with expected behaviour.

There were two observed changes in the behaviour of Chimney Swifts associated with the Main St. site. First, and throughout the summer, Chimney Swifts were observed hovering ~3 m over workers framing the south end of the condominium, which was the side closest to the nest chimney; it is uncertain the number of times this occurred because peripheral observations of the construction sites were made while watching the chimney rim. Head movements by the hovering birds were evident, suggesting the birds were observing the human activity at the construction site below. Second, Chimney Swifts typically exited to the north/northwest from the Main St. nest site. As building construction progressed, it appeared this trajectory shifted to the northwest/west; i.e., Chimney Swifts flew around the new condominium instead of over it.

Building demolition—Church, 2017

Chimney Swifts arrived at the Church site on 20 May and demolition of the adjacent 3.5-storey, 2787 m^2 personal care home took place on 23 May (Braun 2017; Ross 2017). Distance from the Church chimney to disturbed earth was 13 m. A hydraulic excavator (CAT 320D; Caterpillar Inc., Irving, Texas, USA) began and largely finished knocking the building down on 23 May. Activity by the excavator and backhoes loading dump trucks continued through 26 June as the site was cleared of debris. Plumes of dust and dirt were nearly constant during work hours.

Observations totalling 23 h 12 min were made between 9 May and 7 August, including five days (26 May–26 June, 4 h 30 min) while demolition and site restoration took place. The birds arrived in St. Adolphe between 9 and 14 May and were first observed using the Church chimney to roost on 20 May. On 26 May, Chimney Swifts were seen feeding over the clean-up area during work hours. There was no daytime use on 30 May, but there was at the next observation, on 2 June, when activity patterns were consistent with nest building (two entries in 38 min). On 26 June, Chimney Swifts collected twigs from a tree near the lot line where the final cleanup of the personal care home was being finished. There was no detectable change in the approach/departure trajectories of Chimney Swifts using this chimney.

It was later determined that the young hatched at the Church on 3–5 July, comparable to hatching dates at Main St. (3–5 July), SE Club Amical (3–5 July), and NE Club Amical (5–6 July; B.E.S. unpubl. data.). The remaining site in St. Adolphe, Brodeur Bros. was not occupied by Chimney Swifts in 2017. Two fledglings emerged from the Church on 31 July.

Major interior building renovations—Brodeur Bros., 2019

The Brodeur Bros. building was converted from its former use as a car dealership and recreational vehicle rental location to a daycare in 2019. The nest chimney remained open at this site, rising through the middle of the building. Nesting birds would likely have been aware of high decibel construction noises inside the building, e.g., pneumatic drill to break concrete and possibly other noisy equipment (power saws, pneumatic nailers, skid steer, etc.).

Chimney Swifts were first seen in St. Adolphe on 12 May. The noise of renovations was first detected by B.E.S. on 15 May and continued through the summer. Assessing this possible disturbance was complicated by two factors. First, B.E.S. was outside, ~90 m away, so noise levels at the chimney could not be quantified. Second, the start of rooftop repairs began on 10 June so we deleted from this renovation analysis any observation hours that included rooftop activity.

Observations totalled 40 h 18 min over 27 days from 19 May to 4 July, the last day when inside noise was detected. In the 10 h 36 min when interior noises were heard by B.E.S., there were four entries (0.4/h) and in 29 h 42 min when there were no loud noises there were 54 entries (1.8/h). The entry rate with noise was less than expected, whereas the rate without noise was consistent with the rate typical for this particular stage of nesting (Table 1).

Rooftop activity—Club Amical, 2016

The effect of people walking and working on a flat roof was assessed at Club Amical by comparing entry rates when workers were present and when they were not (Table 2). Observations totalling 9 h were made on 11–17 and 19 July. Nesting was ongoing in both Club Amical chimneys when rooftop repairs began on 11 July. Roofing activities occurred daily through normal working hours on 11, 12, and 14 July; heavy rain fell on 13 July. Previous data indicated the breeding pair at NE Club Amical was tending non-brooded young for the duration of rooftop repairs, whereas the SE Club Amical Chimney Swifts were feeding brooded young. Both Club Amical chimneys were monitored simultaneously, so monitoring hours were equal. However, as the NE Club Amical breeding attempt failed earlier than the SE Club Amical breeding attempt (see below), the monitoring time of Chimney Swift response to potential disturbance was less.

The nest in NE Club Amical failed on 16 July. Entry rates with and without workers present were much lower than the expected 4/h when feeding non-brooded young (Table 1) and much lower than at a comparable site. In 2016, the breeding pair at the Church was at the same nesting stage and was observed on one day when NE Club Amical was monitored. There were three entries to the Church nesting chimney in 35 min (5/h).

At SE Club Amical, the entry rate when workers were present was slightly lower than when they were not, although both rates were above what would be expected when tending brooded young (2/h, Table 1). Additional data on entries and exits established that three adults were tending these brooded young, i.e., there was a "helper" (Dexter 1981). The nest at Brodeur Bros. was also at the feeding brooded young stage on 11 and 14 July 2016 (unpubl. data) and showed the expected two entries/hour when a helper is not present. A single exit was observed from SE Club Amical on 19 July 2016 after which the nest failed. There was no access to a cleanout trap for either of these chimneys so there is no further information about the nest failures.

Rooftop activity—Brodeur Bros., 2019

The effect of people walking and working on a flat roof was also assessed at Brodeur Bros. (Table 2). While the interior was being renovated in 2019 (see above), rain in June revealed leaks in the roof, near the chimney, that resulted in interior water damage and an emergency rooftop repair. Rooftop repairs were carried out on 10–12 and 27 June, and 8–9 and 15 July. Subsequent observations determined that hatching occurred on 10 July; 27 days of observations were made during nest building and incubation (Table 2) and seven days were during the feeding of brooded young stage. The data were partitioned to reflect this change in behaviour (Table 2). The parents stopped attending the nest after 16 July, which is the last day of data used.

During incubation, there were no entries when workers were on the roof, but the entry rate was as expected when workers were not on the roof (1.5/h; Tables 1 and 2). At this rate, one would expect 12 entries in the hours when workers were present.

Concurrent observations (3 h 26 min) on 10–12 June were made opportunistically at Main St. Subsequently, it was determined that hatching at Main St. and Brodeur Bros. were within 24 h of each other, so

TABLE 2. Number of daytime entries and hourly rates of entries of Chimney Swifts (*Chaetura pelagica*) at three nest sites in St. Adolphe, Manitoba, Canada in the presence of workers on the flat roofs and when there were no workers on the roof.

Site (stage of nesting)	Date	Workers on roof			No workers present		
		Obs. (h)	Entries (*n*)	Entries /h	Obs. (h)	Entries (*n*)	Entries /h
NE Club Amical (feeding non-brooded young)	11–15 July 2016	2.1	2	1.0	3.1	2	0.6
SE Club Amical (feeding brooded young)	11–17 July 2016	2.1	6	2.9	6.9	22	3.2
Brodeur Bros. (incubation/nest building)	10 June–9 July 2019	8.1	0	0.0	38.6	58	1.5
Brodeur Bros. (feeding brooded young)	10–16 July 2019	0.5	0	0.0	12.3	11	0.9

they were at the same stage of nesting (incubation) on those days. There were three observed entries at Main St. in 3 h 24 min or 0.9/h, which is in agreement with rates typical for this stage of nesting (Table 1) but higher than the entry rate seen at Brodeur Bros. (0/h).

There were fewer data when the parents were feeding brooded young at Brodeur Bros. (Table 2). There were no entries during the presence of workers. The one time (15 July) that workers left during an observation period was the last day of rooftop work, and the first Chimney Swift entry was seven minutes later. There was a single Chimney Swift entry in 2 h of observation on 16 July and none on 17–19 July. The nest had failed. Additional rooftop repairs were made on 25 and 31 July.

Behaviour observations indicated that hatching took place on 10 July (day 1); the predicted fledging dates were calculated as 6–8 August (day 28–30). Parental attendance waned below expected feeding rates (Stewart and Stewart 2010, 2013) on 15–16 July, then did not occur on 17–19 July (day 8–10). A nest failure was indicated. The eight half eggshells at the cleanout trap in September indicated that four eggs hatched. The 2019 nest remained on the wall of the chimney until it was dislodged by commercial cleaners in March 2020.

Rooftop activity and Chimney Swift approaches to nest site

Chimney Swifts sometimes approach their nest sites and depart without entering. At Brodeur Bros. in 2019, on days when observations were made both without and with workers on the roof, 5/19 approaches by the birds (26%, 11 h 42 min of observation) resulted in no entry when there were no workers on the roof. However, when workers were present, 9/9 (100%, 7 h 36 min of observation) approaches resulted in no entry.

At Club Amical in 2016, observations were made without and with workers present only on 12 July, so we used 13 and 15 July (workers absent) and 11 and 14 July (workers present) for comparison. In the absence of workers, 3/10 (30%, 3 h 6 min of observation) approaches did not result in entries. When workers were present, 11/18 (61%, 2 h 6 min of observation) approaches were followed by no entry.

Discussion

We found that Chimney Swift behaviour and nest site activity was not overtly influenced by building demolition and construction conducted on adjacent lots within 13–30 m of nest chimneys. In contrast, Chimney Swift behaviour and breeding success appeared to be negatively affected by loud interior renovations and rooftop work conducted in or on the same building as the nest chimneys. These findings are, to our knowledge, the first of their kind to be documented for this species. Given the protected status of Chimney Swifts in Canada, these findings can be used by regulatory authorities to provide guidelines on how to reduce disturbances from renovation and construction projects relating to buildings with nesting Chimney Swifts.

Chimney Swifts that nest in urban areas are routinely exposed to anthropogenic noise and road dust. Many MCSI sites are adjacent to busy thoroughfares and the St. Adolphe nest sites are all 20–45 m from a four-lane road. Construction of a three-storey condominium spanned the whole Chimney Swift nesting season. Slow, incremental changes to the height of the new building were accommodated by the Main St. breeding Chimney Swifts. The only impact was an apparent shift in exit trajectories. There was no discernible effect on nesting success. Demolition of the personal care home was brief and occurred before nest building began at the Church. Debris removal and site restoration spanned nest building, egg laying, and incubation. The breeding attempts at the Main St. and Church sites resulted in successful fledging. Overall, there was no apparent change in chimney use associated with either the condominium construction or demolition site restoration. We have no information on the possible deleterious effects of dust and noise during chick-feeding stages. Future demolition cases involving Chimney Swifts should be monitored diligently to document potential disturbances from dust, equipment movement, noise, etc., at this critical stage.

Renovations to the Brodeur Bros. building began before, then overlapped, rooftop activity. Before roof repairs started and while the Chimney Swifts were nest-building and incubating, the birds entered the chimney at lower rates during periods of loud noises, such as jackhammers breaking up the concrete floor, but entered at higher rates when it was quiet and no work was occurring. During those times, entry rates were at the higher end of the expected range and it is possible that the Chimney Swifts attempted to compensate for lost time in nest building and incubation. Several studies have shown that noise alone negatively impacts habitat use, feeding rates, nesting success, and nestling quality in birds and acute, unpredictable noise had greater impacts than chronic, more predictable noise (e.g., Merrall and Evans 2020; Mulholland *et al.* 2018; Rosa and Koper 2021). Similar effects may occur in Chimney Swifts based on our results. Breeding Chimney Swifts in Manitoba appear vulnerable to disturbance as a complete nesting cycle requires at least nine weeks and the reproductive season is short (< 14 weeks). No documented primary nesting attempt in St. Adolphe has succeeded if initiated after 4–6 June and no secondary nesting attempt has ever been successful (Stewart and Stewart 2010, 2013; B.E.S. unpubl. data).

The duration of incubation in St. Adolphe appeared to be variable (16–21 days) as reported elsewhere (Steeves *et al.* 2020). Chimney Swifts can prolong incubation for several days during cool weather (Steeves *et al.* 2020) and, similar to other species of swifts (Apodidae spp.), the eggs might have a high tolerance to cool temperatures (O'Connor 1979; Malacarne *et al.* 1992). It is generally thought that unhatched Chimney Swift eggs are constantly attended as the parents take turns to leave the chimney to feed (Fischer 1958; Stewart and Stewart 2013). Sometimes we were unable to determine if an absence of entries by an adult during incubation meant the eggs were unattended or if one parent remained on the nest for an abnormally long time. The former might delay embryonic development and the latter might compromise the energetic reserves of the sitting (fasting) adult. Both parents share chick-rearing responsibilities (Kyle and Kyle 2005; Steeves *et al.* 2020). If one parent is on the nest and the other is excluded due to anthropogenic disturbance, the energetic costs to the parent on the nest may be acutely or chronically detrimental, potentially causing an energy shortage that might limit its subsequent capacity to feed its young (Moreno 1989). Therefore, it is reasonable to conclude that delays in the progression of nest building or incubation due to anthropogenic disturbance, particularly multiple cumulative delays over the course of a single nest cycle, may have negative impacts on reproductive success of nesting Chimney Swifts.

The presence of workers on the Brodeur Bros. roof stopped entries from 9 July onwards and the eggs hatched on 10 July. Roofers' presence was during a crucial period when the newly hatched young need to be fed. Unlike delayed nest building or incubation, lost feeding time cannot be compensated for by more frequent feedings later. Intense anthropogenic disturbances have also been shown to slow development in Blue Tit (*Cyanistes caeruleus*) chicks and cause them to fledge in poor body condition (Remacha *et al.* 2016). Poor fledgling physical condition, including low body mass and shorter wing length, is one factor that reduces survival rates of post-fledging birds, which in turn influences demographic rates, including annual survival and recruitment (Naef-Daenzer and Grüebler 2016).

We documented nest-site avoidance in the presence of rooftop workers and loud interior building noises surrounding the chimney base. Reduced activity in response to the threat of predation has been documented around nest sites in songbird species (e.g., Rohwer and Purcell 2019). Similarly, nest avoidance due to anthropogenic disturbance has been observed in European Pied Flycatcher (*Ficedula hypoleuca*) nesting near busy footpaths (Goodenough 2014). Chimney Swifts will fly over a nest chimney and disappear from sight before returning shortly afterwards, making a rapid entry into the chimney (Kyle and Kyle 2005; MCSI unpubl. data), possibly as they have satisfied themselves that no threat is present. We found that more approaches resulted in immediate departure without entry when workers were present on the rooftop. Indeed, during nest building, egg laying, and incubation at Brodeur Bros., no approaches resulted in entries when workers were on the rooftop. At both Club Amical nest sites, where chicks were being fed (assisted by a helper at the SE Club Amical site), there were more approach-departure events when workers were present than on contiguous days when there was no rooftop work being done. Chimney Swift behaviour that was negatively associated with anthropogenic rooftop activity included single or repeated instances of an approach followed by quick deflection or veering off, rapid altitudinal changes before immediate departure, circling of the site before departure, and hovering before departure.

Many birds respond to anthropogenic disturbances as if they were akin to a predation threat (Frid and Dill 2002). The behaviours we documented would suggest that human presence on the roof of a building, and the generation of loud noises surrounding the chimney base, elicit similar avoidance behaviours in Chimney Swifts to those observed in other bird species in response to perceived predation events (Frid and Dill 2002). Similarly, in London, Ontario, sandblasting and repointing of two chimneys was associated with two failed breeding attempts, while loud noises near the chimney from fireworks, a roaring crowd, and a drone flying near the nest chimney rim all resulted in apparent disruption of the birds' behaviour (W. Wake pers. comm. 13 November 2021).

At Brodeur Bros. in 2019, the young hatched on 10 July, roofers were present on 15 July, and the nest failed on 16 July. At Club Amical in 2016, there was roofing activity while the birds using both chimneys were feeding young on 11–12 and 14 July; heavy rain fell on 13 July. The NE nest failed on 16 July and the SE nest failed on 19 July. The low rate of feeding over several days at the NE chimney suggests that the nest attempt might already have been in the process of failing. At Brodeur Bros. it is possible that one or both parents entered the feeding-young stage energetically compromised due to enforced longer incubation periods brought on by anthropogenic disturbance. In turn, this may have contributed to nest failure.

Nest failures can be associated with a number of environmental stressors, but we consider the primary cause of nest failure at Brodeur Bros. was the roofing activity. Extreme temperatures, especially low temperatures, and high precipitation have been associated with reduced body mass and low survival rate of juvenile swifts and swallows (Hirundinidae spp.; Cucco and Malacarne 1996; Winkler *et al.* 2013; Cox *et al.* 2019; Steeves *et al.* 2020). However, average daily maximum and minimum temperatures for July at Winnipeg Richardson International Airport, 28 km NW of St Adolphe, (2016: 25.1°C and 13.4°C; 2019: 26.7°C and 13.6°C; ECCC 2021) were not different than long term averages at Winnipeg (1981–2010: 25.9°C and 13.5°C; ECCC 2022b), suggesting that prolonged extreme temperatures were not a factor contributing to nest failure. Rainfall in July 2016 (82.7 mm) approximated the long-term average of 79.5 mm while July 2019 was drier (44.8 mm), which suggests that prolonged extreme rainfall was also not a factor contributing to nest failure. We are unaware of any alternative factors, in addition to rooftop activity, that might better explain the influences on swift behavior and reproductive success that we observed, although they may very well exist.

We have shown that rooftop activities and elevated noise levels correlate with diminished parental care in Chimney Swifts. With only one instance each of building construction and demolition, our study and its conclusions would have been stronger with increased sample sizes. Construction or demolition of a taller building, for example, might have greater impacts, or other unknown variation not captured by our sample might exist. Further quantitative studies of anthropogenic disturbances and Chimney Swift responses are required. Controlled experiments that purposely cause disturbance remain unacceptable. Monitoring Chimney Swift behaviour before, during, and after expected disturbances could be a permitting requirement when emergency repairs at a nest site are needed. Until more data become available, our results can be used to formulate best practices to mitigate potential negative effects of building construction and maintenance projects on this Threatened species and its habitat during the breeding season.

Recommended best practices

Our results suggest that rooftop activity and loud noises within the building containing the nest chimney (i.e., loud being audible from outside the building, 90 m away) cause reduced frequency of chimney entries by breeding adults. This reduction in attendance likely leads to avoidance of nesting habitat, reduced incubation activity, reduced rate of feeding young, and nest failure. These behavioural changes might be viewed as harassing individual birds or disturbing nests or eggs as prohibited by s. 5 and s. 6 of the Migratory Birds Regulations (2022) or as damaging the residence of Chimney Swifts as prohibited by s. 33 of SARA (2002). Our study supports regulators as they seek guidance on describing activities that demonstrably disturb Chimney Swifts and developing best practices for limiting the impacts of those activities.

It is best practice, therefore, to entirely avoid generating loud noises and any rooftop activities within or on the building containing the nest chimney during the usual season of Chimney Swift occupancy, and especially during known or suspected occupancy of any chimneys by nesting or roosting swifts. We note that having strong trusting relationships with property owners in St. Adolphe led to deferred work on three roofs in 2020 and 2021. Additionally, landowner letters and outreach from the Province of Manitoba led to other property owners avoiding disturbance by doing rooftop work when the birds were absent. Based on such successes, we highly recommend that these types of proactive efforts be made with landowners in instances where anthropogenic disturbance might negatively impact nesting Chimney Swifts.

In addition, we also recommend the following due diligence to help ensure protection and conservation of the swifts:

- monitor the nest site intensively to establish the pre-disturbance behaviour baseline, including typical approach and departure paths, nesting stage, activity sequences, and entry rates;
- monitor during potential disturbance events to identify avoidance behaviour that indicates displacement (e.g., increased frequency of approaches followed by quick deflection/veering off, rapid altitudinal adjustments and immediate departure, and circling or hovering prior to departure). Manage anthropogenic activities immediately to enable Chimney Swifts to access the nest site;
- establish a setback distance for storage and operation of equipment with movable arms as a precautionary approach to limit noise and movement of larger vehicles, which may interfere with flight lines (e.g., large hydraulic excavators, cement pumper trucks);
- limit the number and duration of events requiring people and equipment above the eaves and on the rooftop;
- avoid noisy interior construction and renovations close to the chimney, or in the same room as the chimney, during the breeding season; and
- avoid cleaning the interior of the chimney during the Chimney Swift breeding season.

When construction occurs at locations where Chimney Swifts are using the site for roosting only, monitoring needs to be particularly intensive.

Conventional wisdom is that the birds enter around sunset and depart around sunrise but entry and exit times are highly variable (Steeves *et al.* 2020; Pearce and Foot 2022). Only monitoring that allows estimating the numbers of birds inside the chimney at any given time can ensure there are no birds there to be disturbed. As well, all rooftop activities at nest and roost sites should cease during periods of increased environmental stress (e.g., storms, extreme temperatures, high winds, poor air quality due to smoke) to allow Chimney Swifts an opportunity to take shelter in the chimney.

Conclusion

Anthropogenic disturbances, notably loud interior noises and rooftop activities, elicit behavioural responses in Chimney Swifts that likely contribute to nest site failure through reduced attendance and feeding frequency. Human activities near nest sites should therefore be managed to limit negative impacts on the birds. This is best achieved through 1) community outreach with targetted landowners to raise awareness and promote cooperation and compliance, and 2) stringent use of the conservation best practices and guidance described above. Enforcement of species-at-risk and migratory bird legislation should only be used as a last resort, if absolutely necessary, when the above approaches fail or seem likely to fail to protect the swifts. Continued monitoring to identify new nest sites remains an ongoing priority as most property owners are unaware that their property is being used by Chimney Swifts. We also recommend further research into behavioural associations with various types of disturbance and the preparation of best practice documents for property owners to inform them how to limit nest site disturbances.

Author Contributions

Writing – Original Draft: T.F.P., B.E.S., and R.E.A.S.; Writing – Review & Editing: T.F.P., B.E.S., and R.E.A.S.; Conceptualization: T.F.P. and B.E.S.; Investigation: B.E.S.; Methodology: B.E.S. and R.E.A.S.; Formal Analysis: R.E.A.S.

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Red-eared Slider (*Trachemys scripta elegans*) nests in the Greater Toronto Area

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Abstract

Red-eared Slider (*Trachemys scripta elegans*) is a non-native turtle found in abundance in Toronto's wetlands as a result of pet releases. Although this species is known to reproduce successfully in southwestern Ontario, Canada, there is yet no evidence to suggest successful reproduction in the Greater Toronto Area (GTA). As part of a native turtle nest protection program, volunteers inadvertently placed nest protector boxes over four slider nests in 2021 and 10 nests in 2022. This gave us the opportunity to determine whether nests produced viable offspring and whether these hatchlings would emerge in the fall. The exact nesting date for each nest was recorded. In 2021, eight of the 41 eggs from the slider nests showed very late-stage arrested embryonic development. In 2022, one of the nests had four hatchlings out of their eggshells but still inside the nest cavity. It is unclear whether the hatchlings would emerge later in the fall or overwinter in the nest cavity and emerge the following spring. If the small population sampled accurately reflects what occurs in the GTA, complete egg development may be possible for this species in some years, in some locations, with the right local micro-climate and micro-habitat. We discuss implications for turtle nest protection in Toronto.

Key words: Red-eared Slider; *Trachemys scripta elegans*; turtle nest protection; arrested development; Toronto; wetlands; turtle embryo; climate change; invasive species

Introduction

Red-eared Slider (*Trachemys scripta elegans*) is native to the central United States and northeastern Mexico but introduced in other parts of North America (Ernst and Lovich 2009) and many countries around the world (Rödder *et al.* 2009). Since the 1950s, these turtles have been favoured by the pet trade. They are now present in more than 90 countries and, at one time, were considered to be among the top 100 invasive species (Lowe *et al.* 2000). Sliders have been reported to outcompete some native turtles for basking sites (Cadi and Joly 2003; Lambert *et al.* 2019), although basking sites are usually not a limiting factor in Ontario (Seburn 2016). In some countries, native turtles have experienced weight loss and higher mortality after the introduction of Red-eared Sliders (Cadi and Joly 2004), and there is always the risk of introducing new pathogens when a pet turtle is released into the environment (Oi *et al.* 2012). In Canada, Red-eared Slider is considered a threat to some populations of native turtles, although population effects are uncertain (COSEWIC 2016a,b, 2018).

The 3-cm (carapace length) hatchlings grow to 30 cm and can quickly outgrow their enclosures, causing pet owners to release them into local wetlands (Ernst and Lovich 2009). Sliders can reproduce successfully outside their native range in a broad range of climatic conditions, including temperate areas (Standfuss *et al.* 2016). Viable hatchlings have been reported in many temperate countries and regions, such as Japan (Taniguchi *et al.* 2017), Spain (Perez-Santigosa *et al.* 2008), France (Cadi *et al.* 2004), Slovenia (Standfuss *et al.* 2016), British Columbia (Mitchell *et al.* 2022), and southern Ontario (Seburn 2016). Slider hatchlings can successfully emerge in southwestern Ontario in the fall and as far north as Oxford and Middlesex counties near London, Ontario (S. Gillingwater pers. comm. 13 May 2022). Since their documentation in Ontario in the 1950s, Red-eared Sliders have been reported in 130 locations, with 67% of Ontario sightings in the Greater Toronto Area (GTA; Seburn 2016). Red-eared Sliders found in many of Toronto's wetlands are known to nest (Dupuis-Desormeaux *et al.* 2019, 2021), but hatchlings had not been discovered.

Every species of turtle subjected to Ontario winters must deal with extended freezing conditions, potential anoxia, and prolonged times in brumation, either under ice or in nest cavities, sometimes unsuccessfully (Dupuis-Desormeaux *et al.* 2022a). Turtles found at northern latitudes dig nests and lay eggs in the late spring and early summer. Incubation periods vary among species, but all eggs will hatch in the fall and hatchlings will either emerge then (as is most common in Snapping Turtle [*Chelydra serpentina*] and Blanding's Turtle [*Emydoidea blandingii*]) or overwinter in the nest cavity and delay emergence until the following spring (typical for Midland Painted Turtle [*Chrysemys picta marginata*] and very occasionally Snapping Turtles). (See Lovich *et al.* 2014 and Ultsch 2006 for a comprehensive review of overwintering strategies and poor outcomes in Ontario [M.D.-D. unpubl. data; S. Gillingwater pers. obs.].) Delayed emergence in North American turtles is suggested to be an evolutionary advantageous trait only possessed by northern turtle populations (Gibbons and Nelson 1978). In its native range, the slider's overwintering strategy varies, with most hatchlings emerging in the fall, but delayed emergence is documented in some areas, such as Illinois (Gibbons and Nelson 1978; Packard *et al.* 1997) and Florida (Jackson 1994).

Temperatures in nest cavities can fall below freezing in winter months; thus, turtle hatchlings that overwinter in the nest cavity at northern latitudes must be able to withstand freezing (St. Clair and Gregory 1990; Packard *et al.* 1999). Hatchlings that typically overwinter in nests, such as Midland Painted Turtles, can withstand lower temperatures for longer periods than turtles that tend to emerge from nest cavities in the fall (Red-eared Sliders, Snapping Turtles, and Blanding's Turtles; Packard *et al.* 1999). Sliders are less adapted to withstand sub-zero temperatures, leading to increased hatchling freezing of these species compared with Painted and Blanding's Turtles (Packard *et al.* 1999).

We oversee a large group of volunteers, who perform a variety of tasks to safeguard native turtle populations, including protecting nests with anti-predator structures. Although sliders are not a species that we target for protection, a few slider nests are inadvertently protected every year. This provided an opportunity to collect data on nesting dates and outcomes at two sites in the GTA. Although our study was limited to two seasons at two study sites, we hope that given the ubiquitous presence of this non-native species in many Canadian cities, including the GTA, and the paucity of published data on their hatching success in Ontario, this small study will add to the knowledge of this species' ability to reproduce and potentially spread.

Methods

Study sites

Nesting sites were discovered by volunteers who observed and followed turtles suspected of being ready to nest. The first nesting location was on a southwest facing hill at Loafer's Lake Park, in Brampton, Regional Municipality of Peel in the GTA region of Ontario, Canada (43.72330°N, 79.80104°W), near the northern limit of the deciduous forest zone (Allen *et al.* 1990). The site is in a highly residential and commercial area. Etobicoke Creek is the primary inflow and outflow to Loafer's Lake.

The second site, High Park, had nesting sites dispersed throughout the park. Volunteers started a nest protection program in 2022. High Park is a large urban park in the city of Toronto, Ontario, Canada (43.64650°N, 79.46370°W). The park is characterized by an oak savannah, a 14-ha naturalized pond with wetlands (Grenadier Pond), smaller wetlands and ponds, and a ravine.

Nest protecting and monitoring

Once a suspected nesting turtle was observed, volunteers followed the female to her nesting spot and allowed her to oviposit while protecting her from animals, vehicular traffic, people, and other disturbances. After successful egg-laying and the turtle's safe return to the wetland, the volunteers placed a protection box over the nest to keep predators from digging up the eggs. The boxes were anchored in the ground with 30-cm nails and marked with a unique number identifier. The boxes were a ~60-cm by 60-cm frame, constructed of standard 2 × 4 inch wood (38 × 89 mm), with exit holes along the side, and covered with a sheet of galvanized steel mesh (1.3-cm mesh), a design commonly used throughout Ontario (M.D.-D. pers. obs.).

In 2021, volunteers placed 75 nests protectors at the Loafer's Lake site and other nearby sites in Brampton, Ontario, protecting 36 Midland Painted Turtle nests, 34 Snapping Turtle nests, and five Red-eared Slider nests. The boxes were placed over the nesting area soon after egg laying in the spring and summer months and left until the fall (Snapping Turtles) or the following spring (Midland Painted and Red-eared Sliders), allowing for safe gestation, hatching, overwintering, and emergence.

The nests were monitored almost daily in the fall (Snapping Turtles) and in the early spring (Midland Painted Turtles and Red-eared Sliders) for signs of emergence. The nest protectors around Red-eared Slider nests laid in the summer of 2021 were removed, and the nests excavated on 10 May 2022, while those in 2022 were excavated in November 2022. We did not want to interfere with the Red-eared Slider nests in 2021 and potentially assist hatchling emergence, but we did monitor for emergence holes in fall 2021 and spring 2022 and found none. The nests were excavated to look for signs of emerged hatchlings (empty eggshells inside the nest cavities or emergence holes) or failed nesting (undeveloped eggs or dead hatchlings in the nest cavities).

In 2022, volunteers protected 63 Midland Painted Turtle nests, 75 Snapping Turtle nests, 10 Red-eared Slider nests, and one Eastern Musk Turtle (*Sternotherus odoratus*) nest. Only Red-eared Slider nests were systematically excavated and inspected in November 2022.

Results

We documented five Red-eared Slider nests and protected four (one nest protector was placed over the wrong area) at Loafer's Lake in 2021 and 10 nests in 2022 (both study sites combined). The four protected nests from 2021 yielded clutch sizes ranging from 8 to 13 eggs (Table 1). There was no successful hatching in any of these nests. All slider nests lacked an exit hole, empty shells inside the nests, and signs that any hatchlings had exited their eggs or the nest cavities before we excavated the nests. Recorded nesting dates for the sliders ranged from 16 June to 13 July 2021.

After excavating the nests, we counted and dissected the eggs and investigated hatchling development of the earliest laid nest in greater detail. Slider egg development in all the nests stopped at the late embryonic stages. Each embryo appeared to be connected to a large yolk sac within the eggshell (Figure 1). Using the 27-stage embryonic developmental scheme of Yntema *et al.* (1968) and based on Greenbaum's (2002) study of Red-eared Sliders, the embryos of the earliest nest (#1) appeared to be arrested at stages 24–26 (Figure 2), close to the hatching stage (stage 27). In contrast, 27/34 (79.4%) protected Snapping Turtle and 26/36 (72.2%) Midland Painted Turtle nests showed successful emergence. The failed Snapping and Midland Painted Turtle nests had suffered from a variety of issues, including flooding, rooting (plant roots invading the eggs), infertile eggs (showing no embryonic development), egg predation, egg desiccation, nest cavity collapse, and hatchling entanglement in grass roots and blades. We were also unable to relocate a small number of the nests because of poor nest protector placement. None of the native species exhibited late-term embryonic arrested development.

In 2022, Red-eared Sliders nested from 11 June to 29 July. We excavated nests between 8 and 14 November. Nine of the 10 excavated nests had eggs

TABLE 1. State of Red-eared Slider (*Trachemys scripta elegans*) nests found in the Greater Toronto Area.

Nest	Nesting date	Clutch size	Outcome*	Stage†
Loafer's Lake				
1	16 June 2021	8	AD	24–26
2	2 July 2021	13	NV + AD	18–21
3	5 July 2021	8	NV	—
4	13 July 2021	12	NV	—
5	22 June 2022	13	AD	17–21
6	27 June 2022	7	AD	24
7	16 July 2022	13	NV + AD	14
8	23 July 2022	3	NV	—
9	26 July 2022	13	NV + AD	12–21
10	5 July 2022	15	NV + AD	14
High Park				
11	11 June 2022	8	NV + H	27
12	27 June 2022	13	AD	20–21
13	28 June 2022	13	NV	—
14	29 July 2022	6	NV	—

*AD = arrested development, H = hatched in nest cavity, NV = non-viable eggs.
†Stages range from 1 to 27, with 27 indicating hatched (Greenbaum 2002).

FIGURE 1. Red-eared Slider (*Trachemys scripta elegans*) embryo from nest #1 at Loafer's Lake, Ontario, Canada, encased in the shell and showing the unabsorbed egg yolk. This embryo was at stage 25 or 26 (detailed dissection required to determine exact stage). Photo: M. Dupuis-Desormeaux.

(3–15 eggs) that had either failed because of arrested embryonic development or were non-viable (eggs were desiccated and sunken; Table 1). We also documented double clutching, confirmed by photographs taken of a female after laying her eggs. The female that laid the eggs in nest #5 at Loafer's Lake on 22 June (13 eggs) also laid a clutch on 16 July (nest #7, 13 eggs). We suspect that the female that laid eggs in nest #8 on 23 July was disturbed as there were only three eggs and the nest was not covered before she left the site.

When we excavated nest #11 (laid on 11 June) in 2022, we found four hatched turtles on top of four non-viable eggs (Figure 3). This nest was found at the side of a road, in full sun. Most other slider nests were found in part shade.

Embryonic development in the other nests from 2022 varied greatly from stage 12 to 24 (Table 1). We removed the live hatchlings from nest #11, and they were adopted by a volunteer. Prospective adopters were educated on the equipment and long-term commitment required to keep this species in captivity and how it is illegal to release pet turtles into Ontario wetlands.

Discussion

Red-eared Slider clutches were not successful at the Loafer's Lake site in 2021 or 2022 despite their location near Painted and Snapping Turtle nests with predominantly successful emergence in both years. The peak nesting time for native turtles at this site was 8–14 June (unpubl. data), and the slider eggs were laid after this peak in both years. Some of the excavated slider eggs at Loafer's Lake showed late embryonic development but no evidence of pipping and hatching. The eggs of the earliest laid nest (#1) were the most developed of the excavated slider clutches, but

FIGURE 2. Seven of the eight Red-eared Slider (*Trachemys scripta elegans*) embryos removed from their eggshells from the earliest nest of 2021 (#1) at the Loafer's Lake site, Ontario. Embryo stage ranges from 24 to 26. The eighth embryo from this nest was damaged during egg dissection. Photo: M. Dupuis-Desormeaux.

FIGURE 3. Hatched Red-eared Slider (*Trachemys scripta elegans*) inside the nesting cavity (nest #11), High Park, Ontario, after excavation on 8 November 2022. Photo: M. Dupuis-Desormeaux.

were still unable to develop fully, suggesting that the local climatic conditions at this site might be a limiting factor (Ficetola *et al.* 2009).

However, the success of one nest at producing viable offspring at our High Park site in 2022 raises more issues. Because we excavated the nest on 8 November 2022, it is uncertain whether the hatchlings would have exited the nest at some point before the first freeze and snowfall (which was 16 November 2022, M.D.-D. pers. obs.). Also worthy of noting is that the volunteers who work diligently at protecting turtles had a strong protective instinct toward these slider hatchlings. Thus, the hatchlings were not euthanized.

Given our small sample size and the fact that only one of the 14 monitored nests was able to produce viable hatchlings, we recommend further investigations into factors limiting Red-eared Slider reproduction in Ontario. With at least one nest with hatched, but not emerged turtles, in the GTA, sliders there might be poised to reproduce successfully during the summer. As climate continues to warm, causing potentially warmer summer and fall temperatures, Red-eared Slider eggs in Toronto may be able to develop fully more frequently and hatch and emerge in the fall as they do further south in Ontario (Seburn 2016). Some of us have argued that having non-native sliders in urban wetlands might not be as bad as often portrayed and may provide important ecosystem functions (Dupuis-Desormeaux *et al.* 2022b), but others have a much more conservative view (Mitchell *et al.* 2022).

Our study also raises questions as to which course of action to take when volunteers discover slider nests now that we know they can produce viable hatchlings. Should we ask volunteers to remove the eggs, destroy the nest, or let nature take its course? Our volunteers felt much more inclined to simulate a predation event and destroy newly laid eggs than to remove hatchlings for euthanasia. Local conservation authorities might discuss a plan to take eggs from all slider nests before any advanced embryonic development happens to avoid creating moral dilemmas among the volunteers.

We suggest that further research on the post-emergence survival of slider hatchlings in Ontario wetlands is also needed to better understand the potential ecological effects of this non-native species and whether these effects pose threats to Ontario's native turtle species.

Author Contributions

Writing – Original Draft: M.D.-D. and G.V.A.; Review & Editing: M.D.-D., G.V.A., M.M., R.T., V.D., and S.E.M.; Conceptualization: M.D.-D.; Data Collection: M.D.-D., G.V.A., M.M., and R.T.; Funding Acquisition: M.D.-D., V.D., and S.E.M.

Acknowledgements

We thank all the volunteers of the Heart Lake Turtle Troopers and the Turtle Protectors High Park who worked tirelessly to protect and monitor nesting sites, specifically the organizational work done by Jamie-Lee Ball, Christina Cicconetti, Lori Leckie, Leah Nacua, and Rebecca Zimmerman for the Troopers and Jenny Davis and Carolynn Crawley for the Protectors. We also thank Scott Gillingwater (Upper Thames River Conservation Authority) and Jeff Lovich for their helpful comments on the first draft and the support and encouragement provided by David Seburn.

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The Canadian Field-Naturalist

Book Reviews

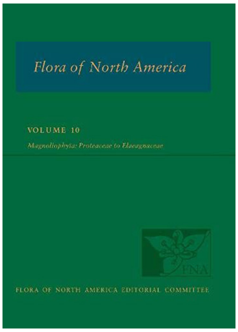
Book Review Editor's Note: *The Canadian Field-Naturalist* is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those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

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

Botany

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, Hardcover.



We're getting near the end. After many years and 22 published volumes, the Flora of North America (FNA) series, that fundamental compendium of North American plants north of Mexico, is in the home stretch. So, I'd like to start this review of Volume 10 with a heartfelt thank you on behalf of botanical workers everywhere to the FNA association, committee, editors, and authors past and present for these massively important works.

Volume 10 is slightly slimmer than past issues, but only because it covers 12 of the (mostly) smaller North American vascular plant families, from Proteaceae (one species) to Elaeagnaceae (nine species) to Onagraceae (277 species). This includes diverse eudicot species from Florida to Kalaallit Nunaat (Greenland), which no doubt kept the expert regional reviewers running from one herbarium cabinet to the next (thanks to them, too!).

Early pages of this volume are devoted to a gorgeous frontispiece: a full-page colour plate of Blue Waxweed (*Cuphea viscosissima*) and a lovely tribute to Walter Judd. From there, the tome dives headlong into the taxonomic treatments, set up (like all FNA volumes) with useful keys, chapters devoted to each family, and within each family further keys and parallel genus and species descriptions. Approximately 25% of the species treated within are illustrated by talented botanical artists, providing important visual context to the descriptions.

Keen to test the wheels on this volume, I ran through the keys and descriptions in the Onagraceae treatment by Warren L. Wagner and Peter C. Hoch, as this family includes Arctic and southwestern USA species of interest to me. For both *Epilobium* and *Chylismia* (my test genera), the keys are easy to follow and provide ample characters for identification of even the most challenging material. This family is also a showcase for one of this volume's greatest strengths—a commitment to parallel species descriptions. The *Epilobium* treatment in particular stands out due to the length of these descriptions—with extensive care taken to fully describe the morphology of these subtle species.

Of particular note, within the Lythraceae, the description of Purple Loosestrife (*Lythrum salicari*) includes information on the status of this invasive species, as well as references regarding ongoing biocontrol research. As a former invasive species ecologist, I found this section particularly interesting, but I also appreciated other efforts like this found throughout this volume, to make this work relevant to as many biological disciplines as possible.

With only seven more volumes of the Flora of North America series to come, my guess is that if you've been collecting this work all along, you likely already have Volume 10 at your home or institutional library. If not, I absolutely recommend adding this useful book to your shopping list (particularly if you work with taxa from the north or southwest deserts)! Nowadays, thanks to hard work from the FNA team, the Flora of North America website contains all the information that the print volumes do in a complementary, easy to navigate, and up-to-date format. While this important effort makes the flora broadly accessible, the print copy is still pleasurable to use, important to archive, and key to supporting the efforts of the FNA committee as they complete this monumental task.

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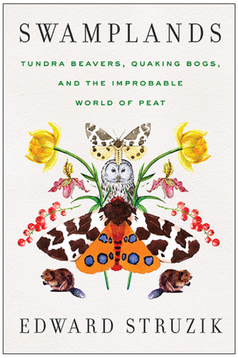
CONSERVATION AND CLIMATE CHANGE

Swamplands: Tundra Beavers, Quaking Bogs, and the Improbable World of Peat

By Edward Struzik. 2021. Island Press. 312 pages, 39.95 CAD, Hardcover, 33.95 CAD, Paper, 29.99 CAD, E-book.



Swamplands focusses on the preservation and restoration of peatlands (swamps, bogs, and fens) in Canada and the United States. Throughout the book, Struzik relies on current research and interviews with active researchers to emphasize that peatlands are globally the most important ecosystem for storing carbon and controlling the effects of climate change. The book will be appreciated by all those readers looking for a comprehensive introduction to these essential and diverse ecosystems.

Each *Swamplands* chapter begins with a short story about an individual researcher followed by the ecological history and current state of preservation or restoration taking place at a particular location. Struzik's conversational writing style effectively brings uninitiated readers into the story. Each chapter stands alone, summarizing the subject with enough depth to leave the reader informed but not overwhelmed, and providing a set of Notes at the back of the book for those wishing to explore topics in more detail. However, reading the book in sequence leads to an improved understanding of the context and challenges facing peatland reclamation and preservation.

The first two chapters set the historical context by contrasting two views of North American swamplands that began with early European settlers and persist today. One perspective views peatland as not only worthless but also a danger to public health. The other, more closely aligned with those of Indigenous people who adapted to peatlands rather than subdued them, is exemplified by Henry David Thoreau—"without wetland the world would fall apart" (p. 60)—and the ironically named George Perkins Marsh, who supported considerations of peatland preservation and restoration during development in the latter half of the 19th century and urged all to become a "co-worker with nature" (p. 60).

Struzik devotes four chapters to the American perspective on species restoration. He looks at North Carolina's swamplands, the preservation of Hawaii's tropical peatlands, peaty wetlands formed around ponds in Mojave Desert oases, and western Alaskan tundra peatlands. Canadian perspectives on preservation issues are described in five chapters, which include discussions of the small Wagner Fen in Alberta, Ontario's Georgian Bay peatlands, Alberta's Crowsnest Pass peatlands, the Hudson Bay Lowlands, and ending in High Arctic peatlands.

Each chapter explores the following points about peatland ecological value, preservation, and restoration:

1. Peatlands are evolutionary petri dishes and often contain endemic species and rich species assemblages (e.g., over 2000 arthropods and 16 of the 26 orchid species native to Alberta are in Wagner Fen, Alberta).
2. They have unique habitats that are critical to individual species. Larval development of rare Aweme Borer (a small brown moth) depends on Buckbean, which only grows in peatland sedge mats. Rattlesnakes use peat for overwintering in Georgian Bay. The Hudson Bay Lowlands serve as breeding grounds for migratory birds (e.g., Hudsonian Godwit), and peaty hillsides provide dens for Polar Bears. As an aside, each of these species has been recently assessed by The Committee on the Status of Endangered Wildlife in Canada (COSEWIC; Government of Canada 2022).
3. Restoration and preservation projects depend on the efforts of dedicated individuals within governments, citizen scientists, local volunteer groups, and non-governmental organizations (NGOs) like The Nature Conservancy, which has made preservation purchases of several peatland sites in Canada and the United States.
4. Restoration and preservation projects commonly

> encounter conflicting objectives among user groups, such as deer hunters fearing that Red Wolf restoration will threaten local deer populations in North Carolina's Albemarle-Pamlico Peninsula wetlands.

The final two chapters of *Swamplands* focus on whole ecosystem restoration of peatlands extracted for resource use and the increasingly precarious areas of warming permafrost that are poised to release large amounts of stored carbon and encourage, rather than mitigate, climate change effects.

Line Rochefort, a scientist at Université Laval, has worked on the restoration of more than 100 peatlands, including work with a company that extracts peat for horticultural products in Saint-Fabien, Quebec. Rochefort's restoration technique depends on the presence of an intact foundation that can be conditioned so that reintroduced sphagnum and brown mosses will promote peat growth. Thus far, restoration of early succession plants has been successful, but restoring the later successional plants requires additional time and work.

The area affected by Alberta's oil sand peatland extraction is much larger than the Saint-Fabien peatland and the production process has not left an intact reclamation foundation. Efforts to restore oil sand peatland have been unsuccessful.

Struzik also provides a comprehensive review of projects directed at reversing or stalling the destruction of peatland from warming permafrost. The mixture of approaches and the intense debates over unintended consequences are summed up by Rebecca Rooney, an aquatic ecologist at the University of Waterloo:

> if this continues without a clear wetland reclamation policy, we will have more than 65 percent less peatland and very little of the plant and animal life that existed there in the past. (p. 246)

Struzik describes the wide variety of environments in which peatlands exist and the large number of diverse projects proposed for their preservation, reclamation, and use. *Swamplands* closes by emphasizing the importance of developing an objective and consistent framework for evaluating the relative costs and benefits of pursuing one peatland restoration project over another. Large-scale comparative experiments, like Spruce and Peatland Responses Under Changing Environments (SPRUCE) managed by the U.S. Forest Service in Minnesota, will be essential for quantifying the costs of restoration, the value of ecosystem functions (e.g., storing carbon, filtering water, mitigating floods, and creating animal refuges), and the economic benefits of resource extraction over a range of environmental conditions.

Swamplands reminds us that each new energy source—peat, coal, and oil—was promoted as essential in its time. The book documents the environmental scars and cumulative effects that remain while we search for new energy sources. Most importantly, *Swamplands* contributes to discussions on how to create a sustainable future and avoid repeating past errors. Whether at home or the library, this book belongs on an accessible shelf next to Aldo Leopold's *A Sand County Almanac* (Oxford University Press, 1949) and Rachel Carson's *Silent Spring* (Houghton Mifflin, 1962). You will be referring to all three soon.

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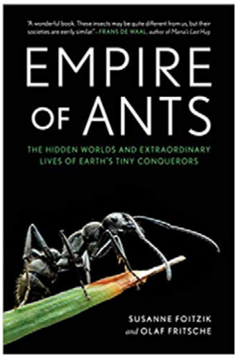
ENTOMOLOGY

Empire of Ants: the Hidden Worlds and Extraordinary Lives of Earth's Tiny Conquerors

By Susanne Foitzik and Olaf Fritsche. Translated by Ayça Türkoğlu. 2021. The Experiment. 352 pages, 36.50 CAD, Hardcover. Also available as an E-book.



I really enjoyed this book. Originally written in German by Susanne Foitzik, Ph.D. (an international authority on ants) and Olaf Fritsche, Ph.D. (a science journalist and biophysicist), this work is an entertaining treatise on why these insects deserve your attention. *Empire of Ants* is easy to read and has an excellent pace and flow. The authors have a sense of humour about their subject, and the playful writing is enjoyable and highly digestible. Credit for the exceptional writing is also owed to Ayça Türkoğlu, who translated *Empire of Ants* to English.

Typical of a nonfiction book, each of the 13 chapters has a central theme (e.g., Chapter 9, Milking It: Ants and Their Livestock) and is comprised of smaller subsections providing specific examples, interesting facts, or anecdotes. These subsections are short, on average two pages each, and many have amusing titles such as Take Me to Your Leader! and Sisters are Doing It for Themselves. Peppered throughout the book are stunning full-colour images. The custom watercolour ant art (by Susanne Foitzik) with accompanying captions that start each new chapter are a welcome and charming addition.

Empire of Ants is a book of ant miscellany executed perfectly. The authors provide both an overview of ant biology and the fascinating specifics—for example, how gene expression determines what an individual ant can or cannot do in the different phases of its life and the consequences of this biology (e.g., ants that cannot migrate when their colony needs to move, because their genes for moving are not active, must be carried by their sisters). Throughout the book, these examples are supported by well-placed photos. In one case, we find a photo of Sahara Desert Ant (*Cataglyphis bicolor*) assuming a characteristically compact 'suitcase' body position so that her sister can easily carry her to a new home (p. 56).

Predictably with insect books, there is a definite 'ick' factor here. This includes a chapter dedicated to unsettling forms of parasitism (such as tapeworms and zombie ants) and, of course, the obligatory mention of the Schmidt Sting Pain Index for all hymenopteran stings, which South American Bullet Ant (*Paraponera clavata*) tops (p. 23). But there is plenty new to me, too, including the concept of a social immune system that prevents colony infections through individual and collective behaviours, and details on ant pharmacology (e.g., leafcutter ants that employ antibiotics to protect their crop against fungus). The authors also provide interesting snippets on their research methods, including first-hand accounts of the challenges associated with digging up ant colonies and detailed instructions on how to dissect an ant brain. As is also typical of insect books, there is discussion of what we still don't know—whole species about which we have next to no information—and some discussion of invasive species and the consequences of their global conquests.

For readers eager to learn more, the authors have included a (non-exhaustive) list of references organized by chapter and specific research subtopic at the end of the book. I have no real criticism of *Empire of Ants*; it is an enjoyable read with excellent writing and useful accompanying images. If you want to know more about your tiny neighbours (who sometimes self-destruct or digest parts of their own brains), this is a great place to start.

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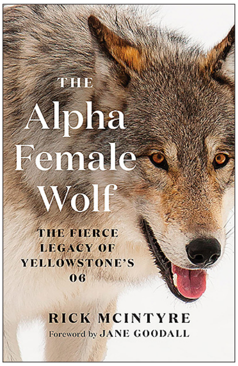
ZOOLOGY

The Alpha Female Wolf: the Fierce Legacy of Yellowstone's 06

By Rick McIntyre. 2022. Greystone Books. 280 pages, 34.95 CAD, Hardcover.



The Alpha Female Wolf, the fourth book in McIntyre's Alpha Wolves of Yellowstone series, picks up where *The Redemption of Wolf 302* (2021, Greystone Books) left off: in 2009, with an introduction to the 3.5 year old 06 Female, or 06F. This book is another page-turning read by McIntyre that will enthrall many readers, including supporters of nature, wolves, carnivores, wildlife, and national parks—especially Yellowstone. McIntyre provides extraordinarily detailed information on wild Gray Wolves (*Canis lupus*), and I was just as mesmerized reading *The Alpha Female Wolf* as I was with his first three books of the series (Way 2019, 2020, 2021).

McIntyre's documentation of the first 20 years of the wolf reintroduction program in Yellowstone has normalized terms for wolves that typically aren't considered in wildlife management jargon: individual, depression, emotional, friendship, play, anguish, joy, and happiness. Through years of observation, McIntyre has learned that wolves are social, sentient, intelligent animals that have a wide range of emotions just like people do. Despite the hardships wolves face in the wild, he shows how wolves live for their families and care deeply about each other, often playing to show affection (e.g., pp. 51, 55, 79, 203). This is in direct opposition to the way they are currently treated by the Rocky Mountain states surrounding Yellowstone that have long hunting seasons with minimal regulations on killing these ecologically important creatures.

According to McIntyre, female wolves are the undisputed leaders of wolf packs, despite conventional (but misinformed) wisdom that males are in charge (pp. xxiv, xxvii, 21, 28–29, 46, 211, 229). This book is refreshing and different, because the author's first three books all focussed on alpha males. This story centres on 06F, who was named for her birth year (pp. xxvii, 18). She was the fourth of seven generations of Yellowstone wolves that McIntyre and his colleagues followed from 1995 to 2015 (pp. xxvii, 230). She was a very independent wolf that didn't pair off with a male until she was ~4 years old, which in wolf years would be considered middle-aged. When she decided to get hitched, she chose two much younger brothers, 754M and 755M, both teenagers in human years (p. 24). 755M became the alpha male and bred with 06, despite 754M's larger size. 754M became a huge asset to the pack as he most often played with and took care of the pups, which were his nieces and nephews (e.g., pp. 64, 79, 83–84, 147–148). The group became known as the Lamar Canyon Pack, named for where the trio was first observed together. They turned out to be a very successful social unit, raising 100% (n = 13) of their pups to adulthood in the three years that 06 had litters (2010–2012).

McIntyre's descriptions are palpable, like you are there in Yellowstone Park with him (a place I have been to many times and have such a fond affection for). The book documents the lives of individual wolves in vivid detail as they hunt for prey—mainly Elk and bison—contend with competitors like Grizzly Bears, and interact with rival wolves. One wolf and one pack in particular—alpha female 686F from the Mollie's Pack—was a real threat to 06's family. 686F was quick to use violence, and her pack killed at least nine other wolves during her tenure (pp. 94, 100, 103, 111, 115, 119, 143, 182). McIntyre often compares 686F to the violent Druid Peak Pack wolf 40F (pp. 94, 115, 209), a major character in his first two books (Way 2019, 2020). Both females ruled their packs with an iron fist and many wolves died as a result. Violent 686F never had any known surviving pups during her tumultuous reign (p. 181).

Despite the danger from rival wolves, the Lamar Pack evaded fatal confrontations, even when standing up to their rivals in some very tense and dramatic moments (e.g., p. 124). 06 was the opposite of 686F, because her pack was not excessively aggressive to other wolves. This behaviour was more similar to famous alpha males, like 21M, that used cooperation over intimidation (pp. xxix, 100; Way 2020). In fact, the first time 06 was documented killing another wolf was when the Mollie's Pack trespassed in the Lamar Pack's territory (p. 141) after previously invading their den site a few months earlier (pp. 119–123). One could say that 06 was an extremely tolerant wolf until she had to protect the vital interests of her family.

The Alpha Female Wolf is arranged into six parts with each section focussed on a calendar year. This organization makes it easy to follow the saga of the park wolves over time, starting in late 2009 and ending in 2015. Given all of the wolves involved in the story, I am continually impressed with how McIntyre makes it manageable to digest the information without leaving out too many details. Further, due to his focus on female wolves in this book, at the end of select chapters McIntyre also returns to his first three books and recounts some of the original famous females, including (in order of appearance in the book): wolves 571F, 9F, 5F, 7F, 217F, 472F, Canyon White Female, 926F, 870F, and 42F. While much of the information is repetitive if you have read the previous books, these passages make *The Alpha Female Wolf* viable as a standalone text.

In later chapters, McIntyre writes about the deaths of 754M and 06 and the grieving that the Lamar Pack (pp. 159, 163) and the humans who watched them (especially McIntyre; pp. 160–161) had to deal with following the loss of these legendary wolves. I had difficulty reading this emotional section, even though I knew it was coming. After 06's passing, 755M had to leave the family he helped establish—he was the father to the rest of the females in the Lamar Pack, and wolves usually don't breed with relatives (pp. 168–169). The concluding chapters show him finding, then losing, other mates until he finally settles in the centre of the park, about 25 miles (40.2 km) from the Lamar Pack's territory, with a white female (pp. 202, 206, 217). These later chapters also describe one of 06's daughters, 926F, taking over as the alpha female of the Lamar Canyon Pack. She restarted the group with multiple males, including the four that killed her previous mate and the father of her 2015 litter. Even though she was a relatively small 37 kg, she dominated the four larger males that joined her pack (p. 229), similar to how her mother, 06, controlled 754M and 755M. That was more proof to McIntyre that females are the ones who really run a wolf pack, especially during the pup-rearing period (p. 229).

McIntyre provides unprecedented levels of detail on wolves throughout this easy-to-read tome on pack dynamics and interactions among individuals. I am amazed with the in-depth understanding that he and his colleagues have on the Yellowstone wolves. But this shouldn't be too much of a surprise, because McIntyre went out every day for over 15 years from 2000 to 2015. I just note some of his experiences here, so reading the full account in this book is a must.

I am continually captivated with McIntyre's Alpha Wolves of Yellowstone series. The first four volumes have now collectively detailed the first 20 years of wolf reintroduction in Yellowstone. Between 1995 and 1997, 41 wolves from Canada and Montana were transported to the area to repopulate the park; the species had been eradicated in the park in the last century due to extermination programs. I already anticipate the release of his fifth instalment in the series, which will likely pick up with 926F's gang and all of the other wolves living in the park in 2015. McIntyre's books are fascinating, because he expands upon his comprehensive field notes to offer insights and perspectives into the amazing wolf behaviours that he has been fortunate to witness over his illustrious career. These books are truly one of a kind and will likely never be replicated again for depth of investigating a particular species in the wild. For the sake of fans of nature and wolves, I hope McIntyre keeps pumping out these books. They are truly a treasure!

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Way, J. 2019. [Book Review] The Rise of Wolf 8: Witnessing the Triumph of Yellowstone's Underdog, by Rick McIntyre. Canadian Field-Naturalist 133: 180–181. https://doi.org/10.22621/cfn.v133i2.2407

Way, J. 2020. [Book Review] The Reign of Wolf 21: the Saga of Yellowstone's Legendary Druid Pack, by Rick McIntyre. Canadian Field-Naturalist 134: 392–393. https://doi.org/10.22621/cfn.v134i4.2739

Way, J. 2021. [Book Review] The Redemption of Wolf 302: from Renegade to Yellowstone Alpha Male, by Rick McIntyre. Canadian Field-Naturalist 135: 323–324. https://doi.org/10.22621/cfn.v135i3.2869

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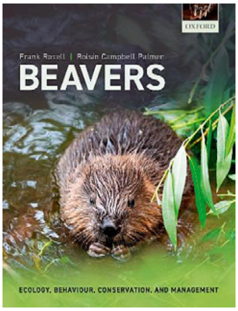
Beavers: Ecology, Behaviour, Conservation, and Management

By Frank Rosell and Róisín Campbell-Palmer. 2022. Oxford University Press. 512 pages, 110.00 CAD, Hardcover, 54.95 CAD, Paper. Also available as an E-book.



Eurasian Beaver (*Castor fiber*) was a mainstay of the fur trade that occurred a millennium or more ago in Europe and Asia where, eventually, it and other furbearers became scarce over a huge area. The search for new sources of fur (and fish) stimulated the discovery and exploitation of wildlife in the New World. In a mere three centuries, between 1600 and 1900, North American Beaver (*Castor canadensis*) was sought and removed from much of its natural range; it survived in only the most inaccessible regions of the continent. Reintroductions sourced from these remote areas after 1900 prevented its extinction and ensured its return to the wider landscape.

Now a detailed and data-rich book has been published, encompassing the significant studies of beavers that have taken place in the 21st century. The authors have included historical information spanning many centuries, but their emphasis is on biology. Improved marking, genetic studies, use of cameras mounted on drones or in a lodge, and landscape models have all contributed to an increased understanding of these large rodents and their habitats. Writing from Europe, the authors tackle both Eurasian Beaver and North American Beaver in one large volume. Reading this book from the land of *canadensis*, one might be skeptical of the result, but the authors carry it off successfully, speaking of all beavers when warranted and noting differences between the two species as needed. *Castor fiber* and *C. canadensis* are genetically distinct, but their lives are more alike than different. How people perceive them also does not vary greatly from continent to continent.

There are many children's books about beavers and quite a few popular and scientific accounts written in North America for adults since 2010. All reveal a fascination with beavers as builders or ecosystem engineers. This book expands the breadth of information available by dealing with the two species in 11 chapters, including the following: Beaver Morphology and Physiology (Chapter 3); Activity Patterns and Life History (Chapter 6); Territoriality, Communication, and Populations (Chapter 7); and Mortality and Morbidity (Chapter 8). Did you know that male beavers have a vestigial uterus? Or that the dried castor sacs sold to perfume manufacturers once contained urine? When it comes to the posterior of the beaver, no part of its unusual anatomy is left unexplained. Indeed, the depth of information throughout this book is excellent.

The reintroduction of native beavers to many European countries, including Scotland, (North American Beaver was successfully introduced into Finland and spread to Russia) and to the mountainous American West has stimulated considerable research in the receiving areas. (North American Beavers introduced to the far south of Argentina have spread to Chile, also stimulating research into the harms to native ecosystems in both countries.) Although Canada has a substantial portion of the world's beaver range, much of the North American research referenced in the book's 44 tables and 164 figures, including photographs, took place in the USA. For instance, in Chapter 8, only 7% of references were derived from research in Canada, although in Chapter 5, 13% of references do so. Perhaps the review of this chapter by Glynnis Hood of the University of Alberta and Ken Tape of the University of Alaska improved that result.

The success of beavers everywhere depends greatly on their interactions with people. Chapter 10 discusses the various techniques used to study beavers in the wild and how to raise them in captivity if needed. Chapter 11 (Living with Beavers: an 'Adorable Nuisance'?) discusses the wetlands formed behind every beaver dam versus those disappearing through human development projects, such as conversion to housing or agricultural use. As a charismatic flagship species, beaver conservation also helps countless other species like sedges, toads, and shrews. The authors muse about the successful reintroductions of Eurasian Beaver into Europe, where beaver hunting is banned, and the relaxation of laws needed to deal with human–beaver conflicts. In the future, they argue that it may be necessary to incorporate green spaces into urban areas to provide more habitats for beavers if populations are likely to expand.

The book is written in a scientific style for academics and professional biologists, but it will also be of interest to amateur naturalists. It includes a detailed Contents and a thorough Index. Each chapter has an extensive References section in the absence of the same at the end of the book, and colour photos make up the majority of the figures. There are occasional misspellings or words missing, which is not unusual in a lengthy book these days. The most grievous error is the use of 'exasperated' when 'exacerbated' was meant, and 'antidotal accounts' is more likely to be a result of autocorrect during editing (p. 391 and p. 423). There are indexing errors; for instance, Chile is not found on p. 387 and flagship species is not found on p. 406 or p. 423. These shortcomings are annoying. However, this work could stimulate more research on North American Beavers across their northern range (in Canada) and better define their role in carbon storage through build-up and storage of sediment and plant material. Just as carbon will persist for decades in rich meadows after beavers move on, this book's overall usefulness as a handy reference about all things beaver will also persist.

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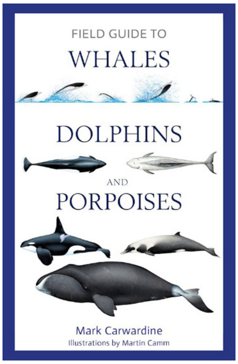
Field Guide to Whales, Dolphins and Porpoises

By Mark Carwardine. Illustrations by Martin Camm. 2022. Bloomsbury Wildlife. 288 pages, 29.00 CAD, Paper, 20.99 CAD, E-book.



The *Field Guide to Whales, Dolphins and Porpoises* is a nice little book that provides a wealth of handy information for identifying cetaceans in the field. It has many of the typical features that you would expect from any field guide: range maps, species descriptions, and a drawing of each species with key characteristics for identification. The author, Mark Carwardine, is a zoologist, wildlife photographer, and science communicator who has written more than 50 books on wildlife, including the precursor to this book, *Handbook of Whales, Dolphins and Porpoises* (Bloomsbury Wildlife, 2020). Unlike the precursor, which is a larger book that is much less portable in the field, this field guide is smaller and more portable.

Field guides are key tools for field biologists to help them with species identification. There are many things that biologists look for in a field guide, including: 1) portability and ability to withstand field conditions, 2) organization, and 3) accuracy and ability to guide the user to the correct species identification. Small books with durable covers and pages are key to satisfying the first requirement, but this is then traded off against the third requirement. There is often far more information available that could be included in a field guide to aid in species identification and provide background that many biologists would find interesting, but authors often must sacrifice relevant information for the sake of space. Organization may seem like an odd component to include in the list above, but a logical organization structure helps readers find information quickly. For example, species might be listed alphabetically, but is this done based on common name or scientific name? If using the common name, which common name, because there are often multiple common names for the same species? Worse still, sometimes multiple species have the same common name. Many biological field guides choose to order alphabetically first by a higher order of taxonomy, like family, and then within family, and then by either the species' scientific or common name. Some field guides do break this mould, though.

So, is *Field Guide to Whales, Dolphins and Porpoises* the one book to bring on a trip, to use up valuable room in your field bag, or perhaps is there a different book you should select? I will not be providing suggestions for other field guides: I leave that up to the individual user. But I will provide a breakdown of this field guide based on the above criteria. Note that in my own research, I mostly study Arctic marine mammals, so I draw heavily on my knowledge of these species when assessing the accuracy of the content.

Portability. This field guide is relatively small (22 × 14 × 1.5 cm, 288 pages), so clearly quite portable. It is a paperback with a glossy finish, and pages are slightly thicker than standard paper. This book could withstand repeated use in dry conditions, but would not stand up in moist field conditions. I would not recommend it for use in an open-hulled boat, and if brought out on a boat at all, it should stay indoors. For those studying whales from shore, this book could be a good choice, assuming it isn't foggy or raining.

Organization. I found myself questioning the organizational strategy of this field guide frequently. The baleen whales are lumped together, as are the toothed whales, and then porpoises. It would have been good to label these larger sections more clearly, and perhaps comment on the ordering in the introduction to the book. For example, Sperm Whales appear right after Humpback Whales, and other than a small label on the bottom denoting a change in taxonomic families, there is little way to tell that there has been a large jump in taxonomy, from baleen whales to toothed whales. Within these larger groupings, sections are labelled based on taxonomic family, but the order is not alphabetical. The species accounts within the sections for each family also follow an unknown organization, which is not alphabetical based on either species or common names. While all of this might seem like too much attention to detail, it does mean that readers have to spend more time flipping pages to find the species that they are looking for.

Accuracy. Overall, this guide is filled with a lot of very useful information. One of the most heavily used features of any field guide are the species illustrations, and the illustrations in this guide are excellent. They point out key features such as body size and shape, colour patterns, and dorsal fin and fluke (tail) shape for identification of the species in the field. A nice addition is the description of blow (water vapour expelled by the whale during an exhale), which can aid in species identification of cetaceans at a distance just based on the size and shape of their blow. The range maps are also good, although some provide more details than others and often lack consistency in terms of colouration and level of detail. For example, Bowhead Whales have four populations (or stocks), and all of these are colour-coded in the map. Meanwhile, Belugas have at least 18 populations, yet the Beluga range is shown as a single population with a single colour on the range map. One suggestion would be to highlight seasonal changes in the population range, as is typically done in field guides for birds. The level of detail within individual species accounts also varies. Many species have one or two pages, as would be expected for most field guides, yet certain more common or popular species, including Killer Whales and Humpback Whales, have many pages. Killer Whales, for example, have 14 pages devoted to them, which seems excessive. The International Union for Conservation of Nature (IUCN) status of each species is listed, and additional population-level status is also provided for some species. Note that the guide's introduction states that only the IUCN status is provided, but clearly this is not the case. For example, Belugas are listed as Least Concern by IUCN, but then the Cook Inlet population is listed as Endangered. I believe this status for the Cook Inlet population is specific to the United States *Endangered Species Act*, rather than IUCN. It seems odd to list one population with a more severe status, but not others, such as the St. Lawrence Estuary population of Belugas in Canada, which is listed as Endangered under Canada's *Species at Risk Act*. Similar examples can be found in multiple other species accounts, including Killer Whales, where the Strait of Gibraltar population is listed as Critically Endangered, but the southern resident Killer Whale population of the North Pacific is not listed, despite being Endangered in both the USA and Canada.

Two other areas could have used strengthening in this book. First, there are quite a few technical terms that remain undefined. The book has a glossary, so the author clearly attempted to deal with the jargon to some extent, but, for example, in the Killer Whale sections terms like 'resident' and 'transient' could have been more thoroughly explained. Also, the subject of acoustics is entirely missing. Marine mammals are some of the most vocally active species on the planet, and their vocalizations can often be a key feature in identifying them; many field-naturalists carry a hydrophone with them on the water for species identification. Including a sentence or two about common vocalizations would have been a good addition. Many bird field guides include short descriptions of vocalizations for each species.

Despite these criticisms, *Field Guide to Whales, Dolphins and Porpoises* is a wonderful resource for people to use in the field for identification of cetaceans, and also for reading at home to learn about the diversity of these interesting marine mammals.

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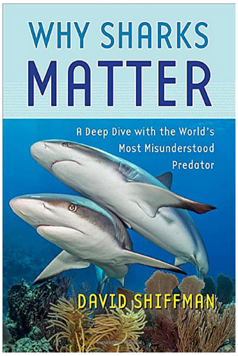
Why Sharks Matter: a Deep Dive with the World's Most Misunderstood Predator

By David Shiffman. 2022. Johns Hopkins University Press. 312 pages, 15 colour illustrations, and 34 black and white illustrations, 24.95 USD, Hardcover or E-book.



Why Sharks Matter is written by David Shiffman, a marine conservation biologist and postdoctoral researcher at Arizona State University with a lifelong passion for and dedication to sharks. The goals of this book, as stated in the introduction, are to teach the reader why sharks are remarkable, what benefits sharks bring, and what you can do to help protect them. Another stated aim is to teach the reader about various options for shark conservation and management, especially those supported by research data but not widely discussed in non-expert circles. Most of the book is dedicated to the latter subject, with a focus on population-level threats and data-driven decision-making.

A more accurate title for this book may have been "Shark Conservation and Management Strategies". Only one chapter covers the subject of the title directly—The Ecological Significance of Sharks (Chapter 3)—whereas the bulk of the book discusses conservation threats and strategies, and what is being done to help shark populations. If you are looking for a book primarily composed of shark miscellany to learn more about these fascinating species and their unique behaviours and adaptations, this is not that book.

The author's enthusiasm for sharks is obvious, and his humour and informal writing style are strengths. Myth-busting is a recurring topic, and the author's frustration with misconceptions about sharks, conservation threats, and management options is apparent throughout the book; it has the whiff of someone who has dealt with one too many Reddit Ask Me Anything sessions. Most sections of chapters are short, a few pages at most, and cover a wide breadth. As a result, the writing can come across as a bit scattered when subjects change abruptly. My favourite chapter was How are Scientists Helping Sharks? (Chapter 8), which includes short vignettes on various shark researchers and their areas of study, providing an inside look at conservation projects and practices.

While there are a few grey-scale images and diagrams embedded in the text, the other images referred to are found as numbered plates in a high quality colour insert, located in the middle of the book. In addition to the Bibliography, the book also has an accompanying website with supplementary information for the curious reader.

Although the writing can occasionally come across as defensive, the author clearly is an expert in his field. This book fills a niche as an accessible, plain-language introduction to shark conservation policy. *Why Sharks Matter* is best suited for those seeking a primer on shark conservation and population management issues and options, especially those interested in the American context. For those seeking an in-depth book about sharks' roles in the ecosystem and their behaviour or biology, I suggest looking elsewhere.

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NEW TITLES

Prepared by Jessica Sims

If you are interested in reviewing a book on this list, please contact Jessica Sims (bookrevieweditor@canadianfieldnaturalist.ca). This list covers a range of upcoming and new releases in field biology, ecology, and natural history. We also welcome your suggestions for new titles and offers to review unlisted books with a Canadian connection, including those on any species (native or non-native) that inhabits Canada, or books covering topics of global relevance, including climate change, biodiversity, species extinction, habitat loss, evolution, and field research experiences.

Please note: Books marked with a * have already been assigned to a *Canadian Field-Naturalist* reviewer. All other books are available for review and review copies of books marked with a † have been explicitly offered by publishers.

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

Biology

The Curious World of Bacteria. By Ludger Wess. Translated by Jamie McIntosh. 2023. Greystone Books. 224 pages, 29.95 CAD, Hardcover.

Evolution of the Ammonoids. By Kate LoMedico Marriott, Donald R. Prothero, and Alexander J. Bartholomew. 2023. CRC Press. 304 pages, 282.50 CAD, Hardcover, 112.95 CAD, Paper.

The Liars of Nature and the Nature of Liars: Cheating and Deception in the Living World. By Lixing Sun. 2023. Princeton University Press. 288 pages, 38.00 CAD, Hardcover. Also available as an E-book.

The Machines of Evolution and the Scope of Meaning. By Gary Tomlinson. 2023. Princeton University Press. 328 pages, 29.95 USD, Hardcover. Also available as an E-book.

Species Tree Inference: a Guide to Methods and Applications. Edited by Laura Kubatko and L. Lacey Knowles. 2023. Princeton University Press. 352 pages and 101 black and white figures, 138.00 CAD, Hardcover, 63.00 CAD, Paper, 49.99 CAD, E-book.

***Understanding Natural Selection.** Cambridge Understanding Life Series. By Michael Ruse. 2023. Cambridge University Press. 225 pages, 56.95 CAD, Hardcover, 22.95 CAD, Paper.

Botany

The Complete Language of Trees: a Definitive and Illustrated History. Complete Illustrated Encyclopedia Series. By S. Theresa Dietz. 2023. Wellfleet Press. 256 pages, 32.99 CAD, Hardcover.

Curieuses Histoires de Plantes du Canada, Tome 5: 1935–1975. Pour Alain Asselin et Jacques Cayouette. 2023. Septentrion. 336 pages, 49.95 CAD, livre de poche, 19.99 CAD, livre électronique.

In the Herbarium: the Hidden World of Collecting and Preserving Plants. By Maura C. Flannery. 2023. Yale University Press. 336 pages and 42 black and white illustrations, 45.50 CAD, Hardcover.

Orchid Muse: a History of Obsession in Fifteen Flowers. By Erica Hannickel. 2023. W.W. Norton. 320 pages, 47.00 CAD, Hardcover, 36.99 CAD, E-book.

Planta Sapiens: the New Science of Plant Intelligence. By Paco Calvo. With Natalie Lawrence. 2023. W.W. Norton. 304 pages, 38.95 CAD, Hardcover, 26.99 CAD, E-book.

Reproductive Biology of Angiosperms: Concepts and Laboratory Methods. By Yash Mangla, Priyanka Khanduri, and Charu Khosla Gupta. 2023. Cambridge University Press. 600 pages, 68.95 CAD, Paper. Also available as an E-book.

Tracking Giants: Big Trees, Tiny Triumphs, and Misadventures in the Forest. By Amanda Lewis. Foreword by Diana Beresford-Kroeger. 2023. Greystone Books. 264 pages, 24.95 CAD, Paper.

Trees: an Illustrated Celebration. By Kelsey Oseid. 2023. Clarkson Potter/Ten Speed. 160 pages, 23.99 CAD, Hardcover, 11.99 CAD, E-book.

Weeds of the Northeast. Second Edition, Revised and Expanded. By Joseph C. Neal, Richard H. Uva, Joseph M. DiTomaso, and Antonio DiTommaso. 2023. Cornell University Press. 608 pages, 1397 colour photos, and 123 black and white line drawings, 44.95 CAD, Paper.

Conservation and Climate Change

Against the Seas: Saving Civilizations from Rising Waters. By Mary Soderstrom. 2023. Dundurn Press. 296 pages, 26.99 CAD, Paper, 8.99 CAD, E-book.

The Anthropocene: 101 Questions and Answers for Understanding the Human Impact on the Global Environment. By B.L. Turner II. 2022. Agenda Publishing. 400 pages, 59.00 CAD, Paper. Also available as an E-book.

Big Bat Year: a Conservation Story. By Nils Bouillard. 2023. Pelagic Publishing. 288 pages, 33.99 CAD, Paper. Also available as an E-book.

Climate Change and Land: IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems. By the Intergovernmental Panel on Climate Change (IPCC). 2023. Cambridge University Press. 906 pages, 126.95 CAD, Paper. Also available as an E-book.

The Climate Crisis: Science, Impacts, Policy, Psychology, Justice, Social Movements. By Adam R. Aron. 2022. Cambridge University Press. 350 pages, 74.95 CAD, Hardcover, 39.95 CAD, Paper. Also available as an E-book.

Conservation Translocations. Edited by Martin J. Gaywood, John G. Ewen, Peter M. Hollingsworth, and Axel Moehrenschlager. 2022. Cambridge University Press. 400 pages, 137.95 CAD, Hardcover, 51.95 CAD, Paper. Also available as an E-book.

A Critical Assessment of the Intergovernmental Panel on Climate Change. Edited by Kari De Pryck and Mike Hulme. 2022. Cambridge University Press. 350 pages, 160.95 CAD, Hardcover. Also available as an E-book.

Crushed: How a Changing Climate is Altering the Way We Drink. By Brian Freedman. 2022. Rowman & Littlefield. 224 pages, 32.00 USD, Hardcover. Also available as an E-book.

***The Deadly Balance: Predators and People in a Crowded World.** By Adam Hart. 2023. Bloomsbury. 368 pages, 37.00 CAD, Hardcover, 25.90 CAD, E-book.

An Environmental Leader's Tool Kit. By Jeffrey W. Hughes. 2023. Cornell University Press. 264 pages, 26.95 CAD, Paper. Also available as an E-book.

Forces of Nature: a History of Florida Land Conservation. By Clay Henderson. 2022. University Press of Florida. 458 pages, 38.00 USD, Hardcover.

How to Fix a Broken Planet: Advice for Surviving the 21st Century. By Julian Cribb. 2023. Cambridge University Press. 130 pages, 18.95 CAD, Paper. Also available as an E-book.

In This Together: Connecting with Your Community to Combat the Climate Crisis. By Marianne E. Krasny. 2023. Cornell University Press. 216 pages, 29.95 CAD, Paper. Also available as an E-book.

The Living Planet: the State of the World's Wildlife. Edited by Norman MacLean. 2023. Cambridge University Press. 446 pages, 137.95 CAD, Hardcover, 57.95 CAD, Paper.

The Making of the Northwest Forest Plan: the Wild Science of Saving Old Growth Ecosystems. By K. Norman Johnson, Jerry F. Franklin, and Gordon H. Reeves. 2023. Oregon State University Press. 472 pages, 52.00 CAD, Paper.

Microplastics: Behavior, Fate, and Remediation. By John Pichtel and Mathew Simpson. 2023. Rowman & Littlefield. 416 pages, 110.00 USD, Paper. Also available as an E-book.

Mr. Mindbomb: Eco-hero and Greenpeace Cofounder Bob Hunter—a Life in Stories. Edited by Bobbi Hunter. Introduction by Captain Paul Watson. Afterword by Elizabeth May. 2023. Rocky Mountain Books. 304 pages, 30.00 CAD, Paper.

New Arctic Cinemas: Media Sovereignty and the Climate Crisis. By Anna Westerstahl Stenport and Scott MacKenzie. 2023. University of California Press. 368 pages, 107.00 CAD, Hardcover, 37.95 CAD, Paper, 29.99 CAD, E-book.

No Miracles Needed: How Today's Technology Can Save our Climate and Clean our Air. By Mark Z. Jacobson. 2023. Cambridge University Press. 454 pages, 16.95 CAD, Paper. Also available as an E-book.

Oil Beach: How Toxic Infrastructure Threatens Life in the Ports of Los Angeles and Beyond. By Christina Dunbar-Hester. 2023. University of Chicago Press. 227 pages, 128.95 CAD, Hardcover, 40.81 CAD, Paper, 29.99 CAD, E-book.

***The Power of Trees: How Ancient Forests Can Save Us if We Let Them.** By Peter Wohlleben. Translated by Jane Billinghurst. 2023. Greystone Books. 280 pages, 34.95 CAD, Hardcover.

†Racial Climates, Ecological Indifference: an Ecointersectional Analysis. By Nancy Tuana. 2023. Oxford University Press. 208 pages, 110.00 USD, Hardcover, 35.00 USD, Paper. Also available as an E-book.

†Re-envisioning the Anthropocene Ocean. Edited by Robin Kundis Craig and Jeffrey Mathes McCarthy. 2023. University of Utah Press. 344 pages, 123.50

CAD, Hardcover, 45.50 CAD, Paper. Also available as an E-book.

Remaking Society: a New Ecological Politics. By Murray Bookchin. Foreword by Marina Sitrin and Debbie Bookchin. 2023. AK Press. 242 pages, 29.95 CAD, Paper, 20.99 CAD, E-book.

***Ring of Fire: High-Stakes Mining in a Lowlands Wilderness.** By Virginia Heffernan. 2023. ECW Press. 224 pages, 26.95 CAD, Paper, 16.99 CAD, E-book.

Seeing the Forest for the Trees: Forests, Climate Change, and our Future. By Gordon Bonan. 2023. Cambridge University Press. 300 pages, 114.95 CAD, Hardcover, 56.95 CAD, Paper. Also available as an E-book.

Solastalgia: an Anthology of Emotion in a Disappearing World. Edited by Paul Bogard. Foreword by Glenn Albrecht. 2023. University of Virginia Press. 188 pages, 33.95 CAD, Paper, 24.99 CAD, E-book.

Tenacious Beasts: Wildlife Recoveries that Change How We Think about Animals. By Christopher J Preston. 2023. MIT Press. 328 pages, 39.95 CAD, Hardcover, 31.99 CAD, E-book.

Threatened and Recently Extinct Vertebrates of the World: a Biogeographic Approach. By Matthew Richardson. Foreword by Stuart L. Pimm. 2023. Cambridge University Press. 750 pages, 126.95 CAD, Hardcover. Also available as an E-book.

Universities on Fire: Higher Education in the Climate Crisis. By Bryan Alexander. 2023. Johns Hopkins University Press. 288 pages, 45.95 CAD, Hardcover. Also available as an E-book.

Urban Jungle: the History and Future of Nature in the City. By Ben Wilson. 2023. Knopf Doubleday Publishing Group. 304 pages, 41.00 CAD, Hardcover, 18.99 CAD, E-book.

Vanishing Sands: Losing Beaches to Mining. By Orrin H. Pilkey, Norma J. Longo, William J. Neal, Nelson G. Rangel-Buitrago, Keith C. Pilkey, and Hannah L. Hayes. 2023. Duke University Press. 272 pages, 33.95 CAD, Paper, 25.99 CAD, E-book.

Wildlife Stewardship on Tribal Lands: our Place is in our Soul. Edited by Serra J. Hoagland and Steven Albert. 2023. Johns Hopkins University Press. 432 pages, 77.95 CAD, Hardcover. Also available as an E-book.

ECOLOGY

The Hidden Company that Trees Keep: Life from Treetops to Root Tips. By James B. Nardi. 2023. Princeton University Press. 320 pages and 357 black and white illustrations, 38.00 CAD, Hardcover, 29.99 CAD, E-book.

Nature's Temples: a Natural History of Old-Growth Forests. Revised and Expanded. By Joan Maloof. 2023. Princeton University Press. 232 pages and 41 black and white illustrations, 24.99 CAD, Paper, 19.99 CAD, E-book.

Reflections Underwater: a Multidisciplinary Exploration of Coral Reef Wonders. By Oded Degany. 2023. Pelagic Publishing. 288 pages, 185 colour photos, and 12 figures, 47.00 CAD, Hardcover, 35.99 CAD, E-book.

Secret Life of the City: How Nature Thrives in the Urban Wild. By Hanna Bjørgaas. Translated by Matt Bagguley. 2023. Greystone Books. 264 pages, 32.95 CAD, Hardcover.

These Trees Tell a Story: the Art of Reading Landscapes. By Noah Charney. 2023. Yale University Press. 432 pages and 129 colour illustrations, 39.00 CAD, Paper.

†Trees and Woodlands. British Wildlife Collection. By George Peterken. 2023. Bloomsbury Wildlife. 416 pages and 300 colour photos, illustrations, and maps, 80.00 CAD, Hardcover. Also available as an E-book.

ENTOMOLOGY

Ants: a Visual Guide. By Heather Campbell and Benjamin Blanchard. 2023. Princeton University Press. 224 pages, 32.00 USD, Hardcover. Also available as an E-book.

Bees of the World: a Guide to Every Family. A Guide to Every Family Series. By Laurence Packer. 2023. Princeton University Press. 240 pages, 217 colour illustrations, 10 black and white illustrations, and 106 maps, 38.00 CAD, Hardcover, 29.99 CAD, E-book.

Of Cockroaches and Crickets: Learning to Love Creatures that Skitter and Jump. By Frank Nischk. Foreword by Carl Safina. 2023. Greystone Books. 232 pages, 32.95 CAD, Hardcover.

Common Bees of Western North America. By Olivia Messinger Carril and Joseph S. Wilson. 2023. Princeton University Press. 400 pages, 581 colour photos, and 198 black and white silhouettes, 49.50 CAD, Paper. Also available as an E-book.

†Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research. Second Edition. Edited by Alex Cordoba-Aguilar, Christopher Beatty, and Jason Bried. 2022. Oxford University Press. 496 pages, 130.00 CAD, Hardcover. Also available as an E-book.

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

Insects of North America. Princeton Field Guides Series. By John C. Abbott and Kendra K. Abbott. 2023. Princeton University Press. 592 pages and 3700+ colour photos and illustrations, 32.00 CAD, Paper, 24.99 CAD, E-book.

The Lives of Beetles: a Natural History of Coleoptera. The Lives of the Natural World Series. By Arthur V. Evans. 2023. Princeton University Press. 288 pages and 150+ colour illustrations, 44.00 CAD, Hardcover, 34.99 CAD, E-book.

What a Bee Knows: Exploring the Thoughts, Memories, and Personalities of Bees. By Stephen Buchmann. 2023. Island Press. 296 pages and 19 photos and illustrations, 39.00 CAD, Hardcover. Also available as an E-book.

HERPETOLOGY

Boas of the West Indies: Evolution, Natural History, and Conservation. By R. Graham Reynolds, Robert W. Henderson, Luis M. Díaz, Tomás M. Rodríguez-Cabrera, and Alberto R. Puente-Rolón. Foreword by Jonathan B. Losos. 2023. Cornell University Press. 288 pages, 122 colour photos, and 21 maps, 80.95 CAD, Hardcover.

Snakes of the World: a Guide to Every Family. A Guide to Every Family Series. By Mark O'Shea. 2023. Princeton University Press. 240 pages, 282 colour illustrations, and 53 maps, 42.50 CAD, Hardcover. Also available as an E-book.

ORNITHOLOGY

The (Big) Year that Flew By: Twelve Months, Six Continents, and the Ultimate Birding Record. By Arjan Dwarshuis. Foreward by Mark Obmascik. 2023. Chelsea Green Publishing. 256 pages, 29.95 CAD, Paper.

Field Guide to North American Flycatchers: Empidonax and Pewees. By Cin-Ty Lee and Andrew Birch. 2023. Princeton University Press. 168 pages, 55 colour and black and white illustrations, and 19 maps, 24.99 CAD, Paper, 19.99 CAD, E-book.

Flight Paths: How a Passionate and Quirky Group of Pioneering Scientists Solved the Mystery of Bird Migration. By Rebecca Heisman. 2023. HarperCollins. 288 pages, 37.00 CAD, Hardcover, 18.99 CAD, E-book.

The Last Cold Place: a Field Season Studying Penguins in Antarctica. By Naira de Gracia. 2023. Scribner. 256 pages, 36.99 CAD, Hardcover, 17.99 CAD, E-book.

†RSPB How to Photograph Garden Birds. By Mark Carwardine. 2023. Bloomsbury Wildlife. 176 pages and 250 colour photos, 35.00 CAD, Paper, 22.99 CAD, E-book.

†Warblers of Eastern North America. Second Edition. By Chris G. Earley. 2023. Firefly Books. 128 pages, 19.95 CAD, Paper.

A Year of Birdsong: 52 Stories of Songbirds. By Dominic Couzens. Illustrations by Madeleine Floyd. 2023. Rizzoli. 224 pages, 37.95 CAD, Hardcover, 20.99 CAD, E-book.

ZOOLOGY

Arctic Fox: Life at the Top of the World. By Garry Hamilton. Photography by Norbert Rosing. 2023. Firefly Books. 232 pages and 90 colour photos, 29.95 CAD, Paper. Also available as an E-book. Hardcover edition published in 2008.

Atlantic Salmon Treasury. 75th Anniversary Edition. Edited by Charles Gaines and Monte Burke. 2023. Goose Lane Editions. 240 pages, 45.00 CAD, Hardcover.

†The Badgers of Wytham Woods: a Model for Behaviour, Ecology, and Evolution. By David Macdonald and Chris Newman. 2022. Oxford University Press. 592 pages and 272 line figures and colour photographs, 286.00 CAD, Hardcover. Also available as an E-book.

Basic Illustrated Animal Tracks. Third Edition. Falcon Guides Series. By Jonathan Hanson and Roseann Hanson. Falcon Guides. 112 pages, 70 colour photos, 39 black and white illustrations, and 34 maps, 25.95 CAD, Paper, 19.99 CAD, E-book.

The Killer Whale Journals: our Love and Fear of Orcas. By Hanne Strager. Photography by Paul Nicklen. 2023. Johns Hopkins University Press. 280 pages, 38.95 CAD, Hardcover. Also available as an E-book.

Tooth and Claw: Top Predators of the World. By Robert M. Johnson III, Sharon L. Gilman, and Daniel C. Abel. Illustrations by Elise Pullen. 2023. Princeton

University Press. 352 pages and 206 colour and black and white illustrations, 57.00 CAD, Hardcover. Also available as an E-book.

OTHER

125 Nature Hot Spots in British Columbia: the Best Parks, Conservation Areas and Wild Places. Second Edition. By Lyndsay Fraser and Christina Smyth. 2023. Firefly Books. 272 pages and 300 colour photos, 29.95 CAD, Paper.

All Things Beautiful: Wonders from the Collections of the Florida Museum of Natural History. By Florida Museum of Natural History. Edited by Beverly Sensbach. Text by Heather Dewar. Photography by Kristen B. Grace. Design by Hollis H. Wooley. 2023. University Press of Florida. 360 pages, 81.00 CAD, Hardcover.

The Biomimicry Revolution: Learning from Nature How to Inhabit the Earth. By Henry Dicks. 2023. Columbia University Press. 320 pages, 46.00 CAD, Paper. Also available as an E-book.

Black Earth Wisdom: Soulful Conversations with Black Environmentalists. By Leah Penniman. 2023. HarperCollins. 352 pages, 33.50 CAD, Hardcover, 16.99 CAD, E-book.

The Correspondence of Charles Darwin. Volume 30 (1882). Edited by Frederick Burkhardt, James A. Secord, and the Editors of the Darwin Correspondence Project. 2023. Cambridge University Press. 766 pages, 143.95 CAD, Hardcover. Also available as an E-book.

The Devil's Element: Phosphorus and a World out of Balance. By Dan Egan. 2023. W.W. Norton. 256 pages, 40.00 CAD, Hardcover, 30.99 CAD, E-book.

The Earth Transformed: an Untold History. By Peter Frankopan. 2023. Knopf. 736 pages, 54.00 CAD, Hardcover, 18.99 CAD, E-book.

Enchanted by Daphne: the Life of an Evolutionary Naturalist. By Peter R. Grant. 2023. Princeton University Press. 360 pages, 44.00 CAD, Hardcover. Also available as an E-book.

Equity for Women in Science: Dismantling Systemic Barriers to Advancement. By Cassidy R. Sugimoto and Vincent Larivière. 2023. Harvard University Press. 272 pages, 45.50 CAD, Hardcover, 34.99 CAD, E-book.

Every Living Thing: the Politics of Life in Common. RSA Series in Transdisciplinary Rhetoric. By Jenell Johnson. 2023. Penn State University Press. 198 pages, 140.95 CAD, Hardcover, 24.95 USD, Paper. Also available as an E-book.

Lapidarium: the Secret Lives of Stones. By Hettie Judah. 2023. Penguin Publishing Group. 336 pages, 41.00 CAD Hardcover, 13.99 CAD, E-book.

The Lichen Museum. Art After Nature Series. By A. Laurie Palmer. 2023. University of Minnesota Press. 184 pages, 19 colour plates, and 21 black and white photos, 100.00 USD, Hardcover, 34.99 CAD, Paper, 24.99 CAD, E-book.

Nature on the Doorstep: a Year of Letters. By Angela E. Douglas. 2023. Cornell University Press. 256 pages, 26.95 CAD, Paper. Also available as an E-book.

Oceans under Glass: Tank Craft and the Sciences of the Sea. By Samantha Muka. 2022. University of Chicago Press. 240 pages, 45.50 CAD, Hardcover, 34.99 CAD, E-book.

Radical by Nature: the Revolutionary Life of Alfred Russel Wallace. By James T. Costa. 2023. Princeton University Press. 552 pages, 44.00 CAD, Hardcover. Also available as an E-book.

Resource Extraction and Arctic Communities: the New Extractivist Paradigm. Edited by Sverker Sörlin. 2022. Cambridge University Press. 350 pages, 143.95 CAD, Hardcover. Also available as an E-book.

A Ribbon of Highway: a Photographic Exploration of Canadian Identity. By Taylor Roades. 2023. Rocky Mountain Books. 176 pages, 40.00 CAD, Hardcover.

†RSPB Handbook of Garden Wildlife. Third Edition. By Peter Holden and Geoffrey Abbott. 2023. Bloomsbury Wildlife. 272 pages and 450+ colour photos, 27.00 CAD, Paper, 17.99 CAD, E-book.

Searching for Happy Valley: a Modern Quest for Shangri-La. By Jane Marshall. 2023. Rocky Mountain Books. 240 pages, 25.00 CAD, Paper.

The Secret World of Weather: How to Read Signs in Every Cloud, Breeze, Hill, Street, Plant, Animal, and Dewdrop. Natural Navigator Series. By Tristan Gooley. 2023. The Experiment. 400 pages, 23.50 CAD, Paper, 19.99 CAD, E-book.

Sensing Disaster: Local Knowledge and Vulnerability in Oceania. By Matthew Lauer. 2023. University of California Press. 292 pages, 107.00 CAD, Hardcover, 37.95 CAD, Paper, 29.99 CAD, E-book.

Snorkelling Adventures Around Vancouver Island and the Gulf Islands: the Ultimate Guide. By Sara Ellison. 2023. Harbour Publishing. 224 pages, 26.95 CAD, Paper.

Spring Rain: a Life Lived in Gardens. By Marc Hamer. 2023. Greystone Books. 216 pages, 32.95 CAD, Hardcover.

This is a Book for People Who Love Mushrooms. This Is a Book for People Who Love Series. By Meg Madden. 2023. Running Press. 128 pages, 22.00 CAD, Hardcover, 13.99 CAD, E-book.

The Vortex: an Environmental History of the Modern World. By Frank Uekötter. 2023. University of Pittsburgh Press. 848 pages, 104.00 CAD, Hardcover.

Wilder Journeys: True Stories of Nature, Adventure and Connection. Edited by Laurie King and Miriam Lancewood. 2023. Watkins Publishing. 224 pages, 27.95 CAD, Hardcover, 9.99 CAD, E-book.

Wildlife Weekends in Southern British Columbia: Day and Multi-day Trips from Vancouver for Wildlife Viewing. By Roy Jantzen. 2023. Rocky Mountain Books. 480 pages, 45.00 CAD, Paper.

Wolfish: Wolf, Self, and the Stories We Tell about Fear. By Erica Berry. 2023. Flatiron Books. 432 pages, 39.99 CAD, Hardcover, 16.99 CAD, E-book.

The Canadian Field-Naturalist

News and Comment

Compiled by Amanda E. Martin

Upcoming Meetings and Workshops

Society of Wetland Scientists Annual Meeting

The annual meeting of the Society of Wetland Specialists to be held 27–30 June 2023 at the Davenport Grand Hotel, Spokane, Washington. The theme of the conference is: 'Wetland Adaptation from Floodplains to Ridgelines'. Registration is currently open. More information is available at https://na.eventscloud.com/website/50365/.

The Animal Behavior Society Conference

The Animal Behavior Society Conference to be held 12–15 July 2023 as a hybrid event, with online content and an in-person meeting at the Oregon Convention Center, Portland, Oregon. Registration is currently open. More information is available at https://www.animalbehaviorsociety.org/2023/.

Mothapolooza

Mothapolooza to be held 14–16 July 2023 at the Highlands Nature Sanctuary, Bainbridge, Ohio. Registration is currently open. More information is available at https://www.arcofappalachia.org/mothapalooza.

The International Mammalogical Congress

The 13th International Mammalogical Congress, cohosted by the American Society of Mammalogists and the International Federation of Mammalogists, to be held 14–20 July 2023 as a hybrid event, with online content and an in-person meeting at the Dena'ina Civic and Convention Center, Anchorage, Alaska. Registration is currently open. More information is available at https://imc13.com/.

Botany 2023

Botany 2023 to be held 22–26 July 2023 as a hybrid event, with online content and an in-person meeting in Boise, Idaho. Registration is currently open. More information is available at https://2023.botanyconference.org/.

Northeast Partners in Amphibian and Reptile Conservation Annual Meeting

The Northeast Partners in Amphibian and Reptile Conservation Annual Meeting to be held 23–25 July 2023 at Wesleyan University, Middletown, Connecticut. Registration is currently open. More information is available at http://northeastparc.org/next-meeting-info/.

Mycological Society of America Annual Meeting

The annual meeting of the Mycological Society of America to be held 30 July–3 August 2023 as a hybrid event, with online content and an in-person meeting at the Little America Hotel and Convention Center, Flagstaff, Arizona. The theme of the conference is: 'Elevating Mycology'. Registration is currently open. More information is available at https://msafungi.org/2023-msa-annual-meeting-elevating-mycology/.

Conservation and Biology of Tortoises and Freshwater Turtles Annual Symposium

The 21st annual Symposium on the Conservation and Biology of Tortoises and Freshwater Turtles to be held 31 July–3 August 2023 in Charleston, South Carolina. Registration is currently open. More information is available at https://turtlesurvival.org/pages/symposium-2023.

Acadian Entomological Society Annual Meeting

The 80th annual meeting of the Acadian Entomological Society to held on 4 August 2023 as a hybrid event, with online content and an in-person meeting at the University of Prince Edward Island, Charlottetown, Prince Edward Island. Registration is currently open. More information is available at https://www.acadianes.ca/.

Ecological Society of America Annual Meeting

The 108th annual meeting of the Ecological Society of America to be held 6–11 August 2023 as a hybrid event, with online content and an in-person meeting at the Oregon Convention Center, Portland, Oregon. The theme of the conference is: ‘ESA for All Ecologists’. Registration is currently open. More information is available at https://esa.org/portland2023/.

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Compiled by William Halliday

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