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COVER: Southern Resident Killer Whale (*Orcinus orca*) female J35 carrying her dead calf. She carried her calf for 17 consecutive days, covering ~1600 km in the Salish Sea off the coast of Washington and British Columbia in July 2018. See the article in this issue by Shedd *et al.* pages 316–320. Photo: T. Shedd. Permit NMFS 21114.

The Canadian Field-Naturalist

Banded Killifish (*Fundulus diaphanus*) and Mummichog (*Fundulus heteroclitus*) distributions in insular Newfoundland waters: implications for a Species at Risk

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Abstract

Newfoundland's Banded Killifish (*Fundulus diaphanus*) population is listed as a species of Special Concern under Canada's *Species at Risk Act* and Vulnerable under *Newfoundland and Labrador's Endangered Species Act*. Mummichog (*Fundulus heteroclitus*) is a similar looking fish species and is currently under review by Newfoundland and Labrador's Species Status Advisory Committee. Both species have limited known distributions in Newfoundland waters that overlap. They may occur sympatrically in estuaries and occasionally hybridize; thus, field identifications can be challenging. We found that dorsal fin position and caudal fin depth were the most useful morphological characters for distinguishing Banded Killifish and Mummichog in the field. We used local ecological knowledge, literature review, museum records, and field surveys to update the known distribution ranges and found both species in more locations than previously documented in Newfoundland. Thus, we extend their known ranges. Our results will be critical in future status assessments of these species in Newfoundland.

Key words: Banded Killifish; distribution range; *Fundulus*; identification; Mummichog; Newfoundland; range extension; species at risk

Introduction

Oviparous cyprinodontiform fishes, commonly known as killifishes and topminnows, occur naturally on all continents except Australia and Antarctica and are common in fresh, brackish, and occasionally coastal seawater (Scott and Scott 1988). In North America, they extend as far north as southern Canada where there are three *Fundulus* species (family Fundulidae): Blackstripe Topminnow (*Fundulus notatus*), Banded Killifish (*Fundulus diaphanus*), and Mummichog (*Fundulus heteroclitus*; Houston 1990). There are two subspecies of Banded Killifish, the eastern subspecies (*Fundulus diaphanus diaphanus*) and the western subspecies (*Fundulus diaphanus menona*), both of which are present in Canada (Scott and Crossman 1973) but only the eastern subspecies occurs in Newfoundland. There are also two subspecies of Mummichog, the southern subspecies (*Fundulus heteroclitus heteroclitus*) and the northern subspecies (*Fundulus heteroclitus macrolepidotus*), of which only the latter occurs in Canadian waters (Able and Felley 1986). In Canada, Blackstripe Topminnow and the Newfoundland population of Banded Killifish were assessed as species of Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2012, 2014) and are listed as such under Canada's *Species At Risk Act* (SARA Registry 2019a,b). The Newfoundland population of Banded Killifish is also listed as Vulnerable under *Newfoundland and Labrador's Endangered Species Act* (Endangered Species List Regulations 2002). Throughout most of its distribution range Banded Killifish is considered Not at Risk (COSEWIC 2014; SARA Registry 2019b). The Newfoundland population's Special Concern and Vulnerable designations are due to a limited and clustered distribution in insular Newfoundland, which makes them vulnerable to catastrophic events and local disturbances (COSEWIC 2014). Also present in Newfoundland waters is Mummichog (Scott and Crossman 1973), whose status is currently under review by the Newfoundland and Labrador Species Status Advisory Committee (T. Knight pers. comm. 28 January 2016). Literature suggests Mummichog distribution is restricted to southwestern Newfoundland (Scott and Scott 1988).

Banded Killifish (Figure 1a) and Mummichog (Figure 1b) are both considered euryhaline, but Banded Killifish is more of a freshwater species, whereas Mummichog is more of a brackish-water species with only a few documented freshwater populations (Klawe 1957; Denoncourt *et al*. 1978; Scott and Scott 1988). Both species are very similar in appearance and may school together where sympatric populations occur in brackish waters (Scott and Crossman 1964). In addition, these two species have been reported to occasionally hybridize (Fritz and Garside 1974; Dawley 1992). These factors make field identification difficult, which may affect population studies and delineation of their respective distribution ranges (Fisheries and Oceans Canada 2011).

Little effort has been spent in delineating the distribution range of Banded Killifish in Newfoundland. Most early reports have been accidental discoveries by anglers and researchers studying other species (Chippett 2004). Localized surveys for Banded Killifish, conducted just prior to the 2003 COSEWIC assessment and update status report (in Terra Nova National Park [Cote *et al.* 2002]; Gros Morne National Park [Knight 2002]; Indian Bay watershed [Chippett 2004]), added only one watershed to their known distribution. Since 2006, the Mi'kmaq Alsumk Mowimsikik Koqoey Association (MAMKA) documented by-catch of Banded Killifish from the American Eel (*Anguilla rostrata*) commercial fishery in western Newfoundland (MAMKA 2006) and conducted Banded Killifish surveys (MAMKA 2011). However, except for a few earlier reports (e.g., Templeman 1951; Scott and Crossman 1964; Day 1993), there was no direct evidence of Banded Killifish at many of the locations presented in COSEWIC (2014).

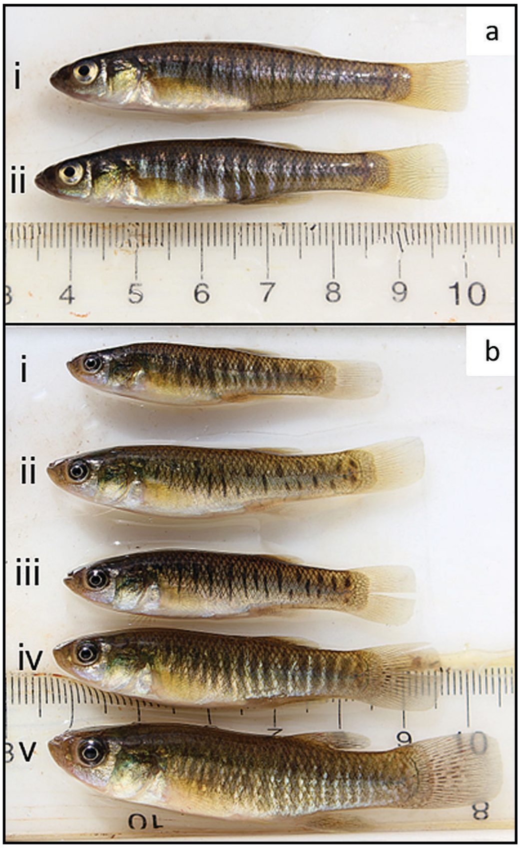

FIGURE 1. a. (i) Female and (ii) male Banded Killifish (*Fundulus diaphanus*); b. (i, iv, v) male and (ii, iii) female Mummichog (*Fundulus heteroclitus*), each exhibiting variations in banding patterns. Photos: Kate Dalley.

The objectives of this study were to determine the morphometric characters that allow for clear differentiation of Banded Killifish and Mummichog in the field and to update their known distribution ranges in insular Newfoundland waters. Field surveys, literature reviews, museum records, and local ecological knowledge (LEK) were used to update distribution ranges. Results from this study will provide new data that will help in the assessment on their listing status both at the federal and provincial levels.

Methods

A literature search was conducted for records of Banded Killifish and Mummichog in Newfoundland. Museums, including the Canadian Museum of Nature (CMN, Ottawa, Ontario [ON]), Royal Ontario Museum (ROM, Toronto, ON), Atlantic Reference Centre (ARC, St. Andrew's, New Brunswick [NB]), The Rooms Natural History Department (The Rooms, St. John's, Newfoundland and Labrador [NL]), Maurice Lamontagne Institute (MLI, Mont-Joli, Quebec [QC]), Ministère des forêts, de la faune et des parcs du Québec (Longueuil, QC), and Nova Scotia Museum (Halifax, Nova Scotia), were also contacted for reports of Banded Killifish. Federal fisheries officers from Fisheries and Oceans Canada, personnel from the Provincial Departments of Fisheries and Aquaculture, and Environment and Conservation, MAMKA river guardians, commercial eel harvesters, academic researchers, and local residents were contacted via telephone, e-mail, or in-person to gather local knowledge and determine potential locations of both species in Newfoundland. Pictures of the species were provided, and people contacted were asked if and where they had been observed. Maps were provided to assist the identification of drainage systems where *Fundulus* spp. were observed, where a 'drainage system' was defined as any water system with a separate drainage to the ocean. Several commercial eel harvesters were requested to retain Banded Killifish/Mummichog specimens captured in their fishing gear and, in some instances, incidental conversations with locals during field surveys were used to gather additional information. Information gathered from the aforementioned sources was used to plan field surveys and focus effort in general areas where there were reports of these species.

A total of 102 sites were sampled for Banded Killifish and Mummichog from 2013 to 2018. Most were sampled using four Gee Minnow Traps (42 cm L × 19 cm D, 22 mm opening, 6.4 mm mesh; Fillmore, New York, USA) that had been presoaked in saltwater for 24 h to remove the surface shine. Traps were each baited with 10 Original Ritz crackers (Mondelēz International, Toronto, Ontario, Canada). Additional opportunistic collection methods included minnow traps baited with sardines, fyke nets, hoop nets, dip nets, pole seines, LR-24 Electrofisher (Smith-Root, Vancouver, Washington, USA), and from stomach contents of Brook Trout (*Salvelinus fontinalis*) caught icefishing with baited hook and line, while other specimens were provided by local residents. Catches from each survey were identified, counted, and standard length (SL) measured. Samples of *Fundulus* spp. (typically 4–6 individuals) were preserved in 70% ethanol from each location for later analysis of morphological and meristic characters for species identification and museum archival. Most Banded Killifish and Mummichog specimens retained in this study were deposited at The Rooms, Provincial Museum of Natural History Annex (St. John's, NL), whereas those sent to the ARC (St. Andrew's, NB) for identification were deposited there (Table S1). Sampling data from this study has been submitted to the Ocean Biogeographic Information System (OBIS) for public archive. Reports of each species were verified using physical specimens or detailed photographs (Figure S1).

In the laboratory, meristic characters (Scott and Crossman 1964) and one morphological character (Scott and Scott 1988) were used to verify field identifications. Meristic characters (Table 1) included the number of dorsal fin rays, the number of gill rakers on the first gill arch, and the number of scale rows, and the stepped forward location (SFL) morphometric were used to identify the species (Table 1; Figure 2). Smaller juveniles were difficult to identify, and several other individuals showed a mix of characteristics suggesting the possibility of hybridization and were sent to L. van Guelpen (ARC) for species identification.

After initial identification of specimens collected from 2013 to 2016, additional morphological measurements were recorded as potential characters to differentiate species for individuals ≥27.5 mm SL in the field (Figure 2). Morphological characters identified from the literature to differentiate these species included the dorsal fin index (DFI; Scott and Crossman 1964; Table 1; Figure 2) and the ratio of the caudal peduncle depth (CD) relative to the distance from the dorsal origin to posterior end of vertebrae (DO–EV); the inverse of the ratio used by Fritz and Garside (1974) and Hernández Chávez and Turgeon (2007).

Data for Banded Killifish, Mummichog, and possible hybrids were plotted using SigmaPlot version 13.0 (Systat 2014) to determine the amount of over-

TABLE 1. Definitions of meristic and morphometric characters used to identify Banded Killifish (*Fundulus diaphanus*) and Mummichog (*Fundulus heteroclitus*) in Newfoundland. See Figure 2 for illustrations of the morphometric measurements.

Character type	Character	Description
Meristic	Number of dorsal fin rays (DFR)	Number of fin rays on the dorsal fin
Meristic	Number of gill rakers (GR)	Number of gill rakers on the first gill arch
Meristic	Number of scale rows (SR)	Number of scales in the longitudinal row from just posterior to the operculum to the end of the caudal peduncle
Morphometric	Caudal depth (CD)	Vertical distance from the dorsal to the ventral part of the caudal peduncle
Morphometric	Dorsal origin to posterior end of vertebrae (DO–EV)	Distance from the anterior origin of the dorsal fin to the posterior end of the vertebral column
Morphometric	Dorsal origin to tip of snout (DO–ST)	Distance from the anterior origin of the dorsal fin to the tip of the snout
Morphometric	Standard length (SL)	Distance from the tip of the snout to the posterior end of the vertebral column
Morphometric	Dorsal fin index (DFI)	Measure the DO–EV distance and subtract it from the DO-ST distance (see Scott and Crossman 1964)
Morphometric	Stepped forward location (SFL)	Measure the DO–EV distance and step that distance anteriorly from the anterior origin of the dorsal fin; the location on the head at which this measurement lands determines the species; if the location lands near the eye it was identified as Banded Killifish, whereas if it landed on the operculum it was identified as Mummichog (Scott and Scott 1988: 612)

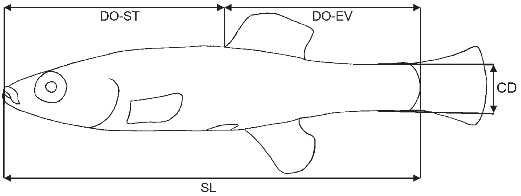

Figure 2. Morphological measurements recorded from killifish (*Fundulus* spp.) in insular Newfoundland. Abbreviations: CD = caudal depth; DO–EV = origin of dorsal fin to end of vertebrae; DO–ST = origin of dorsal fin to snout tip; SL = standard length.

lap of each character. Characteristics with <5% overlap were identified as the most useful for differentiating Banded Killifish and Mummichog.

Results

In general, Banded Killifish (Figure 1a) has a more slender and compressed body form with a more tapered mouth compared to Mummichog (Figure 1b). Mummichog has a stout, robust body form and deeper caudal peduncle compared to Banded Killifish. Females of both species exhibit thin vertical black bands along their sides, but on Mummichog, these bands, posterior to the anal fin, are usually shortened and do not span the width of the body (Figure 1). Males of both species do not have black bands but instead have alternating dark olive and lighter white/silver/blue bands during the breeding season that are closer together compared to bands of females (Figure 1).

From our measurements and analyses (Table S2; Figure S2), we developed the following identification key from the most useful meristic and morphometric characters. Individuals that exhibited characters that when keyed out did not clearly identify as either Banded Killifish or Mummichog were considered potential hybrids.

Number of gill rakers on the first gill arch, 4–7 (usually five); number of scale rows, 42–55; stepped forward location reaches just anterior to the eye to between the eye and operculum (usually middle of the eye); ratio of caudal peduncle depth relative to the distance between the origin of the dorsal fin and the end of the vertebrae, 0.15–0.25 .... Banded Killifish, *Fundulus diaphanus*

Number of gill rakers on the first gill arch 6–10 (usually eight); number of scale rows, 32–39; stepped forward location reaches posterior to the eye to posterior to the operculum (usually posterior operculum); ratio of caudal depth relative to the distance between the origin of the dorsal fin and the end of the vertebrae, 0.25–0.40 .... Mummichog, *Fundulus heteroclitus*

Two adult specimens from Little Paradise Park (>50 mm SL) and eight juvenile specimens (<20 mm SL) from Saltwater Pond sent to the ARC for identification could only be identified as *Fundulus* sp. (Table S2; Figure S2). The juveniles from Saltwater Pond appeared to be Mummichog but the adults from Little Paradise Park exhibited a mix of characters from both species (L. van Guelpen pers. comm. 13 June 2014; Figure S2).

We confirmed the presence of Banded Killifish at 45 sites within 35 drainage systems (Figure 3) and Mummichog at 30 sites within 24 drainage systems (Figure 4) in insular Newfoundland (Tables 2 and S1). From the 102 sites surveyed during this study, 30 and 18 were new (i.e., previously undocumented or unconfirmed from LEK and grey literature, such as internal reports; Table S1) for Banded Killifish and Mummichog, respectively. Locations were considered unconfirmed when grey literature and LEK lacked sufficient physical evidence for accurate species identification. Banded Killifish and Mummichog were not detected at 70 and 82 sites, respectively (Figures S3 and S4). Potential locations of Banded Killifish and Mummichog occur where unconfirmed reports were not investigated (Figures S3 and S4). Banded Killifish and Mummichog were detected sympatrically at two unnamed ponds that connect directly to estuaries at high tide: one near Little Paradise Park, St. Andrew's and the other near Stephenville Crossing (Table S1). When present, catch numbers from minnow traps ranged up to 102 individuals with catch per unit effort (CPUE) from 0.04 to 16.92 fish/h for Banded Killifish and up to 159 individuals with CPUE from 0.04 to 12.52 fish/h for Mummichog.

We found two unreported museum records for Banded Killifish (Burin and Gravels Pond; Table S1) and one unreported record for Mummichog (Terrenceville; Table S1). We also detected two erroneous reports of Banded Killifish from Star Lake and York Harbour, Newfoundland. The Star Lake record was reported by Chippett (2004) based on a personal communication, but we found that the original source indicated Banded Killifish was actually observed in Stag Lake (B. Dennis pers. comm. 9 January 2015). We sampled Stag Lake but could not confirm the presence of Banded Killifish. Fisheries and Oceans Canada (2011) and COSEWIC (2014) reported Banded Killifish from York Harbour, however, no specimens were retained from the original sampling, only photographs. Morphological features measured from these photos (Figure S1d–f) indicated Mummichog, not Banded Killifish. In addition, our surveys at this site yielded only Mummichog.

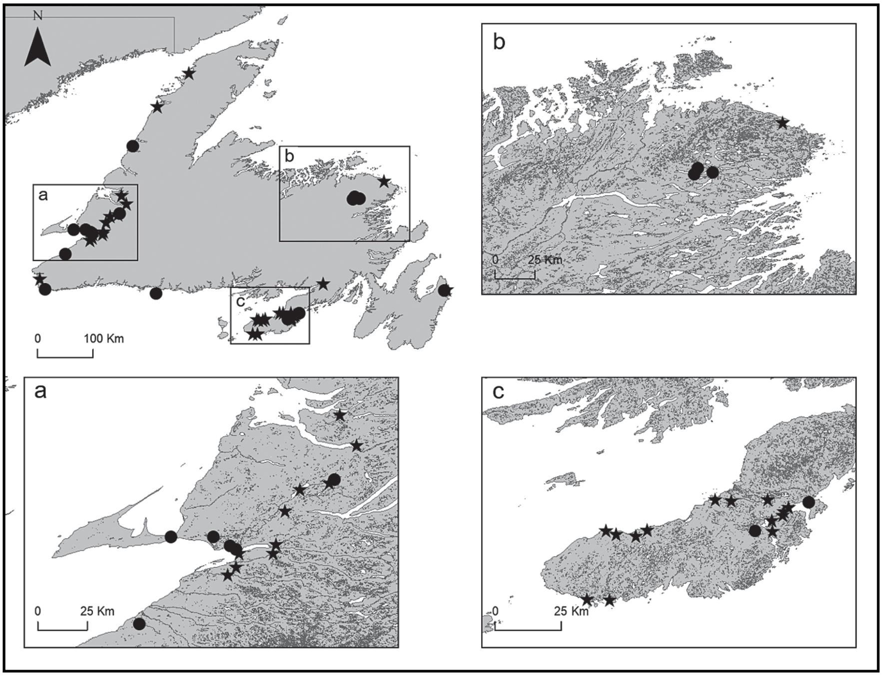

FIGURE 3. Confirmed locations of Banded Killifish (*Fundulus diaphanus*) in insular Newfoundland. ★ = locations confirmed through direct sample collection or samples provided by residents during this study. ● = locations confirmed by museum and literature records, or unpublished data with substantial evidence of species identification (e.g., high quality photographs).

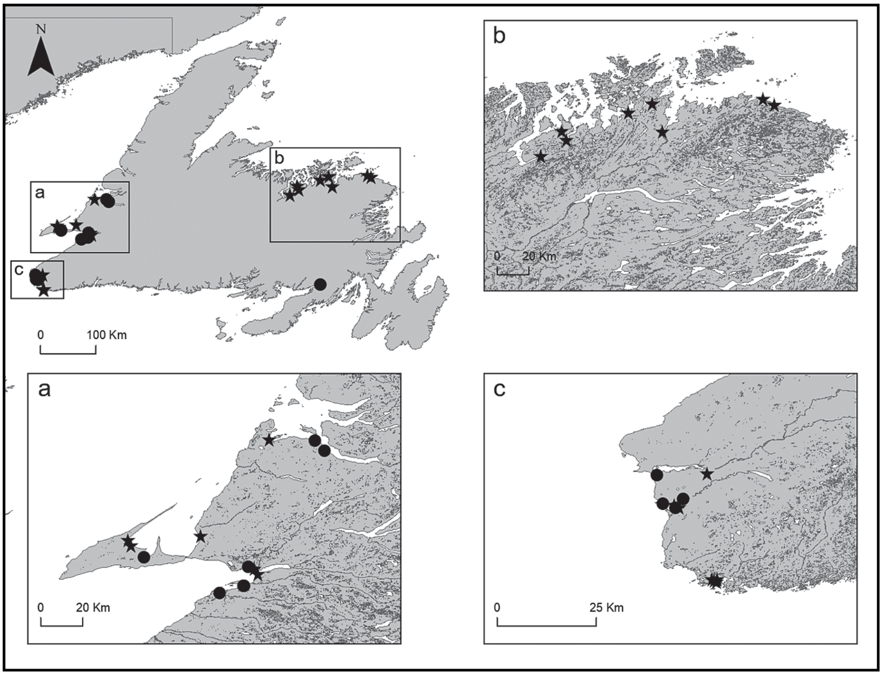

FIGURE 4. Confirmed locations of Mummichog (*Fundulus heteroclitus*) in insular Newfoundland. ★ = locations confirmed through direct sample collection or samples provided by residents during this study. ● = locations confirmed by museum and literature records, or unpublished data with substantial evidence of species identification (e.g., high quality photographs).

Table 2. Sources of site confirmations of Banded Killifish (*Fundulus diaphanus*) and Mummichog (*Fundulus heteroclitus*) in insular Newfoundland.

Species	Literature* only	Literature* with corresponding museum records	Museum records only	LEK with photos	Surveys confirming LEK	Surveys confirm-ing grey literature	Specimens provided by locals	Surveys alone	Totals
Banded Killifish	7	4	2†	2‡	10	0	2	18	45
Mummichog§	3	5	3	0	7	6	1	5	30

*Literature sources included: Johansen (1926); Templeman (1951); Scott and Crossman (1964); van Vliet (1970); Dickinson and Threlfall (1975); Gibson *et al*. (1984); Day (1993); Chippett (2004); Mann and Nambudiri (2005); Mitchell and Purchase (2014).

†One site (Burin) could not be counted in total as site co-ordinates were not provided with sample.

‡See Figure S1a–c used to confirm Banded Killifish reports from LEK (local ecological knowledge).

§Site confirmations based on LEK and grey literature (internal documents) were for reports believed to be Banded Killifish.

Discussion

As previously identified by Scott and Crossman (1964) and Hernández Chávez and Turgeon (2007), the number of scale rows along the lateral line was the most useful meristic character to differentiate these species, because there is no overlap. We found the stepped forward position and the ratio of caudal depth to the distance between the origin of the dorsal fin and the end of the vertebrae to be the most effective morphometric characters for differentiating these species in the field. These characters, previously identified by Scott and Scott (1988) and Fritz and Garside (1974), respectively, only require three measurements in the field, minimizing handling stress and even allow identifications from high quality lateral view photographs.

Several of our specimens could only be identified as *Fundulus* sp.; two individuals from Little Paradise Park (Little Codroy River estuary) were considered potential hybrids, as the species were sympatric in a pond that connects to the estuary near the collection site. Hybridization has been documented at two locations in Nova Scotia (Fritz and Garside 1974) but is probably more widespread (Hernández Chávez and Turgeon 2007). However, hybridization has yet to be confirmed in Newfoundland.

Several previously reported locations of Banded Killifish are likely in error due to misidentification. Similar to the erroneous York Harbour record, specimens were not retained from locations in West Bay of the Port au Port Peninsula (MAMKA 2011). We surveyed most of these West Bay sites and several were surveyed earlier by Johansen (1926) and van Vliet (1970) but only Mummichog were detected.

Our results greatly expanded the known number of locations for Banded Killifish and Mummichog in insular Newfoundland and extended their known ranges. We confirmed Banded Killifish at nearly four times as many sites in more than three times as many drainage systems as previously reported in COSEWIC (2014). Two new locations were considerably further north (77 and 146 km respectively), than previously reported (COSEWIC 2014) and we documented them in one additional drainage system on the northeast coast where only one was previously reported (Chippett 2004). We also corrected two Banded Killifish locations previously misreported by Chippett (2004) and Fisheries and Oceans Canada (2011) due to a miscommunication of a location and a misidentification of Mummichog, respectively. Mummichog was previously reported at ten locations from eight drainage systems along the southwest coast of insular Newfoundland (Johansen 1926; Scott and Crossman 1964; van Vliet 1970; Dickinson and Threlfall 1975; Scott and Scott 1988). We confirmed them at three times as many sites and drainage systems, including eight sites along the northeast coast where they have never been previously reported. The previously reported limited distributions of both Banded Killifish and Mummichog was most likely due to a lack of survey data; the new locations we identified highlight a general lack of basic aquatic biodiversity data for insular Newfoundland.

Banded Killifish can colonize new territory and expand their range when conditions are suitable. A population of Banded Killifish was reportedly introduced into a pond in the city of St. John's (east coast) in 1999 (Mitchell and Purchase 2014). In 2014, we detected a downstream expansion of this population into a lake but did not detect an expansion upstream likely because of a ~4 m high waterfall, which may present a significant barrier (Gibson *et al*. 1984). The expansion of this population over the last 20 years suggests resilience and the potential for population restocking (Mitchell and Purchase 2014) elsewhere if deemed necessary. Expansion of at-risk populations of Banded Killifish in the United States (Illinois) have also been reported (Mankowski 2012). Populations of the eastern and the western subspecies have been rapidly expanding in Lake Michigan since 2001 and the Mississippi

River since 2009 (Willink *et al.* 2018). Recent changes in environmental conditions within the Great Lakes due to introduced species and climate change may have benefited the eastern subspecies in this area, while the western subspecies may have been introduced into the Mississippi River (Willink *et al.* 2018).

In light of the expanded distribution we found, the status of Newfoundland's Banded Killifish population should be reassessed by COSEWIC. This population was initially designated as Vulnerable (renamed Special Concern since 2000; COSEWIC 2003, 2014) in 1989 (Houston 1989, 1990), based on only two known widely separated localities reported by Scott and Crossman (1964) and Gibson *et al*. (1984). The Special Concern status was maintained in the 2003 and 2014 assessments despite the addition of four locations (COSEWIC 2003) and five locations (COSEWIC 2014), two of which (Star Lake and York Harbour) we have found to be in error.

To date, targetted surveys for Banded Killifish have been extremely limited. Including the present study, fewer than 200 (<1%) of Newfoundland's ponds, lakes, brooks, and barachois have been surveyed specifically for Banded Killifish (see Gibson *et al*. 1984; Cote *et al.* 2002; Knight 2002; Chippett 2004; MAMKA 2006, 2011). Given the vast number of water bodies in insular Newfoundland, future sampling must be prioritized and optimized. Representative water bodies from each drainage system with suitable environmental conditions for Banded Killifish should be considered first. We recommend sampling: 1) areas with suitable habitat including shallow quiet waters of ponds and lakes with a sand, gravel, or detritus-covered bottom and patches of submerged aquatic plants (Scott and Crossman 1973); 2) water bodies in the lowest parts of each drainage system without steep gradients that may create barriers to upstream migration (Gibson *et al*. 1984); 3) using minnow traps baited with Ritz crackers, the most efficient sampling method for Banded Killifish and Mummichog >30 mm (SL) during our study; 4) when the water temperature is ≥17°C (Chippett 2004), typically between July and mid-September; and 5) during sunny days, when Banded Killifish were more readily observed during our study. Additionally, detection may depend on size of the water body surveyed. To increase chances of detecting Banded Killifish in larger water bodies, sampling effort should be increased proportionally to water body size. Future surveys should also explore the distribution of Banded Killifish on the northeast coast, as it is unclear how the species arrived there and how widespread it is in this region. To confirm the presence of hybrids in Newfoundland, morphometric and genetic data (both mitochondrial and nuclear sequence polymorphism) from specimens would have to be examined, as suggested by Hernández Chávez and Turgeon (2007).

Author Contributions

Writing – Original Draft: P.S.S.; Writing – Review & Editing: D.R.O., K.L.D., and P.S.S.; Conceptualization: P.S.S.; Investigation: K.L.D. and P.S.S.; Methodology: K.L.D. and P.S.S.; Formal Analysis: P.S.S.; Data Curation: P.S.S.; Project Administration: P.S.S.; Resources: P.S.S. and D.R.O; Supervision: P.S.S.; Validation: P.S.S. and K.L.D.; Funding Acquisition: P.S.S.

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TABLE S1. List of museum collection records of Banded Killifish (*Fundulus diaphanus*), Mummichog (*Fundulus heteroclitus*), and potential hybrids (*Fundulus* sp.) from insular Newfoundland.

TABLE S2. Meristics and morphometrics of Banded Killifish (*Fundulus diaphanus*), Mummichog (*Fundulus heteroclitus*), and potential hybrids (*Fundulus* sp.), collected throughout insular Newfoundland (2013–2016).

FIGURE S1. Photographs used to verify presence of Banded Killifish (*Fundulus diaphanus*) and Mummichog (*Fundulus heteroclitus*) in insular Newfoundland where physical specimens could not be acquired.

FIGURE S2. Frequency distributions comparing meristic and morphological characters of Banded Killifish (*Fundulus diaphanus*), Mummichog (*Fundulus heteroclitus*), and potential hybrids (*Fundulus* sp.) collected in insular Newfoundland (2013–2016).

FIGURE S3. Locations where Banded Killifish (*Fundulus diaphanus*) were not detected in insular Newfoundland.

FIGURE S4. Locations where Mummichog (*Fundulus heteroclitus*) were not detected in insular Newfoundland.

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Note

Epimeletic behaviour in a Southern Resident Killer Whale (*Orcinus orca*)

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Abstract

Southern Resident Killer Whale (SRKW, *Orcinus orca*) may be found year round in the Salish Sea. These orcas comprise three matrilineal pods (J, K, and L) and were listed as Endangered under the Canadian *Species at Risk Act* in 2003 and under the United States *Endangered Species Act* in 2005 because of prey scarcity, vessel noise and disturbance, small population size, and exposure to toxins. Since 1993, the Whale Museum has been operating Soundwatch, a boater education program for vessels. Soundwatch personnel are on the water in the central Salish Sea throughout the summer educating boaters on how to maneuver near marine mammals legally and documenting vessel regulation violations and marine mammal presence and behaviour. Starting on 24 July 2018, Soundwatch documented an adult female SRKW of J pod (J35) carrying a dead neonate calf. J35 continued to carry her dead calf for 17 consecutive days covering ~1600 km. Her story riveted the attention of the people of the Salish Sea as well as people around the world, evoking empathy for J35 and her loss as well as the plight of the Endangered SRKW population. Here, we tell her story and evaluate whether the behaviour J35 displayed toward her dead calf was an example of epimeletic behaviour, animal grief.

Key words: Animal grief; epimeletic behaviour; *Orcinus orca*; Southern Resident Killer Whale

The Southern Resident Killer Whale (SRKW) population is a distinct population of Killer Whale (*Orcinus orca*) that ranges widely along the west coast of North America. They aggregate in the summer months in the United States–Canada transboundary region of the Salish Sea near southern Vancouver Island; these waters include the Southern Strait of Georgia, Puget Sound, the Southern Gulf Islands, the San Juan Islands, and the Strait of Juan de Fuca (Hauser *et al.* 2007). SRKWs are a fish-eating ecotype of orcas that specialize primarily in Chinook Salmon (*Oncorhynchus tshawytscha*), which is estimated to make up 90% of their summer diet (Ford and Ellis 2006; Hanson *et al.* 2010). In the summer months, most SRKWs typically aggregate in the waters of the central Salish Sea, often along the western nearshore area of San Juan Island to feed on returning salmon runs (Ford and Ellis 2006; Hanson *et al.* 2010; Olsen *et al.* 2018).

SRKWs are socially segregated into three pods (J, K, and L), which are structured by matrilines (Parsons *et al.* 2009). Since 1976, the 74 whales making up the current (October 2020) population have been photo-identified, with each member given an identity based on unique physical characteristics, making each whale easily identifiable for tracking by the Center for Whale Research and others (J Pod = 24, K Pod = 17, L Pod = 33 individuals of all ages; Center for Whale Research 2020). In 2003, the SRKWs were listed as Endangered under Canada's *Species at Risk Act* (SARA; SARA Registry 2019) and, in 2005, the population was listed as Endangered under the United States *Endangered Species Act* (ESA; Krahn *et al.* 2004). Under SARA, the population's Critical Habitat was delineated as the transboundary waters of Haro Strait, Boundary Pass, the eastern portion of Juan de Fuca Strait, and southern portions of the Strait of Georgia (Fisheries and Oceans Canada 2017). Under the ESA, the population's critical habitat was established as all inland waters of Washington State, because of this area's importance to the whales for foraging for Chinook Salmon (Krahn *et al.* 2004).

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Three main risk factors have been identified as threatening SRKWs: limited prey, toxic contaminants, and vessel disturbance with its associated presence and noise pollution (Krahn *et al.* 2004). Studies in both Canada and the United States have shown that increased vessel traffic and incidents of boats not adhering to vessel regulations and/or whale guidelines regarding noise pollution near orcas are associated with an increase in the amount of time SRKWs spend travelling and, thus, a decrease in the amount of time spent foraging and resting (COSEWIC 2008; Lusseau *et al.* 2009; Noren, *et al.* 2009; Seely *et al.* 2017). In addition, this population is hypothesized to be most impacted by food limitation, with declines in Chinook Salmon strongly correlated with increased mortality, decreased fecundity, changes in social cohesion, and decreases in adult size (Ford *et al.* 2009; Parsons *et al.* 2009; Ward *et al.* 2009; Fearnbach *et al.* 2011; Foster *et al.* 2012; SRKW Workgroup 2020). In several recent cases, declines in the body condition of individual SRKWs have been documented preceding mortality (Fearnbach *et al.* 2018). In addition, reproductive success in SRKWs has been limited, with only seven successful births leading to young surviving between 2012 and 2019; 72% of the calves being male has resulted in a sexual skew in the population that limits its reproductive potential and chances of recovery (Center for Whale Research 2020; Marine Mammal Commission 2020).

Orcas and other animals with a high level of social structure are thought to have larger brains, with cognitive capacities similar to humans. SRKWs have been reported as staying in tight social structures or pods for their entire lives and often showing signs of affection and caring for each other, such as food sharing (Ford *et al.* 2009; Parsons *et al.* 2009; Ward *et al.* 2009). Furthermore, post-reproductive matriarch whales help kin raise their offspring, presumably to enhance the survival of younger females' offspring; they are also repositories of ecological information, such as foraging sites, that benefit the entire matriline (Wright *et al.* 2016; Nattrass *et al.* 2019).

Caring and emotional responses are thought to be an indicator of higher cognitive function (Simmonds 2006). Several animal species have been described as showing signs of emotions, such as stress, aggression, grief, and joy (Simmonds 2006). Emotions observed in cetaceans, particularly orcas, include parental love and prolonged grieving following the loss of a calf (Herzing 2000; Rose 2000). In fact, it is common enough that a term, epimeletic, is used to describe cetacean behaviour toward the dead or dying (Bearzi *et al.* 2017). Epimeletic refers to a range of behaviours displayed by distressed individuals in a social unit, such as a pod, including rescue attempts, attentiveness, postmortem carrying, carrying an impaired individual or surrogates for the dead, and other compulsive and apparently non-constructive behaviours (Bearzi *et al.* 2017). These behaviours are typically seen in healthy adults, usually females, and have no obvious benefit to the adult (Bearzi *et al.* 2017). Several reports of epimeletic behaviour in captive and free-ranging cetaceans exist, as well as several unpublished reports of SRKWs carrying dead neonates and one published record of epimeletic behaviour in orcas where a female (L72) was documented carrying a dead neonate in her mouth (Reggente *et al.* 2016, 2018; J. Hyde pers. comm. June 2019). Durban *et al.* (2016) also observed K27 carrying a dead neonate in their study on body condition.

The summer of 2018 was significant in the continued viability of the SRKW population because of the loss of three individuals. Here we report on J35 and her behaviour toward her dead neonate (see Appendix S1 for day-to-day field observations).

Soundwatch, an on-the-water boater education and research program, run through the Whale Museum in Friday Harbor, Washington, operates in the central Salish Sea in and around the Haro Strait Region (48°33′49.9″N, 123°13′47.7″W) from 1 May to 31 September under a federal research permit (National Marine Fisheries Service permit 21114; Seeley *et al.* 2017). Once J35 was observed carrying her dead neonate calf on 24 July, Soundwatch collaborated with other researchers and partners to observe and document her movements and behaviour (Figures 1 and 2). Our objectives were to (1) confirm the location of J35 daily, (2) confirm the presence or absence of her deceased calf at appropriate intervals, (3) monitor J35's health and behaviour, (4) work with whale watch companies to provide extra space as a protective buffer, and (5) educate private boaters on the unique situation. All data were collected by T.S. and A.N. and Soundwatch interns and volunteers. Identification of J35 was confirmed each day through binocular observations based on her natural individual markings.

J35 carried her dead neonate calf for 17 days, with Soundwatch directly tracking her location via the global positioning system (GPS) for eight days (88.8 h). Soundwatch was on the water with J pod for two days but did not directly monitor J35's position, resulting in only estimates of where she travelled. In addition, during this time there were seven days when J pod went west to the mouth of the Strait of Juan de Fuca and data received from Fisheries and Oceans Canada sightings indicated that the whales swam along the southern shore of Vancouver Island out to the mouth of the Strait of Juan de Fuca then back into the inland waters. From our GPS tracks and estimated route, we calculate that J35 carried her calf

FIGURE 1. Southern Resident Killer Whale (*Orcinus orca*) J35 carrying her calf on her rostrum while the calf was still buoyant. Photo: Taylor Shedd. Permit NMFS 21114.

FIGURE 2. Southern Resident Killer Whale (*Orcinus orca*) J35 carrying her calf by the pectoral fin in her mouth, making it difficult to determine proof of presence of the calf as it became more negatively buoyant. Photo: Taylor Shedd. Permit NMFS 21114.

for a minimum of 1090.57 km during the 17 days. Because J35, and her pod, were seen only a handful of times during one week in early August, she could have carried her calf for a minimum of ~1600 km.

J35 is not the first SRKW observed carrying a deceased calf, but this is the first documented case of a deceased neonate being carried for an extended period. In the past, other SRKW females (K27, J31, and L72), were observed carrying calves for a few hours or a few days (Durban *et al.* 2016; Reggente *et al.* 2016; J. Hyde pers. comm. June 2019). The extended duration in this case may be an example of epimeletic behaviour or behaviour consistent with grief and mourning; future incidents of this type of behaviour should be carefully documented.

There have been several other cases of odontocetes carrying calves in advanced stages of decomposition for days and even weeks (Bearzi *et al.* 2017; Reggente *et al.* 2018). Only primates have been known to carry dead infants as long as cetaceans (Bearzi *et al.* 2017). The benefit of this type of behaviour to the individual performing it is unclear, although it has been speculated to be initially adaptive, as being attentive and caring for a weak or sick neonate may aid in its recovery (Bearzi *et al.* 2017). The reasons for extending the carrying behaviour after the carcass is markedly decomposed and then stopping are difficult to explain, although it is plausible that the mother continues this behaviour because of the emotional challenge of accepting the loss of her young. It is this extended period of apparent grieving by J35 for her calf that makes this carrying instance noteworthy. Observations of J35's laboured breathing and falling behind her pod suggest that she was struggling to keep her calf with her (see Appendix S1). Perhaps the tight social structure of some odontocetes, such as SRKWs, may make it possible for mothers to carry dead calves for protracted periods because the pod may offer assistance. Assisting and caring behaviour, such as prey sharing (Wright *et al.* 2016), has been observed within SRKW pods; however, no such assistance was directly observed in this case.

SRKWs are Endangered. The loss of even a single individual is critical, because the population is small and reproductively failing (Wasser *et al.* 2017). Conservation actions and human intervention, such as policy changes to increase prey availability and reduce stressors such as pollutants and vessel noise, are needed. Empathy toward individual animals and even populations or species can influence the likelihood of pro-environmental behaviours (Young *et al.* 2018). The story of J35 that we describe drew attention to and empathy for J35 and the SRKWs from people throughout the Salish Sea region and around the world.

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APPENDIX S1. Field observations of J35, 24 July to 11 August 2018, and October 2020 update.

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Habitat use by Veery (*Catharus fuscescens*) in southern Ontario

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Abstract

Veery (*Catharus fuscescens*) is a breeding migrant thrush that nests throughout much of the temperate forests within Canada. Habitat loss and degradation is thought to be responsible for a steady decline in Veery populations since 1970. We studied habitat characteristics of occupied Veery territories versus unoccupied adjacent areas in southern Ontario during the 2016 breeding season. Occupied territories were characterized as riparian deciduous forests dominated by ash (*Fraxinus* spp.), Black Cherry (*Prunus serotina*), and Red Maple (*Acer rubrum)* trees with an understorey of Balsam Fir (*Abies balsamea*) and ferns (order Polypodiales); the presence of fruit-producing plants such as Riverbank Grape (*Vitis riparia*) and Bunchberry (*Cornus canadensis*) also was important.

Key words: *Catharus fuscescens*; nesting habitat; habitat use; Veery

Introduction

Veery (*Catharus fuscescens*) is a migrant thrush that breeds in Canada and the northern United States (Heckscher *et al.* 2020). According to the North American Breeding Bird Surveys, Veery has experienced a 25–50% population decline since 1970 in its breeding grounds in Ontario (Environment and Climate Change Canada 2017). The steady decline in Veery populations has warranted calls for a re-evaluation of the conservation status of Veery and further research on threats to their breeding habitat (Heckscher 2004, 2020).

Disturbances to forest structure and species composition can have a strong impact on the abundance and diversity of bird species in an area; therefore, it is important to have a detailed understanding of the habitat needs of individual bird species (Fleishman *et al.* 2003; Bennett *et al.* 2014; Meyer *et al.* 2015). Studies of habitat use in birds aim to describe how habitat features determine species abundance (Jones 2001). Although habitat use is largely determined by forest structure and species composition, additional factors include prey abundance, conspecific-attraction, and physical boundaries such as forest edges (Ramsay *et al.* 1999; Jones and Robertson 2001; Harper *et al.* 2005).

Preferred breeding habitat of Veery generally consists of large tracts of deciduous forest with riparian areas, but the species can also be found in second-growth forest fragments and mesic upland forests (Bertin 1977; Herkert 1995; Burke and Nol 2000). Previous studies have described the importance of a well-developed forest floor and shrub understorey as necessary for Veery foraging and nesting (Paszkowski 1984; Heckscher 2004; Kearns *et al.* 2006). However, Heckscher (2004) noted that more research is needed on particular mechanisms of habitat use for Veery with emphasis on regional studies to understand which plant communities are important for Veery conservation.

The objective of our study was to compare habitat characteristics of occupied Veery territories with adjacent unoccupied areas in mixed forests of the Great Lakes/St. Lawrence lowlands of southern Ontario, Canada. These data could help inform regional species-specific conservation and environmental management actions by describing habitat types and plant species associated with Veery territories.

Study Area

The study sites were situated within five forest tracts (mean area 0.35 km^2; range 0.15–0.86 km^2) located across a 150 km^2 area in the southern region of the Lake Simcoe watershed in south-central Ontario, Canada (44.2233°N, 79.3278°W). This area of

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the Lake Simcoe region is associated with a mix of large riparian areas, upland hardwood forests, and reforested Red Pine (*Pinus resinosa* Aiton) plantations (Harpley and Milne 1996). The research sites varied from relatively undisturbed forests and wetlands along the Black River and Zephyr Creek, to recreational public forests. The area has recently seen fairly widespread establishment of common invasive species including Dog-strangling Vine (*Vincetoxicum rossicum* (Kleopow) Barbaricz), Garlic Mustard (*Alliaria petiolata* (M. Bieberstein) Cavara & Grande; C.H., P.H., and R.M. pers. obs.), and Emerald Ash Borer (*Agrilus planipennis*; Marchant 2011).

Following a year of preliminary study and site selection in 2015, the study areas were selected for the presence of breeding Veery. The forest sites tended to be dominated by an overstorey of Sugar Maple (*Acer saccharum* Marshall), Red Maple (*Acer rubrum* L.), and ash (*Fraxinus* spp.). Additional tree species in these forest sites included Black Cherry (*Prunus serotina* Ehrhart), Ironwood (*Ostrya virginiana* (Miller) K. Koch), and Red Pine. Understories were well developed and included large numbers of Balsam Fir (*Abies balsamea* (L.) Miller), Alternate-leaved Dogwood (*Cornus alternifolia* L. f.), Common Buckthorn (*Rhamnus cathartica* L.), and saplings of Sugar Maple, Red Maple, and White Ash (*Fraxinus americana* L.).

Climate normals from 1981 to 2010 from the Udora weather station (44.2625°N, 79.1614°W), 15 km from the furthest field site, indicate that May 2016 had comparable temperature to the climate mean (13.5°C versus 12.2°C) and lower rainfall than the climate mean (31.2 mm versus 82.1mm). Similarly, June 2016 had comparable temperatures (17.8°C versus 18°C) and substantially lower rainfall (40.6 mm versus 106.6 mm) to the climate mean (Environment and Climate Change Canada 2016).

Methods

Bird surveys

Surveys occurred daily by one observer from 16 May to 1 July 2016 using transects at each of the five study areas (Calmé and Desrochers 2000; Kearns *et al.* 2006). We surveyed 16 transect routes in total each ~250 m in length. Each transect was walked at a steady pace over 30 min once a week for a total of seven weeks. Transect routes were arranged to cover as much accessible area as possible at each of these five study sites; transects within a site were located at least 1 km apart. Veeries were initially detected by sound, followed by visual confirmation when possible. The detection range on a transect was 300 m. We recorded the initial location of each bird on a handheld global positioning system (GPS) unit (Garmin eTrex 10; Garmin Ltd., Olathe, Kansas, USA; Kearns *et al.* 2006; Ballantyne and Nol 2011). Because the birds were not marked and to reduce the risk of double-counting, we excluded observations with similar GPS coordinates on adjacent transects; pairs were counted as a single observation (Kearns *et al.* 2006).

Sites were surveyed primarily during the morning from 0700 to 1100 EDT with occasional surveys completed during the evening from 1600 to 2000 because Veery vocalizes at both dawn and dusk (Heckscher 2007; Belinsky *et al.* 2012). We did not experienced problems detecting Veery later in the morning, when singing rates can decline, because the transect routes were done quite slowly over a small area and we detected at least one on each route. The survey period of 16 May to 1 July encompasses Veery arrival to nesting areas, breeding, and fledging of young (Robbins *et al.* 1989; Gauthier and Aubry 1996; Heckscher 2007; Heckscher *et al.* 2020). Surveys were not conducted when there was inclement weather, including any precipitation or strong winds (>28 km/h; Nol *et al.* 2005).

Veery territories were estimated using the plot mapping technique, where territory is approximated based on initial point observations taken during repeated visits along a transect route (Christman 1984; Jones and Robertson 2001). We used the "kernel density" function in ArcMap 10.4 (ESRI, Redlands, California, USA) to produce territory maps from the point observations based on the seven visits conducted at each site (Ferrato *et al.* 2017). Veery territories ($n = 12$) ranged in size from 0.2 to 0.8 ha (mean 0.31 ha) and did not overlap.

Vegetation sampling

Vegetation sampling was completed in July 2016, using a nested quadrat approach consisting of tree survey ($n = 24$: 12 in Veery territories and 12 in adjacent areas) and forest floor survey quadrats ($n = 93$: 57 in Veery territories and 36 in adjacent areas). To compare habitat characteristics between occupied territories and unoccupied adjacent areas, each Veery territory was paired with an available unoccupied adjacent area within the same continuous woodlot within each forest study area; thus, each pair was not subject to landscape level boundaries such as forest edges (Burke and Nol 2000). Unoccupied adjacent areas were circular and ~0.4 ha in size, to match the size of the Veery territories. The centre of an unoccupied adjacent area was chosen using a random number generator that determined direction (0–359º) from the centre of the paired occupied territory and distance (50–1000 m) from the edge of the paired territory or forest edges (Jones and Robertson 2001; Heckscher 2004). The maximum 1 km was chosen because the largest Veery territory was ~1 km wide. The minimum distance acts as a buffer area between the unoccupied adjacent areas and paired territory and 50 m was chosen because it is the approximate radius of a 0.4 ha circle.

Tree composition was surveyed with 250 m^2 (15.8 m × 15.8 m) survey quadrats centred on the mean point between all Veery observations in each territory as determined by the "meancenter" function in ArcMap. Another 250 m^2 tree composition plot was completed in the centre of the adjacent unoccupied area. All trees with >8 cm diameter at breast height (dbh) were counted within one of three size categories: small (8–22 cm dbh), medium (23–38 cm dbh), and large (>38 cm dbh). All individual trees and shrubs were counted by species within the forest quadrat area (Bergeron 2000). Three types of trees were counted in groups because we had low numbers of individual species despite the group being a large part of the forest: (1) ash, (2) poplar (*Populus* spp.), and (3) conifer (excluding Balsam Fir). Species in the conifer category included pine (*Pinus* spp.), spruce (*Picea* spp.), and Eastern White Cedar (*Thuja occidentalis* L.).

Forest floor quadrats were established within each of the 12 Veery territories and 12 adjacent unoccupied areas. Forest floor habitat was sampled with 0.25 m^2 Daubenmire quadrats (Daubenmire 1959) at randomly determined points using ArcMap's "create random points" function, which generated random GPS coordinates (Ballantyne and Nol 2011). We sampled larger Veery territories (0.4–0.8 ha, n = 7) with six sampling points and smaller territories (<0.4 ha, n = 5) with three sampling points. Three sampling points also were used in the adjacent unoccupied areas.

We measured percentage cover of: (1) forbs, (2) grass, (3) leaf litter, (4) bare ground, (5) fruit-producing plants, (6) moss, (7) water, (8) fern (order Polypodiales), (9) horsetail (*Equisetum* spp.), and (10) canopy cover in each Daubermire forest floor quadrat. We also counted (11) logs (>8 cm diameter), (12) dead trees (>8 cm diameter), (13) vines, and measured (14) canopy height. As well, landscape-level variables included (15) minimum distance to edge, (16) minimum distance to water, and (17) forest patch size. In our estimation of vegetation cover for forest floor quadrat surveys, we combined all fern species into one category that included primarily: Ostrich Fern (*Matteuccia struthiopteris* (L.) Todaro), Sensitive Fern (*Onoclea sensibilis* L.), and Bracken Fern (*Pteridium aquilinum* (L.) Kuhn). We noted several fruit-producing plant species which we observed Veeries consuming (C.H. pers. obs.) that we also combined. The dominant species were Canada Mayflower (*Maianthemum canadense* Desfontaines), Woodland Strawberry (*Fragaria vesca* L.), Riverbank Grape (*Vitis riparia* Michaux), and Bunchberry (*Cornus canadensis* L.).

Statistical analyses

Statistical analyses were performed using the "vegan" (Oksanen *et al.* 2015) package in R 3.3.0 (R Core Team 2016). Habitat variables which were not normally distributed according to Shapiro-Wilk tests in R were transformed using log transformations (Ramsay *et al.* 1999). Mean and SE values are presented as untransformed data to allow for clear interpretation.

We compared occupied territories versus unoccupied adjacent areas using principal components analysis (PCA) with the "prcomp" function in R (Ramsay *et al.* 1999; R Core Team 2016). Sites were evaluated based on measurements within the following categories: (1) physical forest characteristics (e.g., canopy height, leaf litter amount) and (2) tree and shrub species (Ramsay *et al.* 1999; Calmé and Derochers 2000; Dellinger *et al.* 2007). We generated PCA biplots for both forest physical characteristics and forest species using the first and second principal components (PC1, PC2) generated during each respective analysis. On the PCA biplots, we plotted 95% confidence ellipses to visualize the variance of occupied territory compared with the variance of available territory. We also compared values for each habitat forest characteristic between occupied and available territory using two-tailed paired Wilcoxon tests (Ramsay *et al.* 1999).

Results

We surveyed 12 Veery territories paired with 12 unoccupied adjacent areas across the five study areas. Tree species composition widely varied across each of the forest sites. Across all Veery territories, 28 species of trees were observed with an average of 8.4 tree species in each territory. Between territories and unoccupied adjacent areas, we found three significant (P < 0.05) differences (Table 1) after adjusting P-values using the Holm-Bonferroni method (Holm 1979). Veery territories had higher mean abundance of Black Cherry trees, a greater number of logs, and a lower number of medium sized trees (23–38 cm dbh).

Principal components analysis (PCA) of physical forest characteristics generated three principal components which explained 57.72% of the total variance (Table 2). PC1 explained 26.26% of the total variance and had high negative loadings from canopy height, canopy cover, leaf litter cover, and number of large-sized trees (≥38 cm dbh). Therefore, PC1 likely differentiates second-growth forest from mature forest communities. PC2 explained 18.01% of the total variance and had high positive loadings from fern cover, moss, number of logs, and number of vines, suggesting that this component is describing humid, riparian habitat. PC3 explained 13.45% of the total variance and likely describes riparian habitat with high negative

TABLE 1. Comparison of habitat between occupied territories and adjacent, unoccupied areas. Veery (*Catharus fuscescens*) territories ($n = 12$) were paired with nearby unoccupied adjacent areas ($n = 12$) in the same forest patch. Comparisons were made using two-tailed paired Wilcoxon signed-rank tests. Non-normal data were log transformed for analysis, but original, untransformed data are shown in table.

Variable	Occupied sites Mean ± SD	Unoccupied sites Mean ± SD	*P*
Fruiting plants (%)	21.48 ± 14.65	9.00 ± 11.96	0.8712
Fern (%)	21.52 ± 24.76	3.00 ± 8.38	0.6534
Canopy cover (%)	79.18 ± 12.24	48.23 ± 33.63	0.2065
No. medium trees (23–38cm dbh)	1.94 ± 0.95	4.20 ± 1.91	0.0430
No. logs	9.43 ± 4.36	2.60 ± 1.84	0.0018
No. Black Cherry (*Prunus serotina*)	1.59 ± 1.10	0.07 ± 0.21	0.0037
No. dogwood	2.63 ± 2.28	0.60 ± 0.80	0.2426
No. Red Maple (*Acer rubrum*)	2.74 ± 2.56	0.80 ± 1.33	0.8157

TABLE 2. Eigenvectors from principal components analysis of habitat structure between Veery (*Catharus fuscescens*) territories and unoccupied adjacent areas. Non-normal data were log transformed. Only the first three principal components are included.

Variable	Principal Components		
	PC1	PC2	PC3
Forbs	−0.0327	0.2465	−0.0696
Grass	0.1541	−0.2568	−0.2148
Leaf litter	−0.3896	−0.1353	0.0227
Bare ground	0.2730	0.0641	−0.3699
Berries	−0.0391	0.2152	−0.2123
Moss	0.2576	0.3142	−0.2052
Standing water	0.1647	−0.0725	0.5384
Fern	0.1234	0.3841	0.1493
Horsetail	−0.3337	0.0774	0.1244
Canopy cover	−0.3501	0.2362	−0.0550
Small trees (8–22cm dbh)	0.2451	0.0223	0.3129
Medium trees (23–38cm dbh)	0.0828	−0.4284	−0.1318
Large trees (>38cm dbh)	−0.3095	0.1664	−0.0105
Canopy height	−0.3675	−0.1096	−0.1935
Logs	−0.2145	0.0503	0.0503
Dead trees	−0.0187	0.4764	0.4764
Vines	0.2285	0.3719	−0.1071
Eigenvalue	2.2916	1.8982	1.6399
Cumulative proportion (%)	26.26	44.27	57.72

contributions from dead trees and standing water and a positive contribution from bare ground cover. The PCA biplot of physical forest characteristics with confidence ellipses ($P < 0.05$) shows a distinction between occupied Veery territories and adjacent areas based on the first two principal components (Figure 1).

PCA of forest tree species generated three principal components which explained 55.4% of the variance (Table 3). PC1 explained 28.81% of the total variance which was composed of high loadings by riparian species including poplar, Red Maple, and alder (*Alnus* spp.) and strong negative components of upland forest species: Sugar Maple, American Beech (*Fagus grandifolia* Ehrhart), and Basswood (*Tilia americana* L.). PC2 explained 15.64% of variance composed of high contributions by deciduous tree species and a strong negative contribution from non-Balsam Fir conifers. PC3 explained 10.95% of the variance and was composed of positive components from lowland species including alder and Paper Birch (*Betula papyrifera*

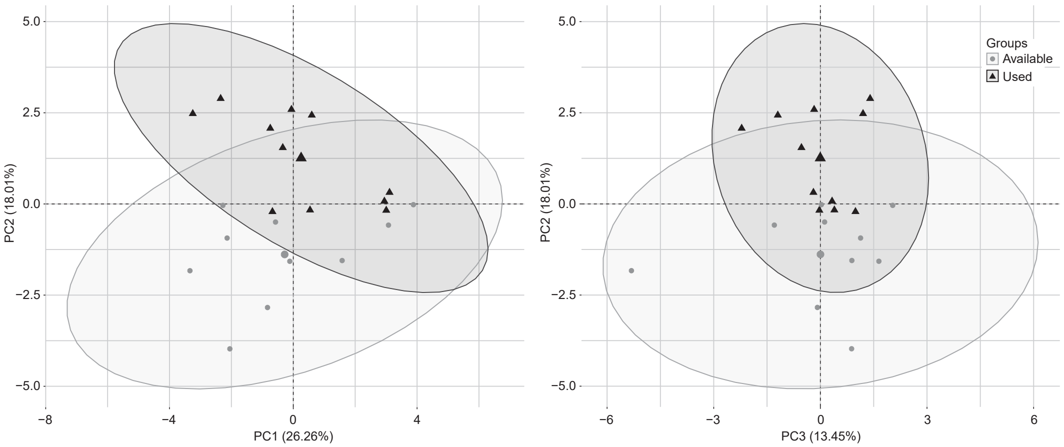

FIGURE 1. Biplots of PC1, PC2, and PC3 scores from principal components analysis (PCA) of habitat structure between Veery (*Catharus fuscescens*) territories and unoccupied adjacent areas in the Lake Simcoe watershed, Ontario, 2016.

TABLE 3. Eigenvectors from principal components analysis of forest tree species between Veery (*Catharus fuscescens*) territories and adjacent unoccupied areas. Non-normal data were log transformed. Only the first three principal components are included.

Variable	Principal Components		
	PC1	PC2	PC3
Alder	0.3151	−0.0515	0.2954
Ash	0.0825	−0.2799	0.0245
Basswood	−0.2732	−0.2199	0.0723
Beech	−0.2719	−0.3019	0.1146
Birch, Paper	0.2104	0.1629	0.5171
Buckthorn	0.2614	−0.2218	0.0471
Cherry, Black	0.1907	−0.4612	−0.2637
Conifer (Cedar, Pine, Spruce)	−0.0172	0.4296	−0.0370
Dogwood	0.2620	−0.3489	0.1086
Fir, Balsam	0.1914	−0.0480	0.1743
Maple, Red	0.3500	−0.2189	−0.1575
Maple, Sugar	−0.4100	−0.2206	0.0491
Ironwood	−0.2439	−0.2757	0.3574
Oak, Red	0.0863	−0.0075	−0.5887
Poplar	0.3651	0.0996	0.0980
Eigenvalue	2.0789	1.5317	1.2812
Cumulative proportion (%)	28.81	44.45	55.40

Marshall) and a strong negative component from Red Oak (*Quercus rubra* L.), a prominent upland species. The PCA biplot of tree species with confidence ellipses ($P < 0.05$) shows a distinction between occupied Veery territories and adjacent areas based on the first two principal components (Figure 2).

Discussion

The results support the hypothesis that there are components of habitat structure and species composition that are significant predictors of Veery habitat use. We found Veery generally occupied sites characterized by the multivariate analysis as second-growth, having low, open forest canopies with standing water and little leaf litter, and few mature trees. In our study area, second-growth habitat was either degraded, regenerating forests, or forests located on floodplains, adjacent to rivers and wetlands. LaRue *et al.* (1994) also found that Veery occupied second-growth forest, could tolerate disturbed sites, and was associated with

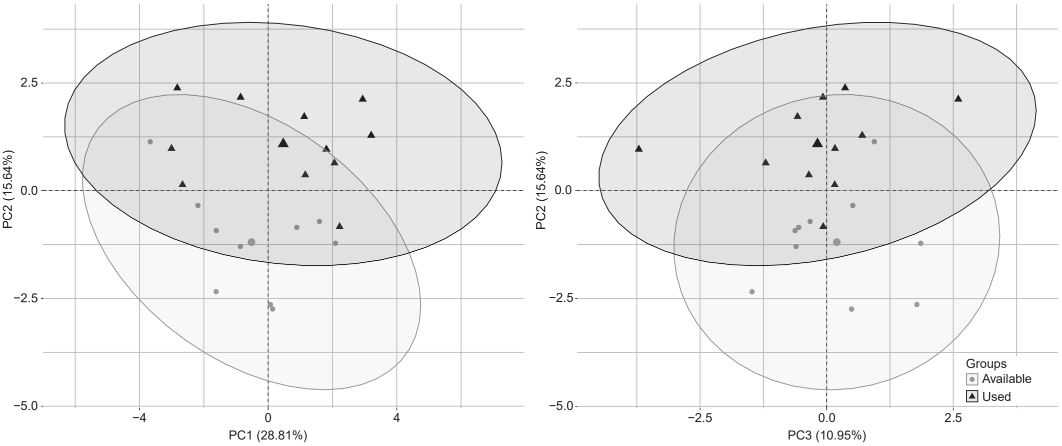

FIGURE 2. Biplots of PC1, PC2, and PC3 scores from principal components analysis (PCA) of forest tree species between Veery (*Catharus fuscescens*) territories and adjacent unoccupied areas in the Lake Simcoe watershed, Ontario, 2016.

riparian habitats. Humid, riparian forests in our study areas were characterized by a forest floor covered by fern and moss, and abundant Riverbank Grape vines hanging from Red Maple, alder, poplar, dogwood, and buckthorn. Our multivariate analysis highlights many of these same features in Veery occupied areas. Veery was found in areas with a high ground cover of fern and moss, as well as large numbers of vines and logs (Table 2) and was associated with each of these riparian tree species (Table 3). Golet *et al.* (2001) highlights Red Maple swamps as an important habitat for Veery.

Our multivariate analyses of tree species composition indicate that Veery were more likely to occupy deciduous forest communities as opposed to coniferous or mixed forests (Table 3). These results are also consistent with findings by Thompson and Capen (1988), who found that Veery was a resident of deciduous, heavily forested habitat with dense understorey. In our study, Veery territories were most commonly located in forests with an overstorey of ash trees and Red Maple (Figure 2). Forests dominated by ash trees and Red Maple most strongly covaried with Black Cherry, American Beech, Ironwood, and dogwood trees. One notable exception to the preference for deciduous trees was the widespread abundance of understorey Balsam Fir in Veery territories. Kearns *et al.* (2006) found that although Veery frequently nested in the dense forest understorey, they also nested within the lower sections of Balsam Fir up to 4 m tall. Veery constructs nests low to the ground in the protection of dense understorey as noted by Heckscher (2004). Thus, we consider Balsam Fir to be a species that significantly contributes to Veery habitat as an understorey species.

Veery primarily forages on insects and to a lesser extent, fruit during the breeding season (Wolfe *et al.* 2014; Heckscher *et al.* 2020). However, Veery and other *Catharus* species readily consume grapes when available, from wild Riverbank Grape or even wine grape vineyards (Beal 1915; Jubb and Cunningham 1976; C.H. pers. obs.). Of the 28 species of tree observed in Veery occupied areas, Black Cherry was the most dominant fruit-bearing tree and there were significantly more Black Cherry trees in occupied compared to unoccupied adjacent areas (Table 1). We suggest that food sources such as Riverbank Grape and Black Cherry may be important components of Veery habitat when available.

The presence of standing water in wet forests was considered a significant habitat variable in our study because Veery has an affinity for moist forested habitats (Paszowski 1984; Heckscher *et al.* 2020). The abundant logs we found in forested wetlands and riparian areas (mostly Paper Birch, Trembling Aspen [*Populus tremuloides* Michaux], and Large-toothed Aspen [*Populus grandidentata* Michaux]) were likely killed by seasonal flooding. However, the greatest proportion of logs by a substantial margin were ash species (C.H. pers. obs.). The large number of dead ash trees and logs is likely due to the presence of the Emerald Ash Borer, which has been highly destructive in Ontario and has been present in our study area since at least 2011 (Poland and McCullough 2006; Marchant 2011). While Veery occupied areas contained significantly more logs than unoccupied areas (Table 1), it is difficult to determine whether this is due to a potential association with ash trees or with riparian habitat.

For habitat management, especially of declining species such as Wood Thrush (*Hylocichla mustelina*) and Veery, it is important to recognize that ideal breeding habitat likely requires a complex arrangement of habitat varied in species composition and structure. Supporting previous research of Veery habitat, we found that riparian areas and second-growth forests were frequently occupied habitats (Paszowski 1984; LaRue *et al.* 1994; Golet *et al.* 2001; Heckscher 2004; Heckscher *et al.* 2020). The status of ash trees is of particular importance for Veery habitat at our forest study areas within the Lake Simcoe watershed. Ash trees are a significant component of Veery habitat and the continued spread of infestations of Emerald Ash Borer may threaten future habitat use in the area. Despite widespread infected and fallen ash trees throughout the study area, there are still many healthy ash trees which may benefit from preventative treatment (Marchant 2011).

Author Contributions

Writing—Original Draft: C.H.; Writing—Review & Editing: C.H., P.H., and R.M.; Conceptualization: C.H., P.H., and R.M.; Investigation: C.H.; Methodology: C.H., P.H., and R.M.; Formal Analysis: C.H.; Funding Acquisition: P.H.

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Nesting ecology and reuse of nest burrows by Bank Swallow (*Riparia riparia*) in southern Yukon

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Abstract

Bank Swallow (*Riparia riparia*) is a declining insectivorous bird that nests colonially in near-vertical surfaces, including natural banks along waterways as well as those created by industrial excavation. Several threats are likely contributing to the population decline, conservation measures have been recommended, and monitoring methods have been developed. However, little is known of this species in the extensive boreal portion of its breeding range. To assess whether recommendations developed in southern areas are likely to be effective in a more northerly region, we investigated aspects of the nesting ecology of Bank Swallow in southern Yukon during 2013–2017. Nesting activity occurred between 20 May and 21 August. We found an exceptional abundance of nest burrows in natural riverbanks along 46 km of the Yukon River near Whitehorse (326 burrows/km), but relatively low percent burrow occupancy in both natural and artificial habitats compared to studies from other regions. Year-to-year persistence of nest burrows and rates of reuse of burrows were high compared to other studies. We highlight the potential importance of the boreal region for recovery of Bank Swallow in Canada, and the importance of using region-specific estimates of percent occupancy when monitoring Bank Swallow using burrow counts. Further study is needed to determine whether unoccupied burrows contribute to nesting success, and whether there are situations in which Bank Swallow burrows should be protected year-round instead of only during nesting.

Key words: Bank Swallow; *Riparia riparia*; nesting ecology; Yukon; colony occupancy; burrow reuse; nesting phenology; aerial insectivore; Species at Risk; boreal region

Introduction

Bank Swallow (*Riparia riparia*) is a colonial breeder. Each nest is in a long, narrow, horizontal burrow (a few centimetres in diameter, with average length ranging from 59 to 90 cm; Garrison 1999) that the birds excavate. Historically, Bank Swallow had centres of abundance in areas where natural banks of friable material occur along rivers and on lake and ocean shores. However, increasing human settlement has provided nesting habitat in other areas, in the form of road cuts and sand and gravel quarries (Erskine 1979). The proportion of the population that nests in naturally, versus artificially-created, substrates varies among regions (Erskine 1979; Garrison 1999).

Louis Bishop (1900: 88), surveying birds along the entire Canadian portion of the Yukon River in 1899, ranked Bank Swallow among the region's most abundant species and noted:

> We were entirely unprepared for the great abundance of this species on Fifty-Mile River above Miles Canyon. There almost every bank was honeycombed with their holes. Along the rest of the Yukon as far as Circle [Alaska] bank swallows were common and often abundant….

Although still a common species in Yukon, Bank Swallow is now listed as Threatened under Canada's federal *Species at Risk Act* (SARA), due to nationwide population declines (SARA Registry 2020). Bank Swallow is widely distributed in North America, and the breeding range includes the boreal region from Alaska to Labrador, extending well beyond areas surveyed by the North American Breeding Bird Survey (BBS; Environment and Climate Change Canada 2019). Little is known of its abundance, trends, habitat use, or breeding biology in northern areas (but see Hickman 1979; Bols 2017). In Yukon, data from the BBS show a steep decline in Bank Swallow numbers (long-term change −90.8% during 1972–2017, short-term change −15.6% during 2007–2017; Smith *et al.* 2019). However, the BBS is conducted along roads, and it is unknown whether this dramatic decline reflects the overall status of the Yukon population or tracks the effect of changing road construction practices on the portion of the population that nests near roads.

Several threats may be driving the Canadian decline of Bank Swallow, which is a long-distance migrant that winters in South America (Garrison and Turner 2020). These include loss of nesting habitat through erosion control and flood control projects that make natural banks unsuitable for nesting, management of sand and gravel quarries, decreased abundance of flying insects due to pesticide use, and poorly-understood threats related to climate change (COSEWIC 2013). Threats specific to Bank Swallows that nest in Yukon are unknown. Recommendations for recovery of Bank Swallow populations have been developed (Falconer *et al.* 2016), along with management recommendations for quarry operations (OSSGA 2013; Environment Canada 2016), and methods for monitoring populations (Bird Studies Canada 2010). Avoiding nesting colony disturbance is recommended during the nesting season, and habitat regulation has been suggested for colonies that have been occupied within the last three breeding seasons (Falconer *et al.* 2016). Burrow counts can be used for monitoring, and an assumption that 50% of burrows are occupied by nesting swallows is recommended for general use, unless local data are available (Cadman and Lebrun-Southcott 2013). Reported percent occupancy of burrows ranges from 63% for lakeshore colonies in Ontario (Burke 2017) to 35.3% for colonies in southern Yukon (Bols 2017).

Yukon Territory is predominantly mountainous, but with wide river valleys. Although a large portion of the territory adjacent to Alaska has been unglaciated for three million years, other regions of the territory feature deep glacial deposits from recent glaciations, including deep deposits in the Whitehorse area from glacial Lake Champagne (Smith *et al.* 2004). Tall riverbanks are found along parts of several major rivers in the territory, including the Yukon, Teslin, Takhini, and Nisutlin rivers in the south, the Liard and Hyland rivers in the southeast, the Stewart River in central Yukon, and the Porcupine and Peel rivers in the north. The human footprint in Yukon is relatively small, with a population of 35 874 (Statistics Canada 2017), although the road system is fairly extensive compared to some northern regions. In a compilation of Yukon Territory bird observations from 1861 to 1998, 78 of 90 (87%) Bank Swallow colonies were in natural banks adjacent to rivers or lakes, while 12 (13%) were in roadside cut banks ("road cuts") or gravel pits (Sinclair *et al.* 2003). This is in contrast to regions such as southern Ontario, Quebec, and British Columbia, where the majority of Bank Swallows nest in artificial habitats (Erskine 1979; Falconer *et al.* 2016).

Bank Swallow is protected in Canada under the federal *Migratory Birds Convention Act* and *Migratory Birds Regulations* (1994), and SARA, which prohibit destruction of nests. However, under SARA the nest burrow is protected only while the birds are actively nesting (Government of Canada 2019). Bank Swallows can excavate new nest burrows each year or occupy old burrows excavated in previous years (Hickman 1979; Garrison *et al.* 1989). In some regions, few burrows persist over winter (Garrison *et al.* 1989; Cadman and Lebrun-Southcott 2013). It is speculated that Bank Swallows may avoid old burrows due to the persistence of ectoparasites from the previous year's nest (Garrison 1999; Cadman and Lebrun-Southcott 2013; Falconer *et al.* 2016). Range-wide, there is little documented information on year-to-year burrow persistence, or reuse frequency of existing burrows. Therefore, it is unknown how the use of nest burrows excavated in previous years contributes to nest success.

Our goal was to assess whether recommendations for management and monitoring, developed in southern areas, are likely to be effective in a more northerly region. To do so, we collected five years of data on: (1) nesting phenology, to inform optimal timing of monitoring as well as avoidance guidelines for industry, (2) percent occupancy of burrows to inform monitoring methods, and (3) persistence and reuse of nest burrows to inform management recommendations regarding protection of burrows in the non-breeding season.

Methods

Study area

Our study was conducted in and near Whitehorse, Yukon, Canada (60.72°N, 135.05°W), located on the section of the Yukon River that was historically known as the "Fifty-Mile River" (Yukon Department of Tourism and Culture 2013). It is in the Yukon Southern Lakes ecoregion, within the Boreal Cordillera ecozone, a mountainous region with major river valleys characterised by deep glacial deposits rich in silt and clay from the most recent McConnell glaciation (Smith *et al.* 2004). Here, the river is typically 100–200 m wide, although it occasionally narrows to <50 m or widens to >500 m. Land adjacent to the river is predominantly forested, but also includes residential, urban, and industrial developments near the city.

Selection of survey sites

To survey Bank Swallow colonies, we boated down two segments of the Yukon River: (A) from the Yukon River Bridge (southeast of Whitehorse on the Alaska Highway) to Schwatka Lake (27.7 river km; Figure 1), and (B) from Shipyards Park in downtown Whitehorse to the Takhini River Bridge north

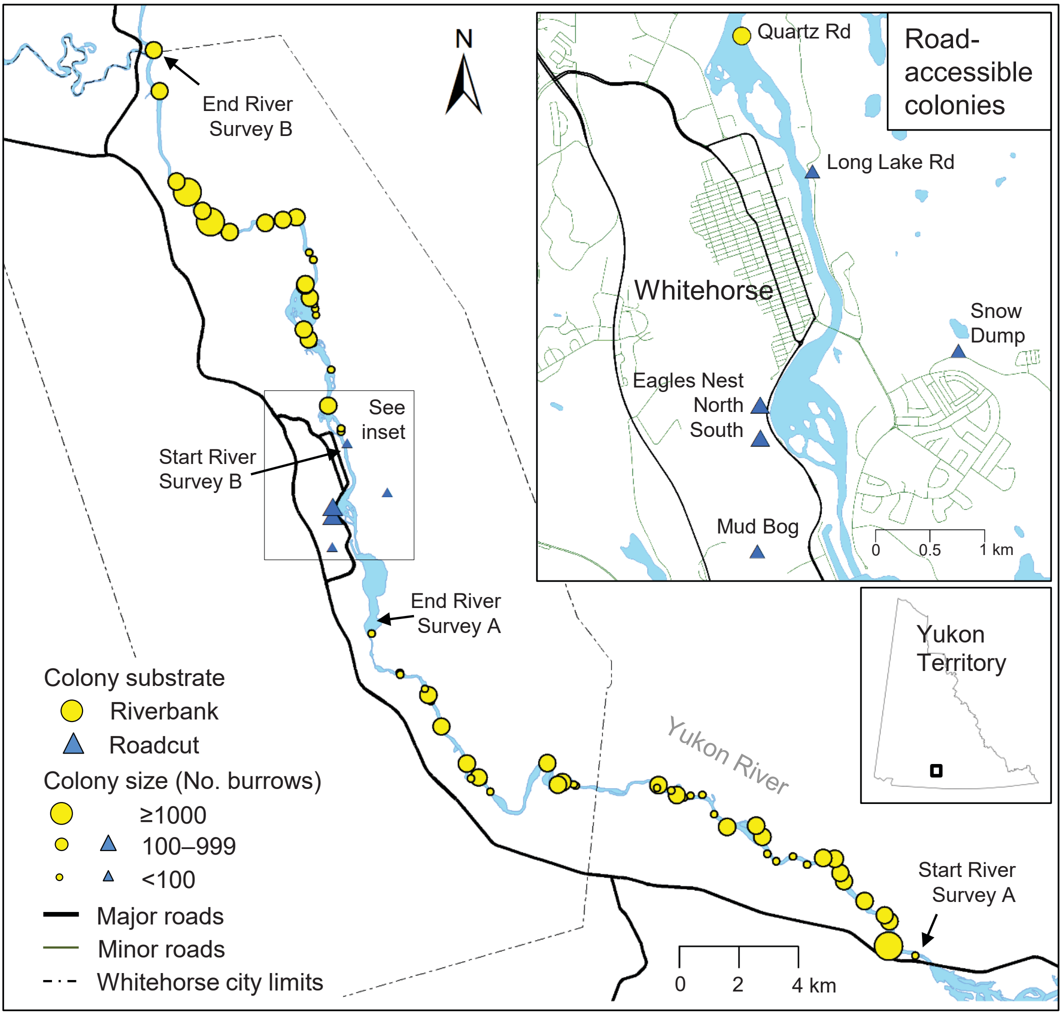

FIGURE 1. Locations of Bank Swallow (*Riparia riparia*) colonies surveyed in the vicinity of Whitehorse, Yukon, Canada.

of Whitehorse (18.3 river km; Figure 1). Both banks of the river were easily visible from its middle, except at three points where the river widens substantially.

In addition to our river survey, we also located Bank Swallow colonies that were visible from public roads within the limits of the City of Whitehorse, for more detailed study. These road-accessible colonies were located by visiting colony sites previously known to the authors and local birders, as well as by searching additional potential habitat. All occupied road-accessible colonies found that could be safely observed and were close enough to obtain clear video footage (i.e., within about 250 m) were included in the study; one colony was excluded because it was too far away (across a lake), and two colonies in active quarries were excluded due to access and safety issues. As a result, we included six road-accessible colonies in the study: five colonies in old road cuts, and one colony in a riverbank which was part of the river survey route described above but could also be observed from land. Road-accessible sites were selected in May 2013, with no new sites added later in the study.

River surveys

River surveys, using two observers, were conducted twice each year from 2013 to 2016: once during 17–26 June and once during 6–17 July. Each river survey was conducted over a two-day period, with segments (A) and (B) each conducted on a separate day. During the first survey in June 2013, a global positioning system (GPS) unit was used to mark the approximate upstream limit of every Bank Swallow colony encountered and we noted on which side of the river the colony occurred. A colony was defined as a group of burrows ≥100 m from other burrows. In June and July of each year (2013–2016) except July 2013, we counted the number of burrows at each colony (by ones, 10s, and 100s depending on the size of the colony), the number of Bank Swallows observed, and the number of occupied burrows. We also noted evidence of nesting stage such as excavation, nestlings visible in burrow entrances, or adults carrying faecal sacs. In July 2013, the first survey year, data collection was limited to the number of Bank Swallows observed and whether the colony was present and occupied. Visits were brief (1–5 min duration at each colony), with shorter visits at smaller colonies with immediate evidence of activity, and longer visits at larger colonies or where activity was not immediately evident. Observations were mostly made with a single pass as we moved down the river, although occasionally, for large colonies, we immediately made a second pass to ensure our counts were correct. Our priorities were counting the total number of burrows and determining whether each colony was occupied. Counts of numbers of birds and occupied burrows were not considered complete, as most swallows presumably remained inside nest burrows or were away foraging. If a new colony was encountered, it was added to the survey and marked with a GPS waypoint. A colony was considered occupied if ≥1 burrow was occupied. A burrow was considered occupied if ≥1 Bank Swallow was seen to enter or exit the burrow or was visible inside the burrow entrance. If a colony was observed to be occupied in ≥1 survey (i.e., June or July), it was considered to be occupied that year.

Road-based surveys

We visited the six road-accessible colonies for more detailed observation between 3 May and 18 July, 2013–2017 (Figure 2). We used photographs to count the total number of burrows, and also to track persistence of individual burrows. At each site we photographed the entire colony at least twice each year (in May before arrival of the birds, and in July when excavation was presumed to be complete, and usually also in June). A complete burrow count was made at each colony 2–9 times per year. We numbered and tracked individual burrows, noting presence or absence of each burrow in each photograph, including newly-excavated burrows as they appeared. At smaller colonies (<100 burrows; *n* = 3), all burrows were tracked this way. At larger colonies (>100 burrows; *n* = 3) we tracked sample sections, including about 20 burrows in each sample, until the samples included about 20% of the colony, as recommended by Bird Studies Canada (2010). The same sample sections

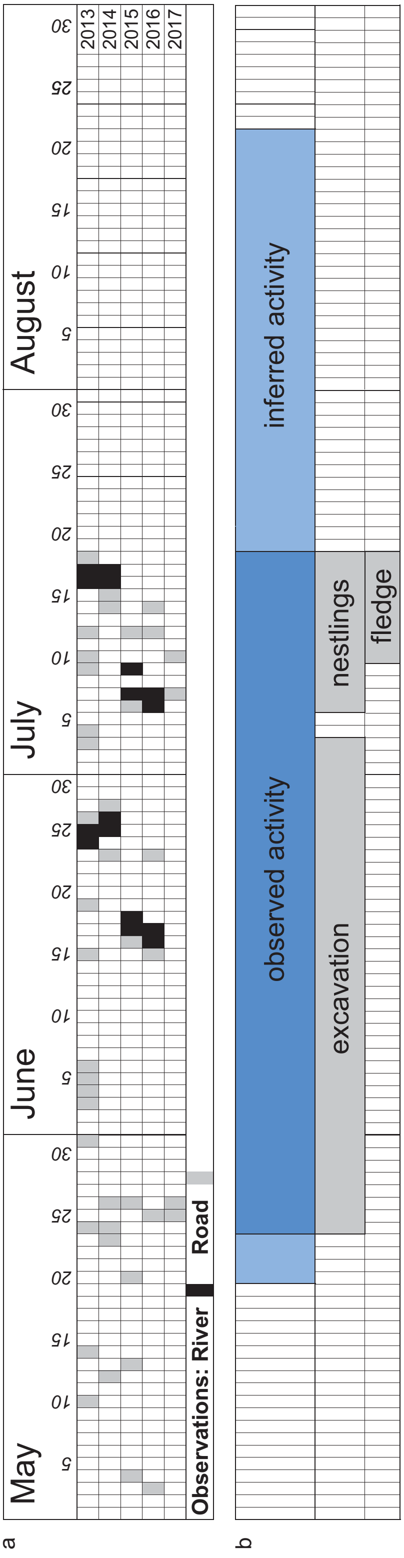

FIGURE 2. Seasonal timing of nesting of Bank Swallows (*Riparia riparia*) near Whitehorse, Yukon, Canada, 2013–2017. a. Survey dates for river (black) and road-accessible (grey) surveys. b. Date ranges of observed and extrapolated nesting activity (dark blue and light blue, respectively), with date range of observed excavation of burrows, nestlings, and fledglings shaded grey.

were used annually, regardless of whether the original burrows remained.

Recording nesting activity

To assess percent occupancy of burrows and track year-to-year reuse of individual burrows, we recorded activity for 20 min by direct observation of the two smallest road-accessible colonies (Long Lake Road and Snow Dump by two observers) and by video recording of sections of the four larger road-accessible colonies (Eagle Nest north and south, Mud Bog, and Quartz Road). Burrow numbers and all entries and exits were recorded along with any additional behaviours indicating nesting stage, such as burrow excavation, adults entering burrows, or nestlings visible in burrows. Video recordings were also made of six river-survey colonies on 16–17 July 2013. For these recordings, a section of burrows was selected which was occupied (i.e., adults entering/exiting burrows) and suitable for recording (i.e., low enough on the bank that the distance and angle allowed a clear image, and in a position where the river current allowed safe landing or steady boating at a distance far enough to avoid disturbing the birds). One to three occupied sections of each colony were thus selected, for a total of nine recordings from six colonies, with 10–15 min long videos.

Data summary and analysis

To calculate linear density of burrows on the river we used mean total burrow counts from six 46-km river surveys (river segments A plus B, completed over a two day period) conducted in June and July 2014–2016. We did not include 2013 data because the June 2013 survey involved a different observer and slightly different technique, and because burrows were not counted in July 2013.

To infer nesting phenology from our observations, we assumed the following: seven days for excavation of burrow (Petersen 1955; Hickman 1979), four days for nest building (Petersen 1955), four days for laying a clutch of four eggs (Hickman 1979) at a rate of one egg per day (Petersen 1955), 14 days incubation (14–15 days in Alaska [Hickman 1979]; 13–15 days in Wisconsin [Petersen 1955]), nestlings moving to the burrow entrance at 15–17 days after hatch (Garrison 1999), fledging (first flight) at 20 days (Petersen 1955; 18–21 days [Beyer 1938]; 18–19 days [Beecher *et al.* 1981]), and fledglings re-entering burrows for up to an additional seven days (Petersen 1955; Beecher *et al.* 1981).

We calculated mean burrow counts for each colony from the six surveys of river colonies (June and July 2014–2016) and the two to nine surveys per road cut colony per year (2013–2017). We used a Wilcoxon Rank Sum test to compare mean colony size of river (n = 74) versus road cut (n = 5) colonies and between colonies that were never occupied versus those that were occupied at least once during the study, and also to compare percent occupancy of burrows in river versus road cut colonies. A Chi-square Test was used to compare year-to-year patterns of occupancy of river colonies, and to compare patterns of burrow reuse for different colony types. We used R version 3.1.1 (R Core Team 2014) for statistical analyses. Results are presented as mean ± SD.

Results

Abundance

We found 74 Bank Swallow colonies along 46 km of the Yukon River, which represented 326 burrows/km (Figure 1). The total number of nest burrows counted on the river averaged 15 017 ± 963 over six surveys during 2014–2016. Fifty-one colonies which were occupied in ≥1 year of the study accounted for 13 947 ± 952 burrows (n = 6 surveys; 303 burrows/km), while 23 colonies which were never occupied during the study had a total of 1069 ± 129 burrows (n = 6; 23 burrows/km). In a given year, 33–37 colonies were occupied, and occupied colonies had a total of 11 624 ± 624 burrows (n = 6; 253 burrows/km).

Mean number of burrows per river colony (203 ± 297, range 1–1670, n = 74) was higher but not significantly different than that of road cut colonies (103 ± 49, range 53–165, n = 5; W = 181, P = 0.9438). Median number of burrows per colony were 95 and 112 for river and road cut, respectively. Colonies that were occupied at least once during the study were larger (259 ± 322 burrows, n = 56) than colonies that were never occupied (46 ± 44, n = 23; W = 200, P < 0.001). Total number of burrows on the river was relatively consistent from year to year (Table 1). However, there was an early-season deficit in the number of burrows in 2016 (presumably from greater-than-usual erosion during the 2015/2016 non-breeding season) compensated for before the July survey (presumably by excavation of new burrows).

Nesting phenology

During river- and road-based surveys, we detected Bank Swallows at colonies between 24 May and 18 July, which was the latest survey date (Figure 2). Specific indications of nesting stage were detected on the following dates: burrow excavation and adults in burrow entrances facing out (“male advertising”; see Garrison 1999) from 24 May to 19 June, birds entering and exiting burrows from 24 May to 18 July, and nestlings visible in burrow entrances and adults carrying faecal sacs from nests during 6–18 July. We observed birds hovering outside burrows without landing during 10–18 July only, which suggests these were fledging juveniles that remain in and around the col-

TABLE 1. Total number of Bank Swallow (*Riparia riparia*) burrows on a 46-km survey of the Yukon River, and percent change between surveys and between years for: all colonies ($n = 72$, 74, and 72 colonies in 2014, 2015, and 2016), colonies that were occupied in ≥1 year ("sometimes-occupied" colonies, $n = 51$), colonies that were never occupied during 2013–2016 ($n = 23$), colonies occupied in a given year ($n = 33$, 35, and 37), and colonies unoccupied in a given year ($n = 39$, 39, and 35).

	2014		2015		2016	
	June	July	June	July	June	July
Total burrows in:						
All colonies	14 240	14 959	15 168	16 091	13 643	16 000
Sometimes occupied	13 021	13 783	14 146	14 954	12 754	15 029
Never occupied	1219	1 176	1 022	1 137	889	971
Occupied this year	10 594	11 198	11 357	11 964	11 258	13 374
Unoccupied this year	3646	3761	3811	4127	2385	2626
Percent change since previous count:						
Sometimes occupied		6	3	6	−15	18
Never occupied		−4	−13	11	−22	9
Occupied this year		6	1	5	−6	19
Unoccupied this year		3	1	8	−42	10
Percent change since previous year, same month:						
Sometimes occupied			9	8	−10	1
Never occupied			−16	−3	−13	−15
Occupied this year			7	7	−1	12
Unoccupied this year			4	10	−37	−36

ony and fly clumsily for several days (Garrison 1999).

Extrapolation from our observations using published information on the duration of Bank Swallow nesting stages (details shown above) indicates the following: clutches were initiated during 2–24 June, hatch occurred between 20 June and 12 July, and juveniles took their first flights during 9–31 July. Excavation of burrows may have started as early as 20 May, and fledglings may have continued to re-enter burrows as late as 7 August. Individual burrows were first occupied (beginning of excavation) between 20 May and 13 June and abandoned for the season between 16 July and 7 August. We had additional incidental observations of later nesting behaviour, including burrow excavation on 3 July 2013 at a small, newly-established road cut colony near the Snow Dump colony, indicating that nesting may extend by two weeks resulting in fledglings potentially continuing to re-enter burrows as late as 21 August. Thus, based on direct observation and inferred nesting activity, the overall period of occupancy of nest burrows in our study was from 20 May to 21 August.

Burrow and colony persistence

Most river colonies (70 of 74; 95%) had burrows present in all four river survey years (2013–2016), while two were newly excavated in the third survey year and still present in the fourth year, and two small never-occupied colonies present for the first three years had no burrows in the fourth year. Burrows were present at all five road cut colonies in all five years of road-based surveys (2013–2017).

Of 203 individually-tracked burrows present in 2013 at four road-accessible colonies (including three road cut colonies and one river colony), 25% persisted for four years into the 2017 season (Figure 3). Of the three road cut colonies, two were apparently

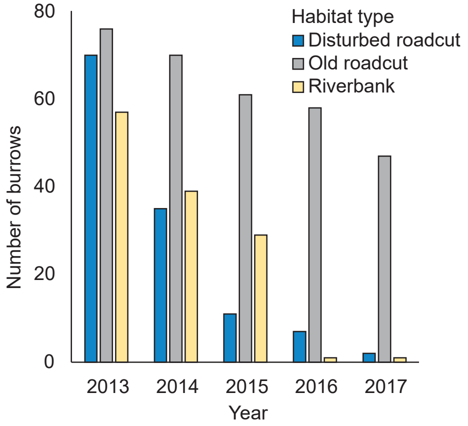

FIGURE 3. Persistence of 203 Bank Swallow (*Riparia riparia*) burrows individually tracked at road-accessible colonies beginning in 2013, for the following four years, for riverbank ($n = 57$ burrows in one colony), old road cut (76 burrows in two colonies), and frequently-disturbed road cut (70 burrows in one colony) substrates near Whitehorse, Yukon.

undisturbed during the study, while we frequently observed human and canine tracks close to nest burrows as well as obvious signs of disturbance from digging at Snow Dump. For this reason, we have summarized the Snow Dump colony separately. Burrows at the two undisturbed road cut colonies persisted longer than burrows at the river colony (road cut: 3.1 ± 1.4 years, *n* = 76 burrows; river: 1.2 ± 0.96 years, *n* = 57 burrows). Burrows at the Snow Dump road cut colony had the lowest rate of persistence (0.79 ± 1.0 years, *n* = 70 burrows). Burrows were not individually tracked at two other road-accessible colonies (Eagles Nest North and South) because many of the photographs and videos at those sites were of poor quality due to poor lighting conditions. Twenty-three river colonies that were unoccupied in all four years retained most (72%) of their burrows, with a total of 1345 burrows in June 2013 declining to 971 burrows in July 2016.

Overwinter persistence of burrows varied among colonies. At the single river colony (Quartz Road), which was also part of the road-based survey and therefore was photographed before the spring arrival of the birds each year, the number of burrows remaining in spring as a percentage of number of burrows present the previous July was on average 47% (*n* = 4 years, range 21–60%); this colony was occupied every year, with a burrow count of 446 ± 75 (*n* = 6 surveys). Two road cut colonies with counts of total burrows each spring and summer had very different rates of persistence of burrows over the winter. The Long Lake Road colony had an average of 94% (*n* = 4 years, range 92–97%) of burrows from the previous July still present the next spring before arrival of the swallows, while the Snow Dump colony, which was often disturbed and damaged by humans and pets, had a mean of 46% (*n* = 4, range 26–61%) of the previous July's burrows still present the following May.

Colony occupancy

Of 74 river colonies, 23 small colonies (31%), which accounted for ~7% of the total burrow count, were never occupied during four survey years and it is uncertain whether they were suitable for occupancy by Bank Swallows during the study. Of the river colonies that were occupied ≥1 year, 45% (23 of 51) were occupied in all four years. Of the five road cut colonies, all were occupied in at least three years and two (40%) were occupied in all five years of the road-based survey.

Considering the 51 river colonies that were occupied at least once and thus known to be suitable for nesting, the year-to-year patterns of occupancy were consistent among consecutive pairs of years (i.e., 2013 to 2014, 2014 to 2015, and 2015 to 2016; χ^2_4 = 2.61, *P* = 0.625; Table 2). There were three instances of river colonies being occupied after at least three years unoccupied, and an additional five instances of colonies being occupied after at least two years unoccupied (Figure 4). Of the 33–37 colonies occupied in a given year, nesting activity was detected on both visits (i.e., June and July) in 74–94% of colonies, only in July for 3–24% of colonies, and only in June for and 0–6% of colonies (Figure 4).

Percent occupancy of burrows

Within colonies, the percent of burrows that were occupied by Bank Swallows was higher for river colonies (47.7 ± 21%, *n* = 32 video samples from seven colonies over five years) than road cut colonies (14.5 ± 13.5%, *n* = 40 video and direct observation samples from five colonies over five years; *W* = 1169.5, *P* < 0.001).

Burrow reuse

Of 119 occupied burrows (i.e., active nests) at four road-accessible colonies tracked by video, direct observation, and photographs, 55% were newly-excavated burrows while 45% were reused burrows (32% in burrows occupied the previous year and 13% in burrows present but unoccupied the previous year). This pattern of burrow reuse differed among colony types (χ^2_4 = 34.4, *P* < 0.001). Active nests at the two undisturbed road cut colonies were more frequently in reused burrows, and active nests at the frequently-disturbed Snow Dump colony were more frequently in newly excavated burrows (Figure 5).

TABLE 2. Year-to-year use patterns of Bank Swallow (*Riparia riparia*) colonies on the Yukon River during 2013–2016. For each pair of years, only colonies that were occupied in at least one of the two years are included. Values are numbers of colonies, with percent in parentheses.

Use pattern	Years		
	2013–2014	2014–2015	2015–2016
Occupied colony occupied previous year	27 (63%)	28 (70%)	30 (71%)
Occupied colony unoccupied previous year	6 (14%)	7 (18%)	7 (17%)
Unoccupied colony occupied previous year	10 (23%)	5 (12%)	5 (12%)
Total	43 (100%)	40 (100%)	42 (100%)

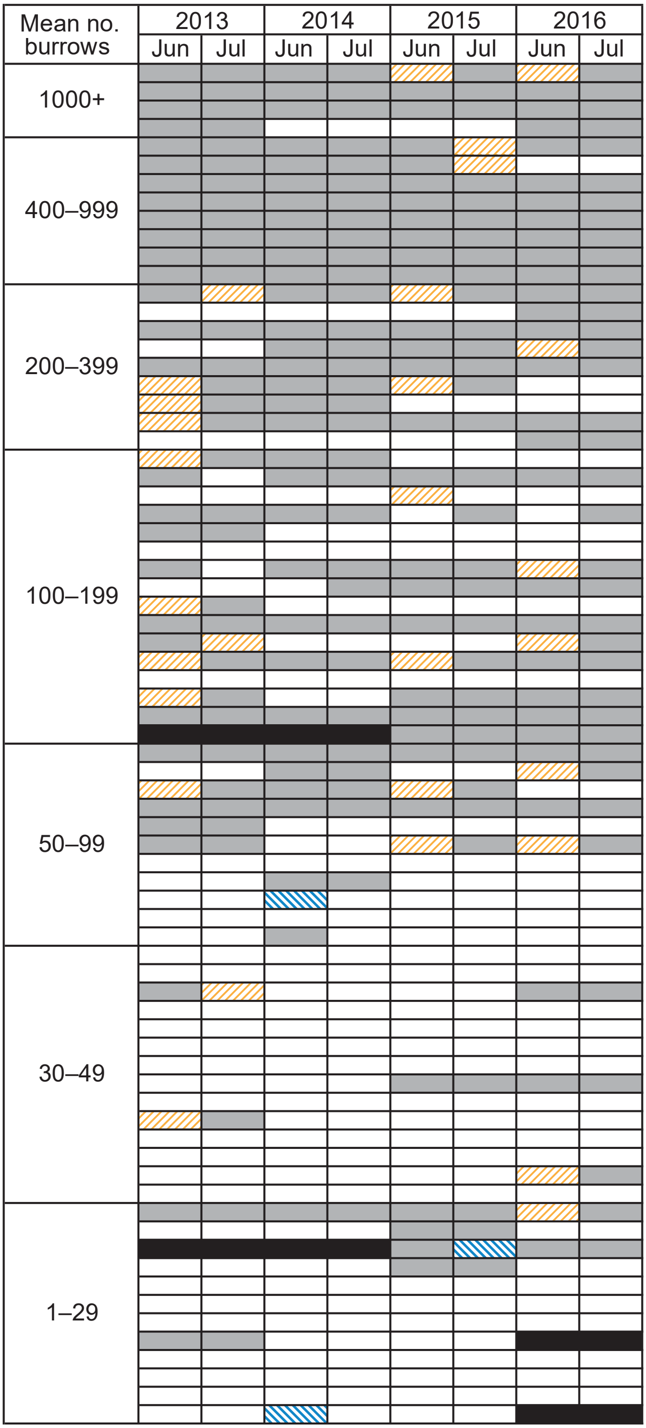

FIGURE 4. Year-to-year occupancy of 74 Bank Swallow (*Riparia riparia*) colonies along the Yukon River, in descending order of colony size (colony size = mean no. burrows from six surveys 2014–2016). Grey = occupied that year, white = unoccupied that year, crosshatching up to right = no evidence of nesting activity during survey but occupied in other survey that year so presumed occupied, crosshatching up to left = unknown, i.e., colony missed on survey; black = no burrows (i.e., no colony at that time).

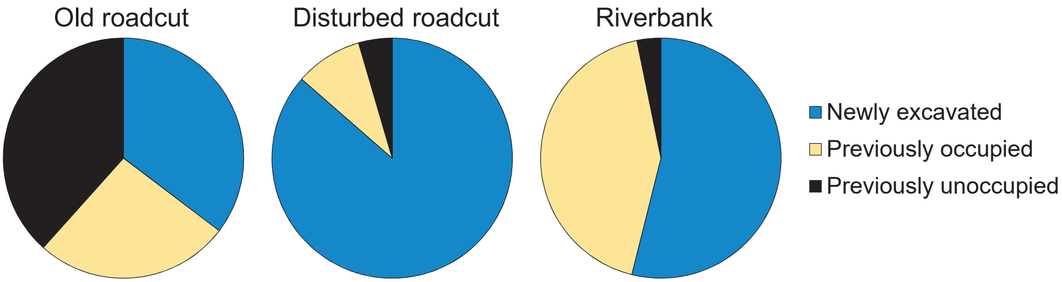

FIGURE 5. Percent of active Bank Swallow (*Riparia riparia*) nests in newly-excavated versus pre-existing burrows (occupied or unoccupied in previous year), in old road cuts (34 nests in Mud Bog and Long Lake Road colonies), a frequently-disturbed road cut (22 nests at Snow Dump colony), and a riverbank (63 nests in two sections of Quartz Road colony); includes 119 active nests from 2014 to 2017 at road-accessible colonies.

Discussion

We found comparatively high densities of nesting Bank Swallows along a 46-km stretch of the Yukon River that suggest northern populations may potentially contribute significantly to the persistence and recovery of this declining species. We documented local nesting phenology, information that is required for designing regional monitoring as well as guidelines to mitigate disturbance by local industry. Low percent occupancy of nest burrows previously found for this region (Bols 2017) is supported by our results, indicating that regional estimates are important for use with burrow counts to estimate local populations. Burrows persisted for much longer than in some other regions, and rates of reuse of nest burrows that have persisted over the winter were higher than in other regions, pointing to the need for further study to determine how old burrows contribute to nest success and whether burrows should be protected year-round in some regions.

Abundance

The abundance of Bank Swallow nesting burrows along the Yukon River near Whitehorse was higher than that along rivers known for high abundance elsewhere in North America. The few published examples include the Sacramento River between Redding and Yolo, estimated to host 80% of California's population of nesting Bank Swallows, with 28 894 burrows along 336 km of river, or 86 burrows/km (Humphrey and Garrison 1987). A three-year study along one of the stretches with highest abundance had 12 000–17 000 burrows along 80 km of river, or 150–212 burrows/km (Garrison *et al.* 1989). In Ontario, a 14.9 km stretch of the Saugeen River had an average of 147 burrows/km, which was considered an exceptionally large population, while other stretches of river in the region had 2.3 to 20.2 burrows/km (Cadman and Lebrun-Southcott 2013). The density of nest burrows that we found along 46 km of the Yukon River (326 burrows/km) was approximately double these densities recorded elsewhere and considered "high". Even considering only the 51 colonies that were occupied in some years (303 burrows/km), or only the colonies occupied in a given year (237–268 burrows/km), the density of burrows was higher than reported elsewhere.

Applying our 47.7% occupancy rate to the 11 624 burrows in active colonies along our river survey route yields an estimated 5545 occupied nests, or 11 090 nesting Bank Swallows on the 46 km stretch of river. This amounts to 0.8% of the estimated Canadian population and 7% of that for Yukon (1 400 000 and 160 000 birds, respectively; COSEWIC 2013). Considering that Bank Swallow is likely also abundant along other major rivers within glaciated areas of the territory (for example the Teslin, Takhini, Nisutlin, Liard, Hyland, Stewart, Peel, and Porcupine rivers), this suggests that the Yukon population may be considerably larger than current estimates based on roadside surveys.

Nesting phenology

The inferred beginning of the nesting period in our study (20 May) and the directly observed start date (24 May) are similar to the earliest date from historical Yukon data (28 May; Sinclair *et al.* 2003). In contrast, the inferred end date (21 August) for the nesting period of Bank Swallow in our study is later than the last calendar date of historically observed burrow occupancy in Yukon (8 August; Sinclair *et al.* 2003). This late end date, although inferred from a late observation of excavation of a burrow which may not have successfully produced young, can be used to inform avoidance guidelines for industrial work in the vicinity of Bank Swallow colonies.

In a two-year study of Bank Swallow in Fairbanks, Alaska, nesting dates were also similar; birds were first noted at colonies on 23 May and leaving by 6 August.

One unusually late nesting was noted in which young were ready to fledge on 18 August (Hickman 1979). An observation of a colony near Old Crow, in northern Yukon, on 30–31 July 1970 (Morlan 1972) also fell within the nesting dates inferred from our observations. Our study shows a longer nesting season for Bank Swallow than indicated in the Bird Nesting Calendar Query Tool (28 May–3 August for Yukon; Hussell and Lepage 2015), which is based on a citizen-science database and is designed to inform avoidance periods for industry (Rousseu and Drolet 2017). Nesting in our study area began later than in southern Ontario (earliest clutch initiation 8 May; Burke *et al*. 2019) and British Columbia (earliest clutch initiation 27 April; Campbell *et al*. 1997). The nesting period found in our study falls within the "possible period of occupancy" stated in the SARA Residence Description for Bank Swallow (May to late August; Government of Canada 2019).

Burrow and colony persistence

The high overwinter persistence of river colonies and burrows in our study (47% of burrows at a river colony; 94% and 46% at two road cut colonies) contrasts with results from elsewhere. On the Sacramento River, California, most burrows eroded away between nesting seasons, particularly in wet years (Garrison *et al*. 1989), and the Saugeen River, Ontario, almost all burrows disappeared due to erosion over the winter (e.g., 2.3% of the previous year's burrows remained in spring one year; Cadman and Lebrun-Southcott 2013). However, a study in Alaska of 11 Bank Swallow colonies at gravel pits found that, on average, 61% of the previous year's nest burrows persisted into the next season (Hickman 1979), which is within the range of burrow persistence that we found at artificial (road cut) sites.

Colony occupancy

If we omit the 23 small river colonies that were never occupied and may not have been suitable for nesting during our study (~7% of all river burrows counted), the 45% of 51 Yukon River colonies that were occupied in all four survey years was similar to the 43% of Saugeen River colony sites that were occupied in all five survey years in Ontario (Cadman and Lebrun-Southcott 2013). For our small sample of road cut colonies, our result of 40% of colonies occupied in all five survey years was higher than the 32% of 19 southern Ontario aggregate pit colony sites occupied in all three survey years (Burke 2017). In that study, annual occupancy was greater at lakeshore sites, with 100% of 11 lakeshore colony sites occupied in all five survey years (Burke 2017).

Occupancy patterns at Yukon River colonies appeared to differ from those found on the Sacramento River, where only 40–56% of sites were occupied colonies that had been occupied the previous year and 21–42% were occupied colonies that had been unoccupied the previous year (Garrison *et al*. 1989). This compares with 63–71% and 14–18%, respectively, in our study, suggesting that the Sacramento River had more inter-annual change in locations of occupied colonies, perhaps due to higher erosion rates changing the suitability of sites more often, or avoidance of previously-occupied sites, possibly due to ectoparasite densities. Colony sites may be unoccupied because of major predation events during the previous breeding season (Freer 1979), or when bank erosion makes a site unsuitable (Cadman and Lebrun-Southcott 2013). Other swallow species, such as Cliff Swallow (*Petrochelidon pyrrhonota*), avoid occupying existing nesting colonies with high densities of ectoparasites (Brown and Brown 1986). Our observations of old colonies with highly persistent burrows no longer in use suggest that changes in river course, or vegetation succession, may have slowed erosion to the extent that these sections of riverbanks are no longer suitable for nesting.

Percent occupancy of burrows

Percent occupancy of nest burrows on the Yukon River (mean 47.7%) was similar to published estimates from river colonies elsewhere, while percent occupancy of our road cut colonies (mean 14.5%) was lower. In Sacramento River colonies, percent occupancy determined by directly checking the contents of nest burrows was 56% (Humphrey and Garrison 1987), 46% and 47% (Garrison *et al*. 1989). Burke (2017) found 63% of burrows occupied in lakeshore colonies, and 60% occupancy in aggregate pit colonies in southern Ontario, based on weekly 20 min videos. Cadman and Lebrun-Southcott (2013) considered 50% occupancy to be a good approximation when estimating number of birds from burrow counts, which agrees with our data from Yukon River colonies, but not those at road cuts.

Because our occupancy estimates were based on single visits and videos ranging from 10 to 20 min, they may have been underestimates. However, we used shorter (10 and 15 min) videos only during the nestling stage, when nest visits are frequent. Also, Bird Studies Canada (2010) recommends 15 min videos to assess occupancy of Bank Swallow colonies, although Burke (2017) used the middle 20 min of 30 min video recordings. In a separate study that assessed occupancy of Bank Swallow colonies along the same stretch of the Yukon River, 91% (range 66–100%, $n = 16$ colonies) of occupied burrows were detected within the first 15 min of 30 min videos used to assess occupancy at 16 colonies between 22 June and 7 July 2015 (Bols 2017).

Although the short duration of our video recordings may have resulted in occupancy being underestimated, the fact that we selected occupied sections of colonies (rather than random sections or whole colonies) suggests they are more likely to be overestimates. Bols (2017) used video recordings of 16 entire occupied colonies to assess occupancy along the same stretch of river, thus avoiding this bias, and found a lower mean occupancy rate of 35%. Using that occupancy rate, with our burrow counts from occupied colonies only (i.e., 0.353 × 11 624 burrows) would indicate 4103 active burrows, or 8206 adult Bank Swallows along the 46 km stretch of river. This is equivalent to a 27% occupancy rate for total burrows counted including occupied and unoccupied colonies (i.e., 4103/15 017).

The relatively low percent occupancy of road cut colonies in our study area may be partly due to the very high persistence of old burrows, many of which may appear usable while actually being incomplete or obstructed (e.g., by roots or eroded material). In general, estimates of local Bank Swallow populations based on burrow counts should either count only occupied colonies (if occupancy rates are based on occupied colonies), or use a lower occupancy rate that accounts for unoccupied colonies (such as the 27% suggested above for our study area), as appropriate for the region.

Burrow reuse

Our study provides the first evidence of frequent reuse of old nest burrows by Bank Swallows nesting in riverbanks. A study in interior Alaska found that at 11 gravel pit colonies over two years, 76% of active nests were in old burrows from previous years while only 24% had been newly excavated (Hickman 1979). This reuse rate is even higher than we found in old road cuts in the Whitehorse area. For riverbank colonies, there is a lack of information on nest burrow reuse, perhaps because the Sacramento and Saugeen rivers, where most burrows erode away over the winter (Garrison *et al*. 1989; Cadman and Lebrun-Southcott 2013), may be typical and few burrows persist long enough to be available for reuse.

Bird species that nest colonially are more likely to have nests infested with ectoparasites (Poulin 1991). Bank Swallow nests host fleas (*Ceratophyllus* spp. and *Celsus* spp.; Haas *et al*. 1980), blowflies (*Protocalliphora* spp.; Whitworth and Bennett 1992), mites (Peters 1936), and lice (Stoner 1936; Emerson 1972), and nestling growth has been shown to be slower in ectoparasite-infested nests of this species (Alves 1997). Some swallow species inspect old nests for ectoparasites and avoid reusing nests that are infested (Brown and Brown 1986; Barclay 1988). There has been speculation that Bank Swallows avoid reusing nests because of the risk of ectoparasites (Garrison 1999; Cadman and Lebrun-Southcott 2013; Falconer *et al*. 2016), but no evidence of this has been documented. It is unknown whether overwinter mortality of Bank Swallow ectoparasites is greater in the north, due to colder winters, and whether this allows greater rates of reuse of old burrows. Nevertheless, it is noteworthy that the highest documented rates of reuse of old nest burrows are from cold regions in Alaska (Hickman 1979) and Yukon.

It is also unknown whether excavation of new burrows is hindered by freeze/thaw patterns of some nesting substrates in the north. Nesting dates of Bank Swallow have not advanced with warming climate as they have for other swallow species (Imlay *et al*. 2018), which invites speculation that the well-insulated nature of Bank Swallow nesting substrates may play a role; e.g., if frozen ground limits excavation of burrows in early spring and/or the northern part of the breeding range.

Conclusions

Our study provides new information from the northern boreal region on the nesting ecology of Bank Swallow, a Threatened species. The comparatively high abundance of Bank Swallow in natural habitats away from roads suggests that numbers may be higher, and declines less severe, than indicated from roadside surveys. Variation in percent occupancy estimates point to the need for further standardization of monitoring methods for this species. The longer persistence of burrows, and higher rates of reuse of temporarily unoccupied colonies as well as old nest burrows within colonies, points to the need for further study to determine how old burrows contribute to future nesting success, and whether nest burrows should be protected even when they are not occupied.

Author Contributions

Writing – Original Draft: P.H.S.; Writing – Review & Editing: M.D.M., P.H.S., and S.A.S.; Conceptualization: S.A.S. and P.H.S.; Investigation: M.D.M., P.H.S., and S.A.S.; Methodology: S.A.S. and P.H.S.; Formal Analysis: P.H.S. and M.D.M.

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Changes among Caribou (*Rangifer tarandus*) in Slate Islands Provincial Park following successive arrivals of Gray Wolves (*Canis lupus*)

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Abstract

From observations of Caribou (*Rangifer tarandus*) during 1974–2017 on the Lake Superior archipelago that makes up Slate Islands Provincial Park, we infer direct and indirect effects of the arrival of Gray Wolves (*Canis lupus*) in the winters of 1993–1994, 2002–2003, and 2013–2014. Arrivals consisted of wolf pairs in the first and third cases, and, in each instance, wolves survived at least one additional winter. Wolves created conditions that led to behavioural changes in Caribou consistent with avoiding predators. Caribou did not frequent calving locations near shoreline areas, nor did they use water to escape from wolves. Wolves occupied a Red Fox (*Vulpes vulpes*) den, and its general location, at one time frequented by Caribou, became the most common area to find Caribou carcasses and was avoided by Caribou when wolves were present. Caribou were functionally extirpated by wolves, with just two to four males remaining in 2017. Wolves also appear to have caused extirpation of American Beaver (*Castor canadensis*) and Red Fox from the archipelago, while Snowshoe Hare (*Lepus americanus*) populations were unaffected by wolves.

Key words: American Beaver; *Canis lupus*; Caribou; *Castor canadensis*; Gray Wolf; *Lepus americanus*; *Rangifer tarandus*; Red Fox; Slate Islands Provincial Park; Snowshoe Hare; *Vulpes vulpes*

Introduction

Quantifying ecological patterns with adequate precision at appropriate spatial and temporal scales and inferring causal relationships from complicated sets of correlations are among the chief challenges in studying natural ecosystems (Peterson *et al.* 2014). Island ecosystems offer several advantages for study: some control on immigration and their limited size and diversity simplify food webs.

Most of the effect of large carnivores on ungulate population demographics is direct (Mech and Peterson 2003). Indirect effects occur when ungulates avoid predation. The “leapfrog effect” (Sih 2005) has been used to describe part of the spatial game of predator and prey, where a predator’s distribution matches the distribution of its prey’s preferred food resources, while its prey sacrifices time spent in areas of highest food resources to reduce predation risk. The direct and indirect relationships among Caribou (*Rangifer tarandus*), Moose (*Alces americanus*), and wolves in boreal forest systems has been described in tracking studies by Rettie and Messier (2000), Bergerud *et al.* (2014), and Courbin *et al.* (2014).

The direct effects of Gray Wolves (*Canis lupus*) on Caribou adults and calves have been previously described for the island ecosystem of Slate Islands Provincial Park (SIPP), Ontario, Canada (Bergerud *et al.* 2007). In this follow-up paper, we summarize observations of Caribou on SIPP during and after three periods of wolf colonization using long-term Caribou survey data, locations of Caribou calving sites, wolf kill sites, and scat analyses. As a nationally Threatened species (SARA Registry 2019), the Boreal population of Woodland Caribou is managed controversially in several parts of Canada by lethal wolf control (Hebblewhite 2017). Recovery of many populations may depend on a better understanding of direct and indirect effects of wolves. Here, we summarize demographic effects on Caribou and examine the leapfrog effect during the first two periods with wolves present and describe the outcome of the third colonization by wolves. We also include some incidental observations of Red Fox (*Vulpes vulpes*), Snowshoe Hare (*Lepus americanus*), and American Beaver (*Castor canadensis*) on SIPP before and during wolf arrival.

Study Area

SIPP is an archipelago of eight islands and some islets in Lake Superior, centred at 48°39′01″N, 87°00′32″W, about 10 km south of Terrace Bay, Ontario (Figure 1). Occasional connectivity of the otherwise isolated archipelago to the mainland 9 km away occurs across winter ice, which allows large mammals to cross in either direction. Caribou are frequently observed swimming between islands of the archipelago, especially between Mortimer Island, the second largest island and the farthest northwest (6.8 km²), and the northeastern peninsula of Patterson Island, the largest and most southerly island (28.4 km²), using McColl and Bowes islands as stopovers. Caribou have not been observed swimming to or from the mainland, and their sign is rare on the more distant Leadman Islands to the northeast.

In 1907, J. King, a lighthouse keeper, saw Caribou tracks crossing on ice to SIPP (Euler *et al.* 1976). With more extensive ice in the first part of the 20th century (Assel 2009), both Caribou and wolves might have moved back and forth frequently between SIPP and the mainland. Although Euler *et al.* (1976) assumed occupation of SIPP by Caribou since 1907, Parsons (1918) conducted extensive mineral explorations of the islands in the decade following and noted no Caribou. Wolf tracks were spotted in February 1965 on Delaute Island (J. Chappel pers. comm. 21 May 1975), but a lighthouse keeper confirmed the absence of wolves during his tenure from 1948 to 1978 (J. Bryson pers. comm. 3 August 1974). Cringan (1956) also saw no sign of wolves during his studies in SIPP in the 1950s. During 1974–1993, we observed no wolf sign on SIPP. Therefore, wolves were likely absent and Caribou were likely free from predators on

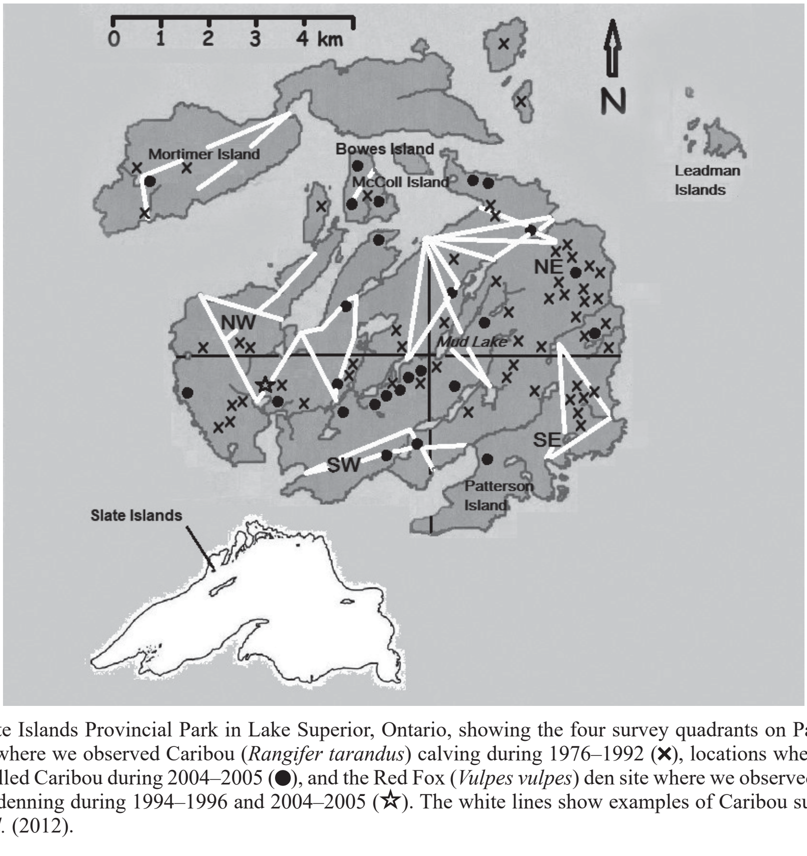

FIGURE 1. Slate Islands Provincial Park in Lake Superior, Ontario, showing the four survey quadrants on Patterson Island and locations where we observed Caribou (*Rangifer tarandus*) calving during 1976–1992 (✕), locations where we encountered a wolf-killed Caribou during 2004–2005 (●), and the Red Fox (*Vulpes vulpes*) den site where we observed Gray Wolves (*Canis lupus*) denning during 1994–1996 and 2004–2005 (☆). The white lines show examples of Caribou survey transects from Carr *et al.* (2012).

SIPP from at least 1948 to 1993. Subsequently, a pair of wolves crossed on ice to the islands in the winter of 1993–1994, and at least one wolf did the same in the winter of 2002–2003 (Bergerud *et al.* 2007). More recently, during the winter of 2013–2014, wolves and Caribou were seen moving back and forth between the mainland and SIPP (B. Patterson pers. comm. 23 October 2017).

SIPP is within the southern range of Ontario's Boreal Forest region (Rowe 1972) and supports plant communities that are generally characteristic of the region. However, as a result of its small size (a total of 36 km²) and relatively large distance from the mainland, the archipelago supports a fractured boreal fauna. Mammals listed in 1949 by Cringan (1956) include Caribou, Red Fox, Snowshoe Hare, American Beaver, Muskrat (*Ondatra zibethicus*), Southern Red-backed Vole (*Myodes gapperi*), Meadow Vole (*Microtus pennsylvanicus*), Short-tailed Weasel (*Mustela erminea*), and Little Brown Myotis (*Myotis lucifugus*). We have also observed that Northern River Otter (*Lontra canadensis*), Moose, American Black Bear (*Ursus americanus*), and Canada Lynx (*Lynx canadensis*) are absent, although Cringan (1956) reported a black bear skull on Bowes Island in 1949.

Methods

Strip transects to estimate Caribou density

A more detailed description of our Caribou survey method using strip transects (King 1937) can be found in Bergerud *et al.* (2007) and Carr *et al.* (2012). Single observers, but not the same observer each year, and usually in teams spread over the transect routes, walked transects in May and June 1974–2001 and again in 2006, 2008, and 2016. Routes for strip transects were chosen to include practical landmarks and turning points (topographic features, lakes, bays, points, etc.) and easy boat access (see Figure 1). The walking schedule coincided with the period after calving, but when vegetation least obscured the view, and the routes were chosen to avoid areas that had been visited the previous day. Using a measuring tape, observers recorded the angular distance to a Caribou spotted or flushed from the transect route; the longest distance each year was considered the maximum line of sight through the vegetation (Table 1). Mortimer Island was always included in the survey transects.

Other Caribou observations

Cringan (1956) mentioned a natural salt lick at the outlet of Mud Lake in the centre of Patterson Island (Figure 1), the island where most Caribou resided during summer. We started placing additional salt at the Mud Lake lick in 1976 and made daily observations of Caribou from this point from mid-May to mid-June each year from 1977 to 1999 and in 2004. These observations allowed a spring classification of Caribou by sex and age, estimates of pregnancy, and a different method for estimating the population, all of which are reported in Bergerud *et al.* (2007); here, we report the directions that Caribou travelled as they entered and left the salt lick during 1988, 1991, and 1992 (our three best observation years before wolf arrival) and during 1994–1996 (three years after wolf arrival).

We divided Patterson Island into four quadrants using Mud Lake as the centre (Figure 1). We labelled them NE (a quadrant of 8.4 km²), NW (5.0 km²), SE (7.3 km²), and SW (7.7 km²). Six main trails led from each quadrant: from the north, northeast, and east to the NE quadrant; from the northwest to the NW quadrant; from the south to the SE quadrant; and from the west to the SW quadrant. From a watchtower, 5 m in height and ~35 m from the salt lick, we observed Caribou as individuals (see next section), including multiple observations of the same individual, entering or leaving the salt lick, and we recorded the trail each used. We used the same quadrants to report calving locations during 1976–1992, based on capturing neonates, observing their tracks, or hearing characteristic grunting by female Caribou for their young calves. We also used the quadrants to report the locations of Caribou aggregations, defined as two or more adult Caribou that we spotted or flushed together, while walking on the survey transects. We also described changes to Caribou distribution across all survey transects using the four quadrants.

In 19 of the study years during 1974–1998, we visited SIPP for a brief period in March to compile age composition tallies (previous-year calves, yearlings, and adults) based on track and sign characteristics. In 20 years during the same period, we obtained age composition tallies (current-year and previous-year calves and adults) from boat and foot surveys in September. During the summers of 2003–2005, we recorded all locations where we encountered a wolf-killed Caribou.

Caribou capture and tagging

We captured Caribou during each fall of 1975–1995 in traps baited with salt, setting two to four box traps and two walk-through traps along regular travel routes. We also herded Caribou from boats toward drive traps at water crossings, and we occasionally used drop nets from trees or from boats when we spotted individuals swimming. During 1980–1995, we tagged captured Caribou with Duflex ear tags (Destron Fearing, Dallas, Texas, USA), numbered in a manner identifiable with binoculars. We released all Caribou at their capture site, after taking measurements including total body weight, estimated by slinging individuals from a collar using a pulley attached to a spring scale. During subsequent summers,

Table 1. Demographic parameters of the Caribou (*Rangifer tarandus*) population in Slate Islands Provincial Park, 1974–2017. Years when Gray Wolves (*Canis lupus*) were present are shown in bold; wolf pairs were seen in 1994–1996 and 2014–2017.

Year	Caribou density from strip transect surveys*				Minimum overwinter survival from tracking tagged individuals†				% calves in classifications‡	
	Total transect length, km	No. Caribou seen	Maximum line of sight, m	Caribou density, no./km^2	No. adult females tagged	Tags (♀) spotted following year, %	No. adult males tagged	Tags (♂) spotted following year, %	Sept. survey	March survey
1974	99	22	29	3.9	—	—	—	—	12	—
1975	105	20	26	3.6	—	—	—	—	12	10
1976	80	41	34	7.5	—	—	—	—	14	—
1977	169	72	38	5.6	—	—	—	—	15	—
1978	65	16	27	4.5	—	—	—	—	18	25
1979	130	43	32	5.1	—	—	—	—	16	17
1980	101	46	33	6.9	17	88	10	70	11	18
1981	162	68	29	7.2	30	93	11	100	18	10
1982	140	74	30	8.7	46	91	25	88	17	—
1983	133	107	31	13.0	50	80	36	84	20	25
1984	83	88	31	16.9	38	84	37	76	15	22
1985	158	96	33	9.3	32	88	38	82	11	5
1986	154	73	33	7.2	24	83	27	93	19	13
1987	62	57	33	13.9	26	85	30	80	16	—
1988	93	41	30	7.3	28	86	29	72	—	6
1989	57	34	36	8.3	26	15	17	12	15	13
1990	168	35	36	2.9	14	100	30	80	—	3
1991	135	24	28	3.2	23	91	6	83	—	4
1992	40	14	50	3.5	23	100	8	100	—	19
1993	55	37	39	8.6	28	89	19	89	25	23
1994	157	54	30	5.7	34	71	38	87	3	28

Table 1. *Continued.*

Year	Caribou density from strip transect surveys*				Minimum overwinter survival from tracking tagged individuals†				% calves in classifications‡	
	Total transect length, km	No. Caribou seen	Maximum line of sight, m	Caribou density, no./km^2	No. adult females tagged	Tags (♀) spotted following year, %	No. adult males tagged	Tags (♂) spotted following year, %	Sept. survey	March survey
1995	190	70	27	6.7	26	81	57	91	5	5
1996	133	58	30	7.2	—	—	—	—	22	2
1997	57	25	29	5.7	—	—	—	—	—	21
1998	43	30	49	7.1	—	—	—	—	11	—
1999	29	16	26	10.6	—	—	—	—	—	—
2000	22	14	45	7.0	—	—	—	—	—	—
2001	59	27	36	5.9	—	—	—	—	—	—
2002	—	—	—	7.4	—	—	—	—	—	—
2003	—	—	—	6.8	—	—	—	—	—	—
2004	—	—	—	7.6	—	—	—	—	—	0.1
2005	—	—	—	7.5	—	—	—	—	—	—
2008	63	11	—	3.6	—	—	—	—	—	—
2014	—	—	—	1.4	—	—	—	—	0	—
2016	114	3	34	0.4	—	—	—	—	—	0
2017	—	—	—	0.1	—	—	—	—	—	0

Note: — = missing data. Data up to 2005 are from Bergerud *et al.* (2007).

*Population density estimates from 2002 to 2008 and 2016 are based on a "best estimate" of line of sight of 33.6 m. Population density estimates in 2014 and 2017 are based on approximate number of Caribou seen during summer field visits and not on strip transect surveys.

†Tagging during 1980–1995 was with ear tags numbered in a manner identifiable with binoculars. Minimum survival is calculated from relocating tagged individuals up to four years after capture ($n = 602$) or recapture ($n = 27$).

‡Classifications in September were by boat and in March from snow track surveys. Absence of calves in 2017 was determined from camera traps (B. Patterson pers. comm. 23 October 2017).

we were able to see and record most tagged individuals at the Mud Lake salt lick.

Observation of other mammals

In 1994 and 1995 during May and June, we counted wolf tracks along the Caribou survey transects by quadrant on Patterson Island. We collected wolf scats during 1995–1998 ($n = 45$) and fox scats in 1986 ($n = 26$) on all spring and summer excursions and examined them for remnants of prey by suspension in water. We regularly observed the fox den at Horace Cove Lake (Figure 1) during 1974–1996, including when it was occupied by wolves during 1994 and 1995. We recorded Snowshoe Hares and approximated their flushing distances during 1974–2001, when we encountered them along the Caribou survey transects. W.D. regularly observed beavers and attempted to count all beaver lodges in the summer during the entire study period, 1974–2017.

Data compilation and analysis

During 1997–2001, L.C. measured the angular distance of Caribou from the walking transects more accurately than in previous years and also measured angle from perpendicular, to create a "best estimate" line of sight to use in density and population-size estimates from 2002 to 2008, a period when none of us was involved in the surveys. We compared this average to the average for all previous years using a two-sample t test. We used the estimate of line of sight to calculate the line transect width for input to estimates of density. We calculated an annual Caribou population by multiplying the number of individuals spotted or flushed in the strip transects by the area of the archipelago (36 km^2), divided by the estimated transect area (transect length × twice line of sight estimate). That is, we applied the density estimate from transects to the entire archipelago.

An estimate of annual adult survival was based on second sightings of tagged Caribou individuals in a following summer, on the last year an individual was seen, waiting three additional years to decide whether the individual had been overlooked, and on estimated date of death for any tagged carcass. If an individual was later seen with tags in good condition, it was added back to the tagged, live pool.

We recorded distances of Snowshoe Hare sightings from the walking transects less accurately than for Caribou sightings, but we adopted the same approach to estimating their abundance for 27 years in the period 1974–2001, when at least three hares were spotted; we substituted a fall survey for the June survey in 1978 when only three hares were spotted in what was part of a series of years of high abundance. We also substituted a best estimate line of sight for 13 years when five or fewer hares were spotted, which we calculated as the mean line of sight for the other 14 years. We made all calculations and t tests using Statistical Package for the Social Sciences, version 25.0 (IBM Corp. 2017).

Results

Caribou demographics

Our best estimate of line of sight in the Caribou surveys was 37.0 m ± 1.0 m (SE), measured most accurately during 1997–2001 (Table 1), when an average of 6.4 ± 0.6 km^2 or ~18% of the archipelago was surveyed; it was not significantly different from the estimates of line of sight during the previous 23 years, 32.4 m ± 1.1 m ($t_{26} = 0.56$, $P = 0.14$). The corresponding mean perpendicular distance from the 1997–2001 measurements, 33.6 m, served as an outer bound of the strip transects in all density calculations during 2002–2016, when lines of sight were not estimated.

Caribou density before wolf arrival ranged from a low of 2.9/km^2 (1990) to a high of 16.9/km^2 (1984; Table 1). Caribou density was 5.7 and 6.7/km^2 in the two springs following the first winter of an observed wolf pair (1994–1995), not much below the average for 1974–2001 of 7.2/km^2. Caribou density was above average, 7.6 and 7.5/km^2, in the two years following the second wolf arrival (2004–2005), but then fell to among the lowest density estimates, 3.6/km^2 in 2008. We visited the archipelago in 2014 and estimated that 50 Caribou remained and we found no calves. In estimates of abundance, this first spring following the second arrival of a wolf pair in 2014 was the first time we observed the population fall below 100 (Figure 2). In September 2016, the second fall after the arrival of the second wolf pair, we walked 114 km searching for Caribou and encountered just three females, all on McColl Island. By summer of 2017, at most four males and no females were photographed with remote cameras deployed throughout the archipelago (B. Patterson pers. comm. 23 October 2017).

Mean calf fraction in the Caribou population in March, excluding the springs of 1995 and 1996, was 15% ± 2% (for 17 years, mean sample size 123 track observations; Table 1). In March 1995 and 1996, the second and third years following the first wolf pair arrival, Caribou calf fractions were just 5% and 2%, respectively. These low fractions corroborated estimates of just 3% and 5% of the population in the previous September, unlike the other low March estimates of 5% (1985) and 3% (1990), which followed years of above average population density and September estimates of 15% calves (both years). In March 2004, the only spring after 1998 when we classified the population, and the first spring after the arrival of the third wolf, our sample comprised 132 females, 36 males, one yearling, and one calf.

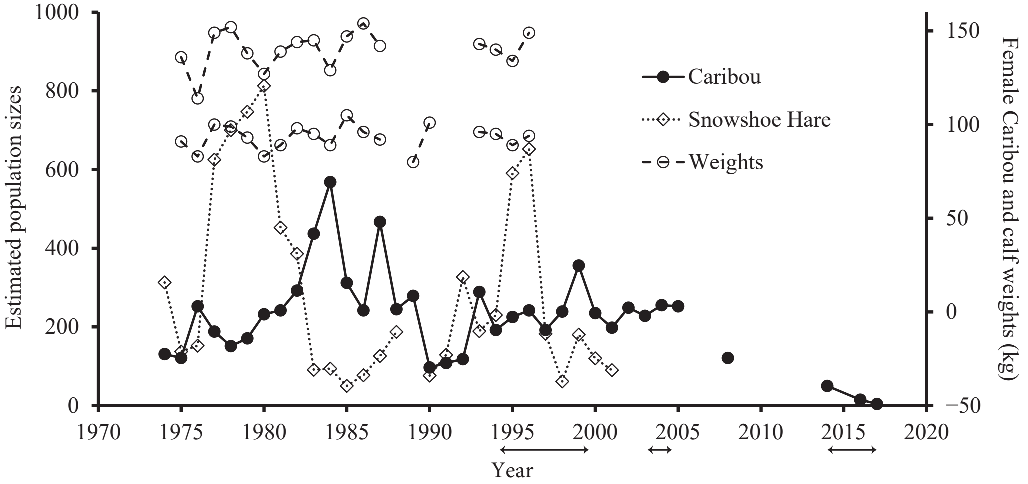

FIGURE 2. Effect of three Gray Wolf (*Canis lupus*) occupancies of Slate Islands Provincial Park (arrows below the x axis) on Caribou (*Rangifer tarandus*) population size; estimated Snowshoe Hare (*Lepus americanus*) population size; and average weights of female Caribou (lower series of open circles) and female Caribou with their calves (upper series) in September. Caribou population estimates up to 2005 and weights are from Bergerud *et al.* (2007). We acknowledge that the transect method could result in overestimates of abundance given that the line transects were conducted over one month and individual Caribou could have been counted more than once.

During 1974–1995, there were 628 adult Caribou capture events, mostly in fall: 602 unique individuals, 13 of which were relocated as carcasses and were included as deaths in the survival analysis. The mean fraction of tagged Caribou seen in the year subsequent to tagging, 1980–1995, was 82% for both females and males (Table 1). The year with lowest adult survival occurred before wolf arrival, in 1989–1990, 15% for females and 12% for males. After the first winter when wolves were spotted, in 1994, only 24 (71%) of 34 tagged adult female Caribou were spotted the following year, the second lowest fraction we recorded for females. Male Caribou, on the other hand, were spotted again in higher fractions after each of the first two winters with the wolf pair present: 33 (87%) of 38 in 1994, and 52 (91%) of 57 in 1995.

Caribou behaviour

Before 1994, Caribou entered the salt lick at Mud Lake most frequently on a trail from the west that took them from the SW quadrant, northeast along the shores of Peninsula Lake, and then just west of Mud Lake (Table 2). After wolf arrival, Caribou rarely used this trail and also substantially reduced their use of trails from the south and northwest. A trail from the east, rarely used before wolf arrival, became among the heavier used in 1994 and 1995; the heaviest used trail was from the northeast during these years.

The distribution of 54 Caribou calving sites on Patterson Island encountered during 1976–1992 was

TABLE 2. Percentage of total Caribou (*Rangifer tarandus*) observations by trail direction leaving/entering the Mud Lake salt lick in three years without Gray Wolves (*Canis lupus*) and in three years following the arrival of a wolf pair that denned southwest of Mud Lake.

Trail	% Caribou with no wolves			% Caribou after arrival of wolf pair		
	1988 (*n* = 340/352)	1991 (*n* = 328/334)	1992 (*n* = 558/563)	1994 (*n* = 980/952)	1995 (*n* = 321/288)	1996 (*n* = 316/365)
South	8/20	14/15	11/15	3/1	2/3	8/1
West	39/34	57/47	43/24	2/5	7/4	10/13
Northwest	44/23	16/14	12/8	5/8	6/10	5/4
North	5/5	1/5	4/6	20/9	12/7	56/21
Northeast	4/16	12/19	30/47	54/56	63/66	12/55
East	0/2	0/0	0/0	16/22	10/10	8/7

Note: Multiple observations of the same individuals are included.

not even, with more than expected in the NE quadrant ($\chi^2_3 = 33.6$, $P < 0.01$; Figure 1; Table 3). More than 50% of calving sites were >1 km from the Lake Superior shoreline and only three sites were adjacent to small inland lakes. Few females calved on Mortimer Island during the pre-wolf years; only during two of 20 spring surveys from 1974 to 1993 did we see calves there (in 1983 and 1984, the first period of unusually high Caribou density). During the first three wolf years, 1994–1996, more Caribou occupied the NW quadrant of Patterson Island, as well as Mortimer Island, and, except in 1995, Caribou aggregations were encountered least often in the SW quadrant (Table 3). In 1994 and 1995, only seven calves were seen during Caribou surveys, and only one of these was in the SW quadrant.

We found no Caribou carcasses after 1996, the first year without a wolf pair, until the arrival of the third wolf in winter of 2003–2004. We then found 26 Caribou carcasses during 2004–2005, 20 of which were on the shorelines or shoals of inland lakes and Lake Superior, the remainder inland at longer distances (Figure 1). Eleven of the carcasses were in the SW quadrant on Patterson Island, and three were on McColl Island. New calving sites were identified on Mortimer Island during these two years. In 2006, we observed another shift in distribution of Caribou, when many occupied the east side of the NW quadrant and the west side of the NE quadrant. This combined area is only 5 km², but we encountered 16 Caribou aggregations in 9.5 km walked in 2006, compared with the rest of Patterson Island, 23 km² (4.6 times the size), where we encountered only 18 aggregations in 26.0 km of walking (1.7 times the distance).

Observations of wolves

The wolf pair arriving in winter 1993–1994, the third wolf arriving in winter 2002–2003, and the second wolf pair arriving in winter 2013–2014 all adopted the same Red Fox den on the northern shore of Horace Cove Lake (SW quadrant); the first pair also used it as a rendezvous site. Wolves were most active around this den, and wolf tracks were most frequent in the SW and SE quadrants during our spring surveys in 1994 and 1995 (SW quadrant) and at Sunday Harbour (SE quadrant). Both wolves of the first pair were observed in March 1996, but from May 1996 only one wolf was observed; until 1999, there was continued wolf sign near the fox den, as well as at Sunday Harbour. Sign of the third wolf persisted only until 2004. Following the winter of 2013–2014, a wolf pair was observed and photographed for three seasons, with one wolf remaining until 2017 (B. Patterson pers. comm. 23 October 2017).

TABLE 3. Percentage of Caribou (*Rangifer tarandus*) calving sites encountered during 1976–1992 on Patterson Island and percentage of aggregations of two or more adult Caribou encountered on survey transects in the years following the arrival of a Gray Wolf (*Canis lupus*) pair in winter of 1993–1994, by quadrant of Patterson Island. Quadrants are by compass direction from Mud Lake. Wolves denned SW of Mud Lake.

Quadrant	% calving sites ($n = 60$)	% aggregations		
		1994 ($n = 151$)	1995 ($n = 110$)	1996 ($n = 36$)
SW	25	15	29	11
NW	10	33	41	42
NE	35	27	14	28
SE	30	25	16	19

Note: n = the total number of calving sites or the total number of aggregations each year.

Wolf scats contained hairs of Caribou calves (21 cases), adult Caribou (13), Snowshoe Hare (12), beaver (12), and Red-backed Vole (two), and berries of Showy Mountain-ash (*Sorbus decora* (Sargent) C.K. Schneider); four), feathers of birds (two), insects (one), and grass (one).

Observations of other mammals

We observed Red Fox using the same den at Horace Cove Lake for 32 years of the study period, including during 1999–2013; we did not find any sign of foxes in SIPP from 2014 onward. The fox scats we collected in 1986 contained hairs of Caribou (four cases), Snowshoe Hare (two), beaver (four), Red-backed Vole (two), and Muskrat (11), as well as feathers of birds (four). Near the den in 1977, we found remnants of 8–10 hares, 6–10 small birds, one Muskrat, two ducks, one Common Raven (*Corvus corax*), one beaver, and one newborn Caribou calf. On another visit in 1985, we found four recent and one older Caribou calf skulls, portions of a Caribou calf pelvis and hindfoot, and the tarsus of a young adult Caribou, along with remnants of Muskrat, beaver, vole, frog, snails, and several birds.

On our Caribou survey transects, maximum flushing distances for Snowshoe Hare varied from 4.0 to 8.9 m, with an average maximum of 6.9 m ± 0.4 m applied to the calculation of strip width during years when five or fewer hares were flushed. In seven years during 1974–2001, more than 15 hares were flushed, and, in those years, population estimates for the archipelago exceeded 450 hares (Figure 2). These high-hare years occurred in two periods: 1977–1981 (15–36 observed, 0.15–0.26/km walked, 450–750 estimated) and 1995–1996 (31 and 46 observed, 0.23/km walked, 600–650 estimated). The second high-hare period corresponded with the wolf pair occupying the archipelago. The average number of hares flushed per km walked was 0.31 ± 0.07 during the six years with at least one wolf present, while in the 22 years of observation without wolves, the same average was only 0.09 ± 0.01 hares, a statistically significant difference ($t_{26} = 9.33$, $P < 0.001$). In the 21 years not identified as high-hare periods, only two cases of more than 10 flushed hares were recorded, and estimates of the number seen per km walked never exceeded 0.10 hares.

Before the arrival of wolves, some beavers constructed their lodges on very shallow creeks, creating just small ponds. Frequently, they did not cover their lodges with mud, and, in some years, they left their lodges in winter to forage over land when their food caches froze to a lake or pond bottom. Their foraging ranged to >400 m from water during 1974–1976. There were 36 active lodges in 1974 (1/km^2) and beavers could have searched for forage over 95% of Patterson and Mortimer islands at that time. By 2006, only six colonies remained, their lodges only occurring on the shores of inland lakes. In 2014, we could not find any sign of beavers in SIPP.

Discussion

Summary of demographic effects of wolves on Caribou

Bergerud *et al.* (2007) concluded that, in the years before the arrival of wolves, Caribou in the SIPP ecosystem were regulated by the availability of summer forage, although they did not experience starvation. Caribou occurred at very high densities compared with other forest-dwelling Caribou populations subject to wolf predation, where densities <0.12/km² are expected (Bergerud 2001). Support for density dependence in Caribou is summarized from Bergerud *et al.* (2007) and relates the SIPP population size and weights of female Caribou in September, which we reproduce in Figure 2: weights are negatively correlated with population size for the previous year. Bergerud *et al.* (2007) also found that Caribou weights were negatively correlated with the number of Caribou carcasses encountered in March of the following year and that the number of carcasses had a positive, exponential regression effect on the Caribou population size in the previous year.

Following the density-dependent period described by Bergerud *et al.* (2007), the Caribou population size did not diminish during or after the first occupancy of SIPP by wolves, nor immediately during or after residence by the third wolf during 2004–2005 (Figure 2). However, arrival of a second pair of wolves in 2014 resulted in Caribou kills throughout Patterson Island and on McColl and Mortimer islands, eventually reducing the number of Caribou to very few, in part because of departures from SIPP beginning at least in the winter of 2013–2014 (InfoSuperior 2017). Why was the Caribou population driven to functional extirpation only after the third wolf colonization? The simplest explanation is that this colonization by two wolves coincided with a much lower Caribou population than what was present in 1994. Alternatively, indirect effects of wolves on Caribou behaviour could have contributed to the final demise of the SIPP population, as we describe below.

Effects of wolves on Caribou behaviour

We propose that the arrival of wolves resulted in Caribou shifting their distribution to the NE quadrant of Patterson Island to reduce their contact with wolves in behaviour conforming with the leapfrog effect (Sih 2005). Bergerud *et al.* (2014) documented a similar effect on Caribou by wolves in Pukaskwa National Park, also on the Lake Superior shoreline. Wolves occupying SIPP were less active in spring and summer in the NE quadrant of Patterson Island, likely because of our activities (at Mud Lake) and that of fishermen and tourists in McGeevy Harbour, between McColl and Patterson islands. But by moving to these smaller islands and the NE part of the archipelago to avoid wolves, Caribou were likely compromising their access to food in an already food-limited environment and becoming more vulnerable to starvation as well as predation, as observed on other Lake Superior islands (Ferguson *et al.* 1980). Concurrently, Caribou increased their contact with people in SIPP, especially on McColl Island. With fitness consequences unknown, such contact has been shown to increase cortisol concentrations in Caribou (Ewacha *et al.* 2017).

Other forest-dwelling Caribou will disperse to higher mountain slopes (Edmonds 1988; Bergerud *et al.* 1990; Nobert *et al.* 2016) or to fen, bog, or island habitats, where escape from predators by swimming is available during calving (Shoesmith 1978; Bergerud 1985; Bergerud *et al.* 1990; Ferguson and Elkie 2004; Carr *et al.* 2007). From the calving locations we documented, many of which were well inland and not near water, we suspect that pre-parturition female Caribou in SIPP never did seek the increased safety of calving near water. Possibly they lost this behaviour after decades without predation. On the other hand, kills of Caribou appeared to have occurred predominantly near inland lake shorelines, consistent with the effectiveness documented for wolves, or even a single wolf, seeking to kill ungulates by wearing them down while they swim in small bodies of water that wolves easily circumnavigate (Jordan *et al.* 2010; Kiss *et al.* 2010). To summarize the leapfrog effect on SIPP, Caribou missed opportunities with summer food in the southern and western part of the archipelago, as they moved north and east to avoid wolves because wolves hunted in the Caribou's preferred space.

Other ecological effects of wolves

Although wolf scats did contain the hairs of Snowshoe Hare, we observed the second highest peak in the hare population during the occupation of the SIPP archipelago by the first wolf pair; thus, wolves did not appear to affect the Snowshoe Hare cycle in SIPP. In contrast, we infer direct and near-complete effects of wolves in reducing an American Beaver population and possibly also a Red Fox population. Our many years in SIPP show that both food limitation (bottom up) and predation (top down) can direct the behaviour and population dynamics of herbivores.

Author Contributions

Writing – Original Draft: A.T.B.; Writing – Review & Editing: B.E.M. and W.D.; Conceptualization: A.T.B. and H.B.; Investigation: A.T.B., W.D., L.C., H.B., and R.S.F.; Methodology: A.T.B., H.B., and R.S.F.; Formal Analysis: A.T.B. and B.E.M.; Funding Acquisition: A.T.B.

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Diel activity patterns of urban Woodchucks (*Marmota monax*) revealed by camera traps at burrows in southwestern Ontario, Canada

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Abstract

Animals display a range of diurnal and nocturnal activity patterns and, among mammals, a high proportion of species are crepuscular or nocturnal. Daily activities are often endogenous and oscillate on a light:dark regime. Such cycles are referred to as 'circadian' and are generally influenced by biotic and abiotic factors. I investigated the daily activity of urban Woodchucks (*Marmota monax*) by using 24-hour camera traps at backyard burrows in London, Ontario, Canada, in June. Cameras enabled the collection of data that would otherwise have been labour intensive by direct observation. Statistical modelling showed that Woodchucks exhibited a strictly diurnal activity pattern. The unimodal activity pattern started at sunrise and ended before sunset. The general daily activity trend was similar to the pattern described by others who used direct observations and telemetry to monitor Woodchucks in more rural settings. Temperature and wind were not included in the best-fit model. Camera trapping is a non-invasive method that could give insight to diel activity as it can easily monitor extended periods and reduce the effort required by direct observation.

Key words: Burrow; circadian; daily activity; diel activity; trail camera; urban; marmot

Introduction

Most animals exhibit daily activity rhythms (Burger 1976; Daan 1981; Robitaille and Baron 1987; Helfrich-förster *et al.* 1998; Jury *et al.* 2005; Williams *et al.* 2014). Daily activities often originate endogenously and oscillate on a light:dark regime, referred to as 'circadian', and are generally influenced by biotic and abiotic factors (Pittendrigh 1981; Aschoff and Tokura 1986). Animals display a range of activity patterns from totally diurnal to totally nocturnal and, among mammals, a high proportion of species are crepuscular or nocturnal (Ashby 1972). Much of an animal's daily activity budget consists of time spent foraging (e.g., Wauters *et al.* 1992) that may be altered by food availability (e.g., Uttley *et al.* 1994), food quality (e.g., Sæther and Andersen 1990), or competition and the risk of predation (e.g., Hughes *et al.* 1994; Cowlishaw 1997).

For some animals, predation risk and mortality are lower when living in urban areas due to the lack of natural predators, although some are negatively affected by introduced predators that follow urbanisation (Fischer *et al.* 2012). Further, in urban environments, animals may alter their anti-predator behaviours in response to urban settings, habituating to the absence of specific predators (Mccleery 2009), or due to human disturbance (Ditchkoff *et al.* 2006)

Monitoring daily activity in the wild is challenging, particularly 24-hour observations. Traditionally, such data have been collected using very high frequency telemetry and global positioning system data (e.g., Coulombe *et al.* 2006), although non-invasive methods (i.e., no physical capture or handling needed) exist. More recently, non-invasive wildlife monitoring has been accomplished using camera traps (e.g., Heilbrun *et al.* 2006; Rowcliffe *et al.* 2008; Athreya *et al.* 2013; Mohamed *et al.* 2013). As date and time are stored along with imagery, it has been possible to analyse daily activity patterns (Akbaba and Ayaş 2012; Lynam *et al.* 2013; Leuchtenberger *et al.* 2014; Steen and Barmoen 2017). I investigated the presence/absence of urban Woodchuck (*Marmota monax*) at burrows in June 2015 using 24-hour camera traps. I defined activity according to Bronson (1962) as any appearance outside the burrow, although restricted to the camera's field of view. Woodchucks (order

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Rodentia) feed on a great variety of plant materials, are overall diurnal, dig burrows, and hibernate in winter (Kwiecinski 1998). The burrows serve as protection from predators and locations to breed and hibernate (Howell 1915; Grizzell 1955; Davis 1967; Hayes 1976; Zervanos *et al.* 2014). During winter, the hibernation burrows are often in woody areas, while in summer, burrows are close to feeding areas that provide cover at the burrow entrance (Grizzel 1955). The main predators of Woodchuck are humans, Domestic Dog (*Canis familiaris*), Coyote (*Canis latrans*), Red Fox (*Vulpes vulpes*), Bobcat (*Lynx rufus*), American Black Bear (*Ursus americanus*), and large hawks and owls (Grizzell 1955; Kwiecinski 1998).

Diel activity is an important aspect of an animal's natural history because the circadian rhythm regulates fundamental processes including responses to abiotic and biotic factors (Halle 2000). It is important to document diel activity patterns of animals in urban areas because activity may be altered by artificial light (e.g., Longcore and Rich 2004), changed predation risk (e.g., Watson 2009; Lehrer 2011; Fischer *et al.* 2012), or human disturbance (Ditchkoff *et al.* 2006). I modelled summer diel activity of urban Woodchucks using camera traps and the cosinor method (Nelson *et al.* 1979; Pita *et al*. 2011; Steen 2017). I expected diurnal activity (Bronson 1962; Conrad and Fidura 1970; Hayes 1976; Meier 1985) and wanted to determine if a non-invasive method gives reliable activity estimates as an alternative to more labour-intensive direct observation.

Methods

Study site and camera traps

I placed trail cameras at four Woodchuck burrows in backyards in the City of London, Ontario, Canada (42.995°N, 81.2707°W), 10–25 June 2015. This urban area is surrounded by wooded parks and green spaces that harbour a variety of mammals and birds. The four Woodchuck burrows were in different private gardens, where all had one or two main entrances and were positioned under trees and bushes. One of the burrows was inhabited by a female with two young-of-the-year; the three other burrows were each inhabited by solitary males. At the adult female's burrow, camera captures of any of the three Woodchuck were analyzed. I could not compare behaviour of the family with that of solitary males due to small sample sizes.

I used camouflaged coloured Browning Dark Ops HD cameras (Browning, Birmingham, Alabama, USA). This small trail camera (11.4 × 8.3 × 6.4 cm) is activated by a passive infrared sensor (PIR) that detects movement at any hour (Swann *et al.* 2004) and features a no glow infrared flash to ensure the animal does not detect the camera. I chose the video recording mode, although still images also would have worked. I mounted the cameras on tree trunks facing the main entrance of the burrows (one at each site) to record activity (Video S1). Each recording was set to last for 10 s, with no delay between each trigger. I only included complete hours of monitoring. I reviewed the videos from the camera traps by using the VideoLAN Client (VLC; Version 2.2.6 Umbrella, free, open source, cross-platform media player). I post-processed the data using R version 3.10.0 (R Core Team 2016), and followed the data processing procedure described in Steen (2017) to create a timeframe for the complete monitoring period for a given hour-block, date, and burrow. Instead of using frequency (number of observations per hour block) in the analysis, I only scored presence or absence of Woodchucks within an hour block (i.e., 'no woodchuck' or 'woodchuck' per observed hour-block; see below). This is a conservative measurement, but is preferred over frequency data because it is likely that not all activity of an individual was recorded (e.g., individuals using an entrance out of view of the camera).

Diel activity and analysis

Statistical analysis was performed using the "lme4" package (R Core Team 2016). The analysis of diel activity rhythms was based on generalized linear mixed-effects regression models (Pinheiro and Bates 2000) in which the periodic component of time series was represented by pairs of sine and cosine functions (Nelson *et al.* 1979; Pita *et al.* 2011; Steen 2017). The response variable was whether there was a Woodchuck observed within an hour-block for each burrow during the 24-h monitoring period each day (Steen and Barmoen 2017). Hence, the response variable had two outcomes: 'no woodchuck' or 'woodchuck' per observed hour-block, modelled using binomial distribution logistic regression models (Galyean and Wester 2010). The fixed explanatory variable, time of the day (i.e., 24 hours), was fitted using the cosinor method (Nelson *et al.* 1979; Pita *et al.* 2011; Steen 2017), first with 24 h as the fundamental period and then with one or two harmonics of 12-h and 8-h periodicity to modulate the signal. The cosinor method uses a fundamental function and one or more harmonics to characterize the waveform of the activity rhythm (Nelson *et al.* 1979; Pita *et al.* 2011; Steen 2017). Each added harmonic improves the fit, although too many harmonics could add too much complexity and cause overfitting (Sheather 2009). I included burrow as a random effect to control for repeated measurements at each site, individual variation among Woodchucks inhabiting burrows (in particular for this study female with young versus solitary male), and different sampling effort among burrows.

Different sampling effort was due to time required to locate the burrows and maintain the cameras.

To control for ambient temperature and wind as possible factors influencing diel activity, I used hourly ambient temperature (°C) and wind speed (km/h) from the nearest weather station (London A climate station, distance ~10.0 km; www.climate.weather.gc.ca) as co-variables. The average 24-h temperature during the June monitoring period was 19.3°C (SD 3.7, range 10.8–29.0°) and average wind speed was 12.1 km/h (SD 6.9, range 1–41).

To avoid overfitting the activity curve (i.e., by adding too many harmonics or including unnecessary co-variables), I calculated the small-sample correction AICc for each model (Burnham and Anderson 1998; Burnham 2002; Aho *et al.* 2014). I evaluated each model by assessing the AICc values against the model that included only the random term (M_0). The model with the lowest AICc value was considered the 'best'. Models in which the difference in AICc relative to $AICc_{min} < 2$ are considered to have substantial support (Burnham and Anderson 1998; Burnham 2002).

I computed the 95% CI of the fitted line by model-based parametric bootstrapping for mixed models (*bootMer* function, 1000 simulations, "lme4" package). I was particularly interested in the global acrophase or time point in the cycle describing an activity peak in the cosinor model and which part of the day that activity was higher than the average (i.e., mid-line estimating statistic of rhythm, hereafter called MESOR). Global acrophases correspond to the time intervals at which the fitted function had peak value (Pita *et al.* 2011). The time of day that the modelled activity was above MESOR could be defined as the main activity period (Navarro *et al.* 2013).

Results

Only a few observations were recorded at night (range 0059–2220) and I monitored the Woodchucks for a total of 900 h in June 2015 (Table S1); Woodchucks were diurnal (presence/absence at the burrow entrance; raw data, Figure 1). The diurnal activity pattern was confirmed by the best-fitted multi-cosinor model (AICc = 902.8 versus AICc = 1128.8 for the null model, Table 1; fitted line, Figure 1; Tables S2 and S3). The most parsimonious model was based on the 1st harmonic component (12 h) in addition to the fundamental period (24 h). Adding the 2nd harmonic (8 h), temperature or wind did not improve model fit (Tables 1 and 2). Including wind and temperature (M_{10} and M_6, respectively) in addition to the time variable in the second and third-best models suggested that wind and temperature had opposite effects (Table S4); the coefficient for wind was positive while temper-

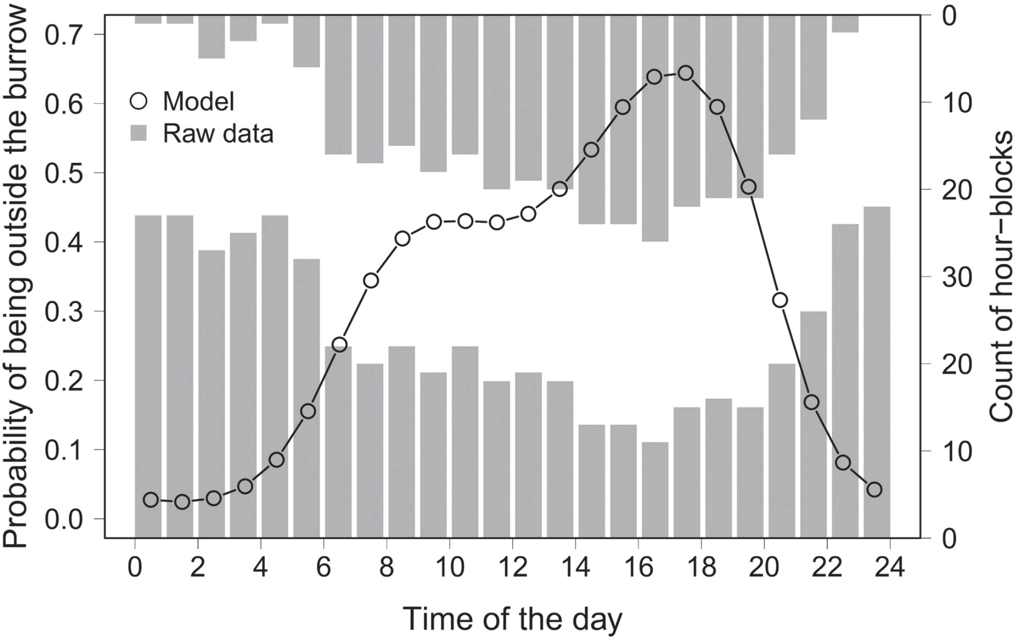

FIGURE 1. Modelled diel activity of Woodchuck (*Marmota monax*), London, Ontario, Canada, June 2015, with the probability of the Woodchuck being outside the burrow in an hour-block (denoted with dot-plot connected with line) and based on the best-fit model (parameter estimates given in Table 1, $n = 900$; random effect = 4). The lower grey bars are the count of hour-blocks with 'no woodchuck' ($n = 574$) and upper grey bars are the count of hour-blocks with 'woodchuck' ($n = 326$).

TABLE 1. Analysis of diel activity rhythm models for Woodchuck (*Marmota monax*), in June 2015, London, Ontario, Canada. The model with the lowest AICc was considered the 'best'. The five highest ranked models are shown. For full model comparison see Tables S2–S4.

Model	K	AICc	ΔAICc
M_2	6	902.81	0.00
M_{10}	7	903.30	0.49
M_6	7	904.82	2.01
M_3	8	905.32	2.51
M_{11}	9	905.49	2.68

ature was negative. This suggests a higher probability of Woodchucks being present at the burrow when it was windy or colder, although these models had low support (Table S3). Further, models only including wind and temperature (M_8 and M_4, respectively) were ranked lowest in comparison to models including the time variable. Thus, there is strong support for Woodchuck activity to oscillate under a light:dark regime with minor influences by abiotic factors such as temperature and wind. The activity pattern at the burrows was unimodal (left skewed) and concentrated in the daylight hours, starting at sunrise and peaking in the afternoon (from 1300–1400 until 1900–2000 hour-blocks, i.e., the global acrophase) and ceasing before sunset (Figure 2). The mean of the modelled activity curve (MESOR) was found to be 0.31 (model M_0, including only intercept and random effect term).

Discussion

I found that Woodchuck had a strictly diurnal activity pattern (presence/absence of the Woodchuck at the burrow entrance) during June as has been found with previous telemetry and direct observation studies (Bronson 1962; Conrad and Fidura 1970; Hayes 1976; Meier 1985). The activity pattern was unimodal, starting with sunrise and ending before sunset. The unimodal pattern corresponds with telemetry data collected during spring and early summer (1–14 June) near the southern range limit of the species (ca. 36° latitude, northern part of Arkansas; Hayes 1976). Although later in June, July, and August, Hayes (1976) found a transition to a bimodal activity pattern before returning to the unimodal state in October. Using direct observation, Bronson (1962) found a bimodal pattern for general activity during the summer months (May–August) and a unimodal pattern early and late in the year (February–April and September–November, ca. 40° latitude, south-central Pennsylvania). Conrad and Fidura (1970) performed systematic sightings during April–May and found that the activity was characteristically unimodal early in this period with a peak at midday and was bimodal with peaks in early morning and late afternoon later in the period (western New York; ca. 42–43° latitude). Further, the onset and cessation of daily activity agreed with Hayes (1976). I found daily activity at the burrow site was low from activity onset until 0700–0800, similar to Merriam (1966) who found by telemetry that, at the onset of daily activity, the proportion of inter-burrow movements was much lower than the proportion of total activity. Merriam (1966) proposed that morning activity might involve a higher proportion of feeding and related movements.

All of these previous studies monitored Woodchucks in more rural settings: old fields with woodlots (Bronson 1962), cultivated hayfields (Hayes 1976), or land previously farmed with old fields and second growth hardwood forest (Conrad and Fidura 1970). Although comparing my results with those of others is limited to examining general trends due to methodological differences (cameras versus direct observations and telemetry), the urban setting in my study did not appear to result in a change in general activity pattern seen in these more rural areas.

The time of day that Woodchuck activity (presence/absence at the burrow entrance) increased from below the MESOR to above the MESOR (i.e., upward crossing) was from 0700 to 0800 (i.e., switched from lower to higher activity). The time of day that the modelled activity decreased from above the MESOR to below the MESOR was at the end of hour block 1900–2000 (i.e., downward crossing, switched from higher to lower activity). Hence, ~12 hours represent the relative length of the main active period, with

TABLE 2. Analysis of diel activity rhythm models of Woodchuck (*Marmota monax*), in June 2015, London, Ontario, Canada. Parameter estimates from the best-fit model (number of observations: 900; random effect: four burrow sites).

Fixed effects:	Estimate	SE	Z-value	*P*
(Intercept)	−1.13	0.45	−2.50	0.012
I(cos(2 · pi · Hour/24))	−1.66	0.15	−11.11	<0.001
I(sin(2 · pi · Hour/24))	−0.74	0.12	−6.34	<0.001
I(cos(2 · 2 · pi · Hour/24))	−0.78	0.13	−6.00	<0.001
I(sin(2 · 2 · pi · Hour/24))	−0.19	0.12	−1.52	0.128

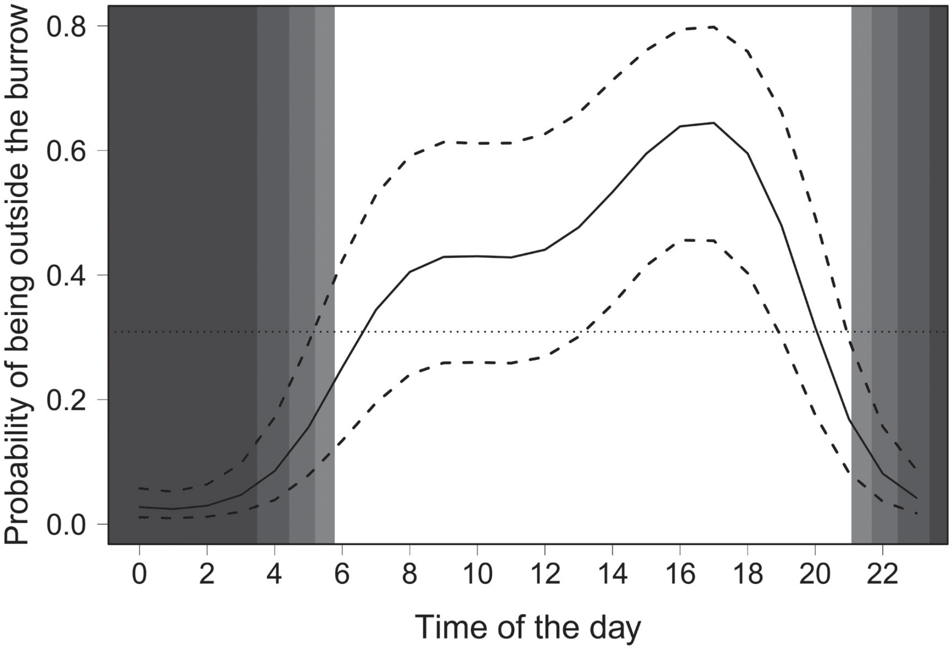

Figure 2. Activity plot with grey shading in accordance to the three types of twilight: astronomical, nautical, and civil (dark to light, respectively, with the white area representing daylight). Modelled activity is of the urban Woodchuck (*Marmota monax*), London, Ontario, Canada, June 2015, outside the burrow site (fitted line in solid and upper and lower 95% CI in dashed line). The MESOR (midline estimating statistic of rhythm) is indicated with a dotted line and parameter estimates are given in Table 1 (*n* = 900; random effect = 4).

an afternoon peak. The period from no activity to MESOR was about three to four hours. The period from MESOR to no activity was about two to three hours. Activity was found to be higher in the afternoon (from 1300–1400 to 1900–2000, i.e., the global acrophase), with a peak in the late afternoon (1500–1700). This pattern corresponded well with inter-burrow movements by Woodchucks revealed by telemetry on one adult and three juveniles conducted in New York mainly in August by Merriam (1966). Woodchucks might become satiated after spending more time foraging during the first part of the day and then spend more time resting at the burrow site.

Temperature and wind were not included in the best-fit model. The two models that included wind and temperature, in addition to the time variable, showed a higher probability of Woodchucks being present at the burrows when it was windy and colder. Because wind and, in particular temperature, are dependent on time-of-day (light:dark regime), the effect of these abiotic weather variables on Woodchuck daily activities might only be unravelled under experimental conditions by dissociating time and weather variables. According to the best-fit model that contained only the time variable, I propose that during the early summer, Woodchuck activity oscillates under a light:dark regime with a minor influence of abiotic factors such as temperature and wind. In contrast, annual activity patterns (i.e., initiation and termination of torpor) are likely driven by both photoperiod length and temperature (Zervanos *et al.* 2010). Hayes (1976) compared early and late season with summer activity and found that the activity curves for early and late season were more irregular compared with the relatively smooth activity curve during summer. Hayes (1976) interpreted this as evidence of weather effects on aboveground activity during the early and late season (with more severe weather). However, during summer, Woodchucks were also found to avoid high temperatures during the middle of the diurnal period. Ambient temperature during these periods showed that temperatures above 31°C reduced aboveground activity (Hayes 1976). Such high temperatures were not registered during my monitoring period (maximum temperature was 29°C).

Conclusions

Camera trapping is a non-invasive method that provides insight to diel activity as it easily monitors extended periods and reduces the effort required for direct observation. My camera data revealed a similar diel activity pattern in urban Woodchucks as previously documented by telemetry and direct observations during summer in more rural settings (Bronson 1962; Hayes 1976; Meier 1985). Adding additional camera traps to monitor foraging activity (e.g., Steen and Barmoen 2017) or combining cameras with telemetry (e.g., Leuchtenberger *et al.* 2014) and extending studies to monitor the complete annual cycle (e.g., Racheva *et al.* 2012) would improve future monitoring.

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SUPPLEMENTARY MATERIALS:

Video S1. Video example of a Woodchuck (*Marmota monax*) revealed by the camera trap. https://www.canadianfieldnaturalist.ca/index.php/cfn/article/view/2110/2601.

TABLE S1. Monitoring effort (number of hours monitored) at each Woodchuck (*Marmota monax*) burrow, London, Ontario, Canada, in June 2015.

TABLE S2. Models used to study Woodchuck (*Marmota monax*) activity, in June 2015, London, Ontario, Canada.

TABLE S3. Analysis of diel activity rhythm models for Woodchuck (*Marmota monax*), in June 2015, London, Ontario, Canada.

TABLE S4. Analysis of diel activity rhythm models for Woodchuck (*Marmota monax*), in June 2015, London, Ontario, Canada.

The Canadian Field-Naturalist

Year-round patterns of mineral lick use by Moose (*Alces americanus*), deer, and Elk (*Cervus canadensis*) in north-central British Columbia

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Abstract

Natural mineral licks are important to the physiological ecology of several species of ungulates in North America and abroad. Information on year-round patterns of mineral lick use by ungulates in Canada is poorly understood. We used camera traps to record patterns of mineral lick use by four ungulate species visiting five naturally occurring mineral licks located within the John Prince Research Forest and surrounding area, near Fort St. James, British Columbia, Canada. Our cameras detected over 1800 mineral lick visits by ungulates from February 2017 to January 2018. Mineral licks were visited year-round, however, most visits were made between May and September during morning hours. We observed variable lick visitations among sites, species, and sex and age classes. The species observed in descending number of lick visits included Moose (*Alces americanus*), White-tailed Deer (*Odocoileus virginianus*), Elk (*Cervus canadensis*), and Mule Deer (*Odocoileus hemionus*). Some licks were visited by all four species, while others were visited by fewer. Female ungulates were recorded at licks more frequently than males or juveniles, which likely reflected the underlying sex and age structure of the population. Elk spent more time at licks than Moose and deer and there was no difference in visit durations between Moose and deer. Most visits were made by single animals, but group visits were also observed. Our findings provide evidence that mineral licks are used year-round by ungulates and appear to be important habitat features on the landscape.

Key words: Camera trap; mineral licks; Moose; Elk; Mule Deer; White-tailed Deer; ungulates

Introduction

Mineral licks (also known as salt licks, mineral springs, and muck licks) are used by a variety of wildlife species (Jones and Hanson 1985). Formed commonly near groundwater springs, on exposed rock faces, along streams, or around tree roots or clay banks, licks are areas where soil solutes can concentrate (Jones and Hanson 1985; Shackleton 1999). Licks are generally classified as dry (e.g., rock faces, clay banks; Jones and Hanson 1985) or wet. Wet licks are frequented by Elk (*Cervus canadensis*) and Moose (*Alces americanus*; Fraser and Hristienko 1981; Parker and Ayotte 2004). Other ungulates, such as White-tailed Deer (*Odocoileus virginianus*) and Mule Deer (*Odocoileus hemionus*) also visit wet licks (Fraser and Hristienko 1981; Shackleton 1999; Jokinen *et al.* 2016) during the early spring and summer months, with little to no visitation in the winter, but see Rea *et al.* (2013a).

Many mineral licks have elevated concentrations of sodium, which is thought to be a key attractant for animals such as Moose (Fraser and Hristienko 1981; Fraser *et al.* 1982; Tankersley and Gasaway 1983) and Elk (Lavelle *et al.* 2014). Several studies have concluded that in addition to sodium, other elements in licks such as carbonates, magnesium, and iron may be attractants to animals (Cowan and Brink 1949; Kreulen 1985; Kennedy *et al.* 1995; Ayotte *et al.* 2006). Visitation to mineral licks by ungulates for sodium and other attractants is thought to be related to milk production (Ayotte *et al.* 2006), the demands of antler growth (Atwood and Weeks 2002), and elements required for improved rumen function (Ayotte *et al.* 2008).

Carbonates (Ayotte *et al.* 2006) and magnesium found in licks may act to combat dietary deficiencies and as compounds necessary for herbivores to regulate high levels of dietary potassium in spring compared to winter forages (Dormaar and Walker 1996; Shackleton 1999; Parker and Ayotte 2004; Jokinen *et al.* 2016). Rea *et al.* (2013a) found that iron concentrations were high at licks in northern British Columbia (BC). Iron could potentially act as an attractant for Moose populations that could use supplemental iron to defend against ticks and improve blood and muscle function (Rea *et al.* 2013a). Iron-rich soils are known to be used by both Snowshoe Hare (*Lepus americanus*; Rea *et al.* 2013b) and Black-tailed Jackrabbit (*Lepus californicus*; Arthur and Gates 1988). In addition to the importance of acquiring minerals, lick sites may also be used for non-dietary needs such as social gathering (Knight and Mudge 1967; Carbyn 1975; Fraser and Hristienko 1981; Atwood and Weeks 2002).

Mineral lick research has predominantly been conducted using daytime visual observations of animals at licks between April and September (Cowan and Brink 1949; Carbyn 1975; Fraser and Hristienko 1981; Ayotte 2004; Parker and Ayotte 2004; Ayotte *et al.* 2006, 2008), which has been termed the 'high use' period. Few studies have been conducted over continuous 24-hour periods (Tankersley and Gasaway 1983) or with camera traps (Atwood and Weeks 2002; Lavelle *et al.* 2014; Jokinen *et al.* 2016). In addition, year-round research into the use of licks using cameras (Rea *et al.* 2004, 2013a) is limited, resulting in an incomplete picture of seasonal patterns of use.

Licks that are used year-round by ungulates may be negatively impacted by land development activities. Because few policies exist that explicitly protect lick sites (Rea *et al*. 2004; Jokinen *et al*. 2016), year-round studies that can delineate time-of-day, season-of-year, and species-specific use patterns could be of value for forest and wildlife managers attempting to balance resource extraction with local wildlife management objectives (Dormaar and Walker 1996; Atwood and Weeks 2002; Parker and Ayotte 2004; Rea *et al.* 2004).

To better understand the daily and year-round seasonal use of mineral licks by ungulates in a managed forest, we installed video-enabled trail cameras at five mineral licks in and adjacent to the John Prince Research Forest in north-central BC, near Fort St. James. Cameras were monitored for one full year to determine which species were using the licks and if use patterns varied by species and among licks. Due to the presumed importance of mineral licks to ungulates, our null hypothesis was that mineral licks would be used by all ungulates equally and that time of day and season of use would not vary among species.

Methods

Study area

We established two wildlife video camera trap stations at each of five mineral licks in and adjacent to the John Prince Research Forest (JPRF; 16 500 ha, 54.833°N, 124.583°W) ~160 km northwest of Prince George, BC, Canada (Figure 1). The area is within the Sub-boreal Spruce Biogeoclimatic Zone, with the local geology comprised of limestone and ultramafic bedrock overlain predominantly by glacial till (Rea *et al.* 2013a). Mean daily average temperatures in the area (2014–2018) were 4.3°C and ranged from a monthly mean daily average of –6.5°C in January, to a monthly mean daily average of 16.7°C in July. Mean annual precipitation was 212.34 mm, with an average of 61.8 cm of it falling as snow (Environment and Climate Change Canada 2019). The maximum for mean monthly snow on the ground typically occurred in February and averaged 37.91 cm (SE 6.30) from 2014 to 2018. In 2017 and 2018, the maximum for mean monthly snow on the ground was 14.88 cm (January) and 58.04 cm (February), respectively (Environment and Climate Change Canada 2019).

Five wet mineral licks within or in close proximity to the JPRF that had been previously documented during field activities were monitored for one year (1 February 2017–31 January 2018). Sites were chosen based on their location within or proximity to the research forest with sites named according to a history of monitoring or their general location. All licks had been known to be used by Moose, some of which are known to migrate seasonally in and out of the research forest (to higher elevations in summer; Chisholm 2018). Deer had also been documented using the lick sites and are known to migrate seasonally in the province (D'Eon and Serrouya 2005), although nothing specific is known about local elevational movements by deer or the seasonal movements or migrations of Elk that inhabit the local area.

Data collection

Two digital passive infrared trail cameras (Trophy Cam HD Model 119477 and 119676, Bushnell Outdoor Products, Overland Park, Missouri, USA) were used at each mineral lick. We used two cameras per site to capture a wide angle of view and to reduce potential errors associated with possible camera malfunctions. Cameras were set on trees at ~1.5 m above ground along the edge of each mineral lick with each camera facing a different direction to maximize coverage of activity areas. Cameras were checked approximately once every three weeks to change memory cards, check batteries, and adjust camera position (sometimes cameras were bumped by animals). Video recording times were set at 20 s, with a 1 s delay be-

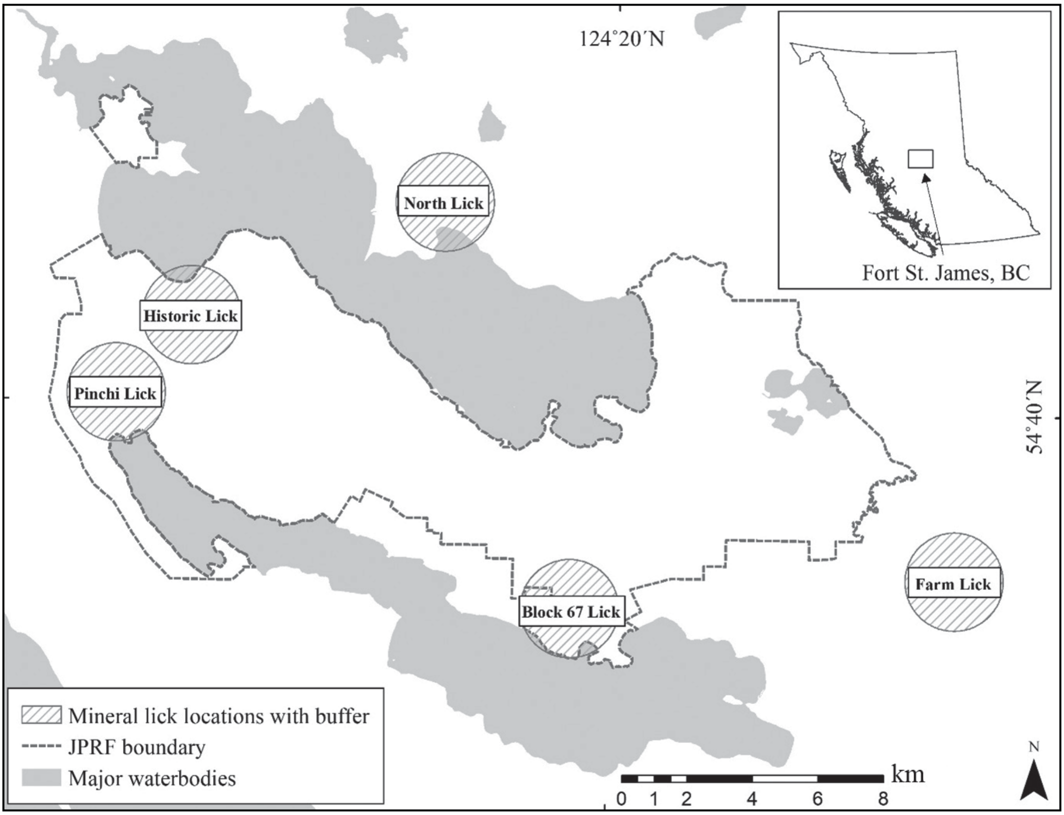

Figure 1. Location of five mineral licks within the John Prince Research Forest and surrounding area near Fort St. James, British Columbia (inset). Buffers added to disguise exact locations of licks.

tween videos to allow for near-continuous videos if an animal remained present and active in front of the camera. Date and time imprints were stamped on each video recording. All cameras were set to daylight savings time for the entire study.

Videos were downloaded, viewed, and information entered into a database. Date, time, temperature, and video number were recorded, then videos were scrutinized to identify the number of individuals, species, sex and age class, the time the animal came into view and left the camera view (in 24-h format) as well as other behaviours. It took 90–120 s to analyze each video.

Animal visits, as captured by cameras, were considered independent and were generally easy to define when different individuals and species were recorded. When the identification of individuals of a species was difficult, which was common in low light conditions, we used average visit times by each species to delineate visits. To determine average visit times for each ungulate species, we recorded how much time individual animals would spend at a lick during a single visit. We then averaged visit times and used the average lengths of these visits as cut-offs to delineate one independent visit from another where an animal of questionable identity moved into and out of the camera's field of view.

Data interpretation

Data were sorted for every ungulate visit. Overlapping dates taken from both cameras at each site were organized and selected to avoid duplicates. To determine length of stay, any data that overlapped from both cameras were merged into one entry, and time of departure was subtracted from time of entry. Data were then grouped for the entire study period, by month, and by day for analyses of trends and patterns.

Moose, Elk, Mule Deer, and White-tailed Deer adult males were identified using antler presence and antler pedicel scars in the months following antler shedding. Moose, Elk, and deer adult females were identified by lack of antlers and lack of antler scars, with female Moose being further identified by the presence of a vulva patch, if visible (Rea *et al.* 2013a). Juveniles were identified based on morphological differences and spotting patterns on coats of younger animals (Ayotte *et al.* 2008).

When animals stepped out of the view of the primary camera, if malfunctions in camera recordings occurred, if data files became corrupt, or if a camera was knocked out of alignment by an animal, data from the second camera at the site were used. During time periods when both cameras at a lick malfunctioned or were not operational (the last two weeks of December at the Farm Lick; Figure 1) we corrected these data to standardize the total number of visitations for that month. We did this by multiplying the number of individual visits during the part of the month in which the camera was recording with the number of days in that month (31 days for December) and then dividing that by the number of days the camera was functioning in that month (as per Rea *et al.* 2013a). This method assumed that the number of visits/day to the lick on the days of the month that the camera was functional equalled the number of visits/day to the lick on the days of the month that the camera malfunctioned.

Statistical testing

We used a series of Kruskal-Wallis (Van Hecke 2013) and multiple comparisons *P* value (two-tailed) tests to determine if there were differences in visit times by species. We used an alpha of 0.05 for all analyses. All statistical tests were completed in Statistica 9.0 (StatSoft 2009).

Results

Our cameras captured 1817 independent ungulate visits to the five mineral licks between 1 February 2017 and 31 January 2018. Most recordings were of Moose (*n* = 621), followed by White-tailed Deer (*n* = 547), Elk (*n* = 495), and Mule Deer (*n* = 154). The majority of mineral lick visits were by single animals: 84% of Moose, 79% of Mule Deer, and 66% of Elk and White-tailed Deer.

Species variability by site

Moose were recorded more often at the Block 67 Lick, the Historic Lick, and the Pinchi Lick, whereas White-tailed Deer were the dominant species recorded at the Farm Lick, and Elk made relatively more visits to the North Lick (Figure 2). The largest number of ungulate visits (*n* = 837) was recorded at the Farm Lick, with White-tailed Deer visits (*n* = 516) at this site accounting for 94% of all White-tailed Deer visits to all licks. Most Moose (*n* = 198) were recorded at the Farm Lick, accounting for 32% of the total Moose visits across all licks; 21% of all Elk and 12.4% of all Mule Deer visits were also recorded at the Farm Lick. There were 552 total ungulate visits recorded at the North Lick, of which 255 were Elk (comprising 52% of the total Elk visits across all licks), 185 were Mule Deer (accounting for 85% of Mule Deer visits across all licks); 22% of all Moose, and 5.2% of all White-tailed Deer visits occurred at the North Lick.

Our cameras recorded 270 ungulate visits at the Block 67 Lick, accounting for 26% of the total Moose visits, 21% of all Elk, 1.3% of all Mule Deer, and 0.5% of all White-tailed Deer visits to all licks. There were 93 ungulate visits recorded at the Historic Lick, accounting for 14% of all Moose, 0.4% of all Elk, and 1.3% of all Mule Deer visits to all licks. No White-tailed Deer were recorded at the Historic Lick. Only Moose and Elk were recorded 65 times at the Pinchi Lick, accounting for about 6% of Moose and Elk visits.

Seasonal trends

More ungulates (*n* = 308) were recorded at licks (all visits pooled for all licks) in June than any other

FIGURE 2. Total number of independent ungulate visits at five mineral licks in the John Prince Research Forest in north-central British Columbia, Canada, February 2017–January 2018. Note: No Mule Deer (*Odocoileus hemionus*) or White-tailed Deer (*Odocoileus virginianus*) were recorded at the Historic Lick and no White-tailed Deer were recorded at the Pinchi Lick.

month of the study period, followed by July (n = 278), August (n = 254), September (n = 240), and May (n = 220; Figure 3). The fewest number of visits were recorded in February (n = 35). Recordings of Moose and Elk were made in all months while White-tailed Deer were recorded from March to January and Mule Deer from May until November. Similar to trends using the pooled results, visits to licks by Moose peaked in June (n = 152; Figure 3). However, peak visits by other species were variable, with White-tailed Deer peaking in September (n = 143), Elk peaking in May (n = 90), and Mule Deer peaking in August (n = 61).

Visits to licks by ungulates outside of the high-use period of May–September (i.e., October–April) were mostly made by Moose (n = 230), with a peak in visits during December (n = 59; Figure 3). White-tailed Deer made 154 lick visits during the winter months, with a peak in April (n = 81). Elk were also recorded visiting licks during this period (n = 125) with a peak in March (n = 33). Mule Deer made eight visits to licks during October–April, with four in October and four in November.

Timing of visits

More ungulates visited licks over the entire year study period (combined visits) at 0700 than any other time of the day. Of the 116 independent visits to licks at 0700, 33% were Elk, 32% Moose, 28% White-tailed Deer, and 7% Mule Deer (Figure 4). The fewest ungulate visits (n = 47) across all licks occurred at 0100. Time of day was divided into four periods (morning: 0600–1159, afternoon: 1200–1759, evening: 1800–2359, and night: 0000–0559; as per Jokinen *et al.* 2016). Most visits combined occurred in the morning (n = 571), of which 41% were White-tailed Deer, 25% Moose, 22% Elk, and 12% Mule Deer. There were 476 ungulate visits during the evening, of which 43% were Moose, 35% Elk, 17% White-tailed Deer, and 5% Mule Deer. There were 389 ungulate visits during the afternoon, of which 45% were White-tailed Deer, 24% Moose, 22% Elk, and 9% Mule Deer. There were 365 ungulate visits during the night, of which 46% were Moose, 32% Elk, 14% White-tailed Deer, and 8% Mule Deer (Figure 4). Although there were fewer visits to licks during winter, the pattern of visits by ungulates by time of day was relatively unchanged, with fewer visits over a 24-h period made from 2100 to 0600, and at mid-day, with most visits occurring from 0600 to 1100 and from 1300 to 2000 (Figure 5).

Visit duration

Ungulates spent an average of 15:33 ± 24:48 (SD) min:sec at licks throughout the study period. The only significant differences in the amount of time spent at licks was between Elk (an average of 22 min per visit) and all other species (n = 1801, H_3 = 26.281, $P < 0.0001$), with specific pairwise differences between Elk and Moose ($P < 0.0001$), Elk and White-tailed Deer ($P < 0.0001$), and Elk and Mule Deer (P = 0.006; Figure 6). Moose made more visits to all the licks over the study period but spent less time on average (14:26 ± 26:31 min:sec) at licks when com-

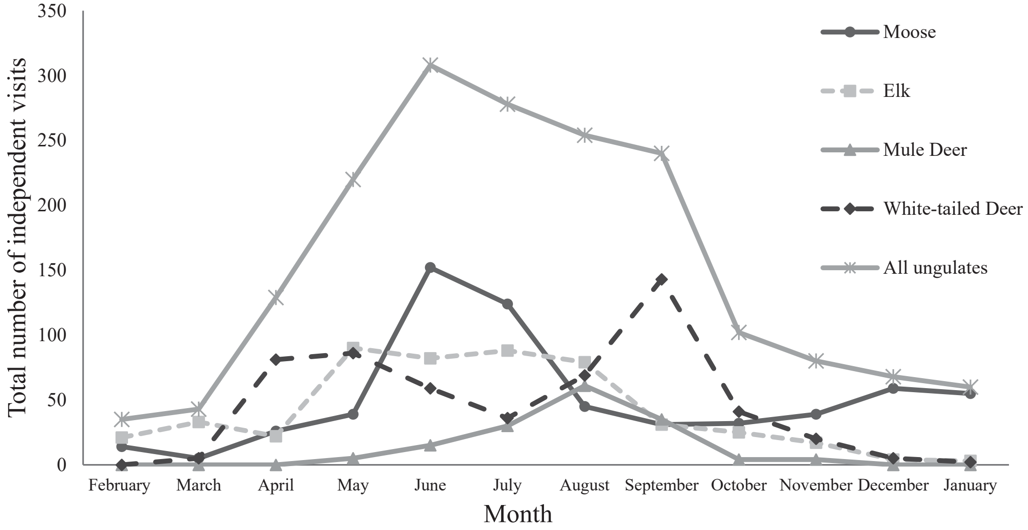

Figure 3. Total number of independent ungulate visits to mineral licks by month in the John Prince Research Forest in north-central British Columbia, Canada, February 2017–January 2018. Visits are pooled across all five licks.

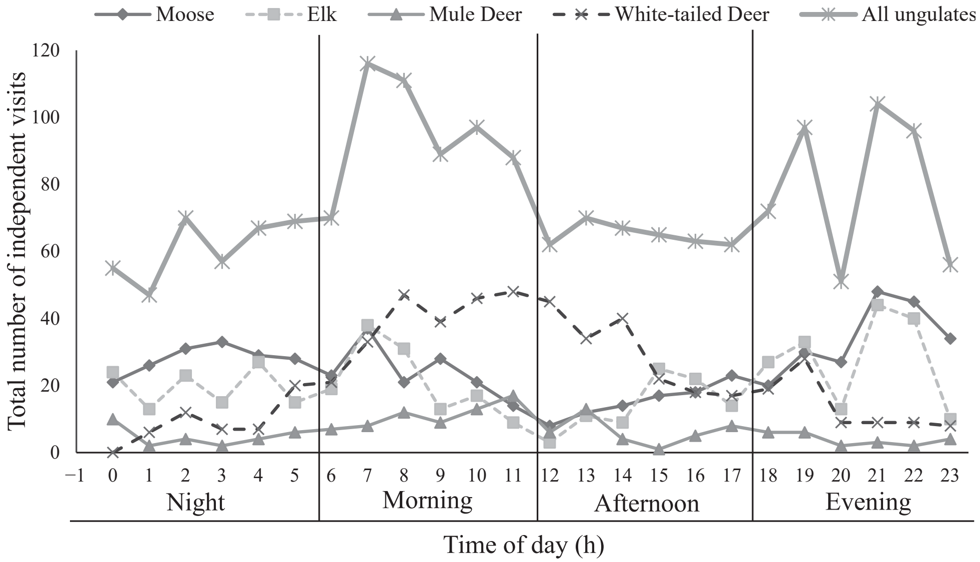

FIGURE 4. Total number of independent ungulate visits to mineral licks by time of day in the John Prince Research Forest in north-central British Columbia, Canada, February 2017–January 2018. Visits are pooled across all five licks.

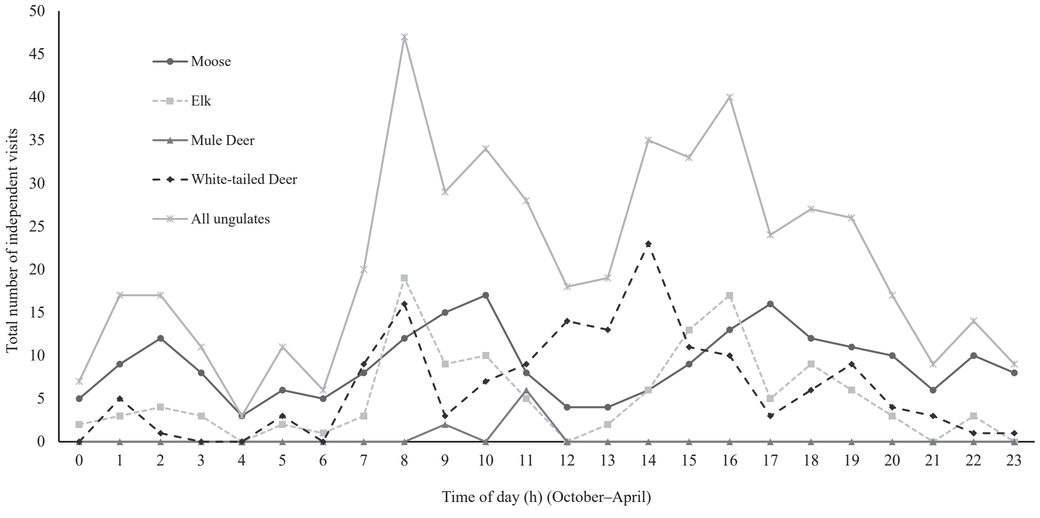

FIGURE 5. Total number of independent ungulate visits to mineral licks outside of the high-use period (i.e., October to December 2017 and January to April 2018) by time of day in the John Prince Research Forest in north-central British Columbia, Canada. Visits are pooled across all five licks.

pared to Elk. Mule deer spent nearly the same amount of time on average (11:49 ± 14:52 min:sec) at licks as White-tailed Deer (12:13 ± 17:29 min:sec), but were recorded having fewer visits on average.

The amount of time Moose spent at licks varied significantly among some licks ($n = 608$, $H_4 = 29.54$, $P < 0.0001$; Figure 7). Moose spent significantly more time per visit at the Farm Lick than the North Lick ($P < 0.0001$) or the Historic Lick ($P = 0.03$). The amount of time Elk spent at licks varied significantly among some licks ($n = 496$, $H_4 = 68.43$, $P < 0.0001$; Figure 7). Elk spent significantly more time per visit at the North Lick than at the Farm Lick ($P < 0.0005$), the Pinchi ($P < 0.0001$), or Block 67 ($P < 0.0001$) licks (Figure 7). The amount of time Mule Deer or White-tailed Deer spent at licks did not vary significantly among licks ($n = 154$, $H_3 = 5.48$, $P = 0.14$; $n = 544$, $H_2 = 4.22$, $P = 0.12$, respectively; Figure 7).

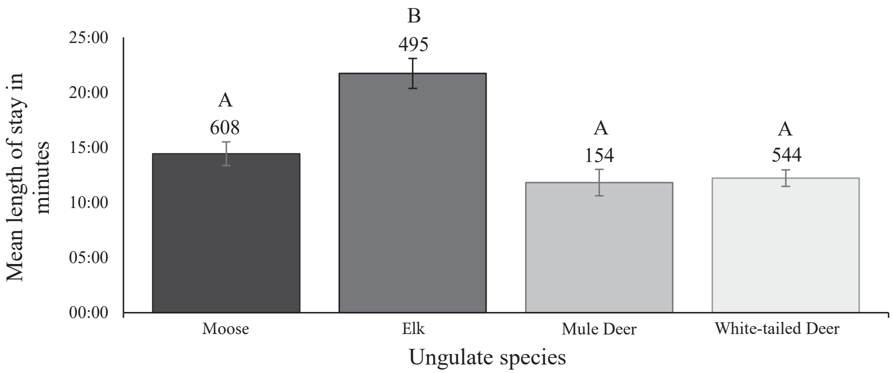

FIGURE 6. Mean (± SE) length of stay in min:sec for each species of ungulate visiting all mineral licks. The sample of independent visits from the beginning of February 2017 to the end of January 2018 is represented by the number above the error bar. If error bars share a common letter they were not statistically significantly different from one another ($P \geq 0.05$).

Sex and age classes

Female ungulates of all species (n = 1026) visited mineral licks more than males (n = 477) or juveniles (n = 298) throughout the study (Figure 8). Males generally visited the licks more than juveniles, but this trend was reversed for White-tailed Deer; Mule deer made up the fewest number of visitors to licks in all sex and age classes (Figure 8). Overall, the total number of visits to licks by female Moose was lowest in March (n = 5) and peaked in June (n = 77; Figure 9). In general, male Moose and juveniles followed a similar pattern as the females. Total visits by female Elk peaked in May (n = 47) and were lowest in December (n = 2; Figure 9). Male Elk followed a similar visitation pattern as female Elk over the course of the year and peaked in June (n = 47). Visits by juvenile Elk peaked in August (n = 22). Visits by female Mule Deer began to rise in April, peaked in August (n = 33), then decreased through to November (Figure 9). Visits by male Mule Deer peaked in July (n = 12) thereafter declining steadily towards winter. Total visits by juvenile Mule Deer peaked in August (n = 17) declining to October when visits stopped. Female White-tailed Deer visits peaked in April (n = 76) with a secondary peak in September, with male visits peaking in May (n = 25) with a secondary peak in August while juveniles visited most often in September (n = 76; Figure 9).

Discussion

With the use of cameras, we determined that over 1800 visits were made by ungulates in a one-year period to the five licks. The majority of visits were made by single animals, with most species visiting licks at various points throughout the year. Visits to licks were made in all months by Moose and Elk, while White-tailed Deer were recorded in every month except February. Mule Deer were recorded at licks in the summer and in October and November, but otherwise did not visit much outside of the high-use period of May to September.

The use of video cameras helped us determine visit lengths and the number of independent visits. With two cameras on each site, we were able to document time of entry and exit from licks by ungulates, giving us a better average length of stay for each animal, and thus a way to determine an independent visit. Additionally, we were able to record ungulate behaviour at lick sites, allowing us to see Moose cratering in the snow to access the lick and could help explain why Moose spent longer periods of time at licks in winter compared to other ungulates we studied. Video footage showed us Moose behaviour that included resting on, or adjacent to, snow-covered licks, behaviours that may otherwise have been missed with non-video cameras that only capture still images when triggered by movement. The use of video cameras may have helped to reduce gaps in our understanding by providing continuous recordings of Moose and other ungulate behaviour that still images could have missed. The audio in video mode also allowed us to hear vocalizations and to detect movements just outside of the camera view that were useful in understanding what was happening during each visit.

Seasonal trends

We recorded more visits to licks during the summer than during any other season. Moose visitations peaked in June, as previously found by Stepanova *et al.* (2017). Moose were also the dominant species recorded at licks in July, November, December, and January. The use of licks by Moose increased from February into May, peaked in June, and decreased in July, which corresponds to findings by Ayotte (2004) and coincides with early summer sodium deficiencies linked to spring plant phenology (Fraser and

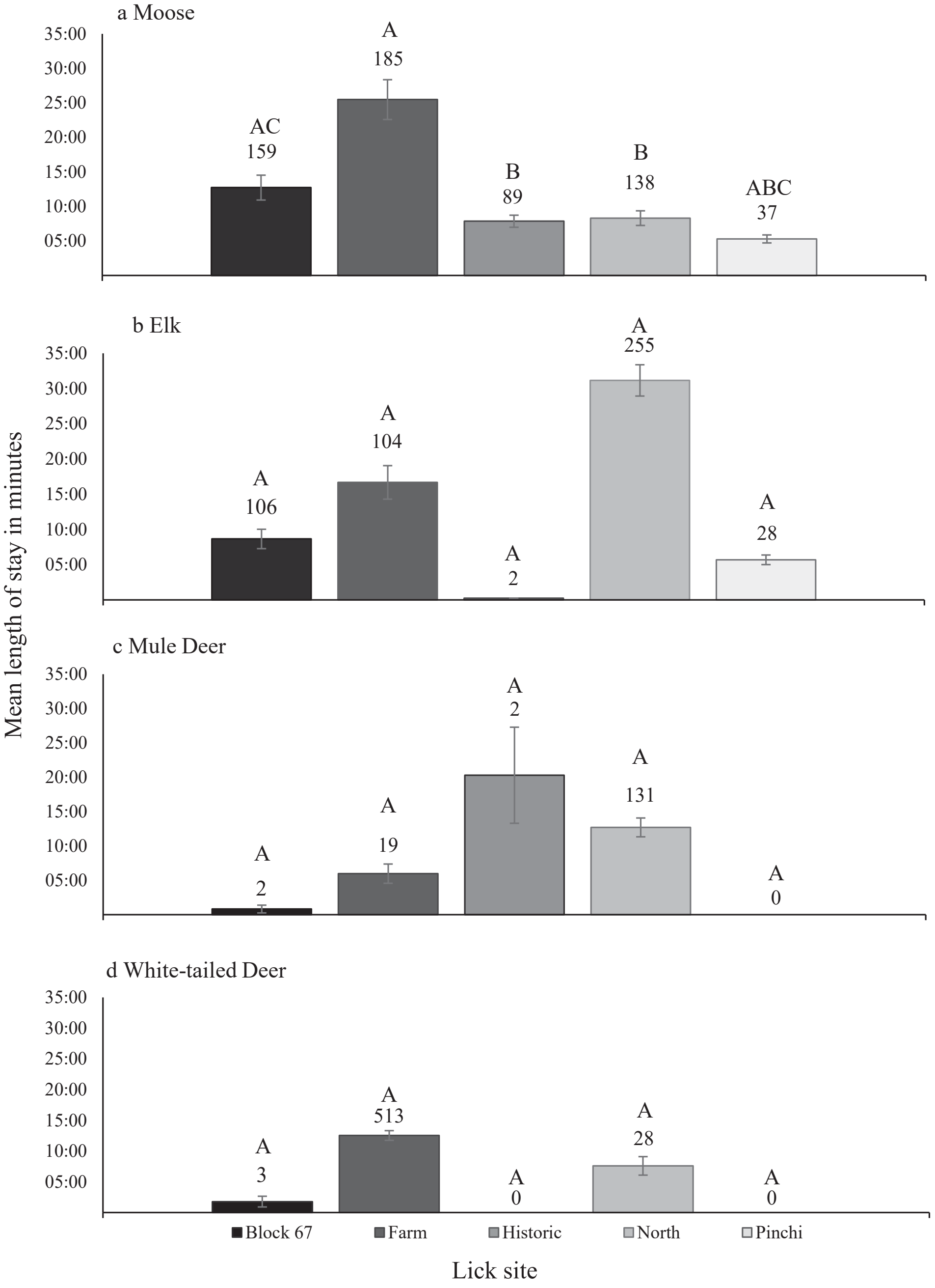

FIGURE 7. Mean (± SE) length of stay in minutes for a. Moose (*Alces americanus*), b. Elk (*Cervus canadensis*), c. Mule Deer (*Odocoileus hemionus*), and d. White-tailed Deer (*Odocoileus virginianus*) across all five licks from the beginning of February 2017 to the end of January 2018. Sample sizes (*n*) are represented by the numbers above the error bars. Note: No Mule Deer were recorded at the Pinchi Lick and no White-tailed Deer were recorded at the Historic or Pinchi Licks. Error bars sharing a common letter are not statistically significantly different from one another ($P \geq 0.05$).

Hristienko 1981; Ayotte *et al.* 2008) as well as calving, moulting, and antler growth (Tankersley and Gasaway 1983). Tankersley and Gasaway (1983) reported no winter lick use by Moose based on lack of tracks in January, April, and early May. However, our study and research done by Rea *et al.* (2013a) showed

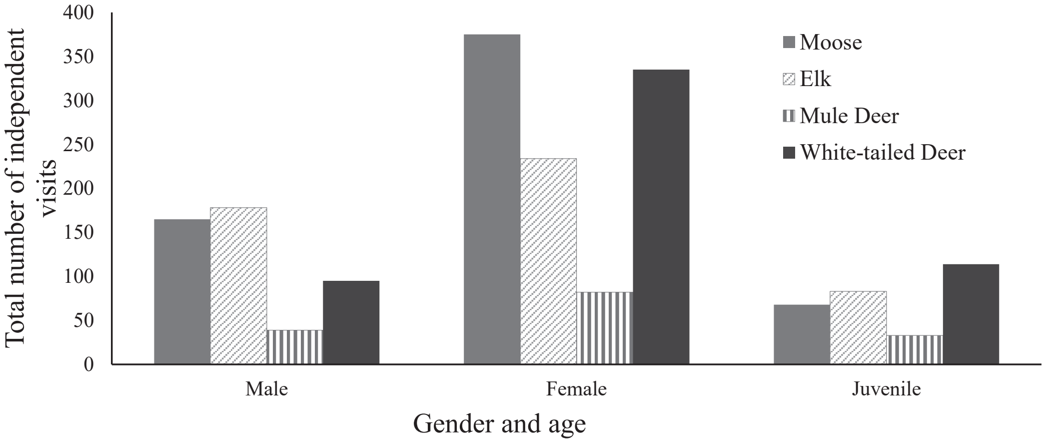

Figure 8. Total number of independent male, female, and juvenile ungulate visits recorded across all five licks from the beginning of February 2017 to the end of January 2018.

increased Moose visits to licks from October onward, which may be attributed to Moose satisfying mineral deficiencies in winter.

Elk visited licks most often in May and were the dominant ungulate at licks in February, March, May, and August. Other studies have also reported high use of licks by Elk in late May and early June following spring forage switching (Ayotte *et al.* 2008) and low elevation vegetation green-up (Parker and Ayotte 2004). Carbyn (1975) also reported an increase in Elk visits in June as large nursery bands passed through their study area following calving (Dalke *et al.* 1965). Rea *et al.* (2013a) reported no Elk in their study based at the Historic Lick in the JPRF during 2002–2005. However, we detected two Elk at the same Historic Lick and 495 Elk at all licks combined in the study area.

Mule Deer were recorded most often in August but were never the most common species at any of the licks. Carbyn (1975) reported peak Mule Deer lick use in June and July and Black (1955) recorded increased observations in April and May with a peak in June. Buss and Harbert (1950) found a striking correlation between lunar phases and Mule Deer visitation rates to lick sites, stating that between July and August, more Mule Deer were counted when the moon was nearly full, having changed their feeding patterns. Although we found a trend in increased early summer use, no such correlation occurred in August when the most Mule Deer were recorded.

White-tailed Deer visits to licks peaked in September, and they were the dominant species at licks in April, September, and October. Atwood and Weeks (2002) recorded more White-tailed Deer visitation between July and August, with another peak in September that they attributed to the minerals required for the growth of winter pelage. The increase in total number of White-tailed Deer visits in September may also be due to the increased number of fawns recorded accompanying does to licks (Atwood and Weeks 2002). Additional studies have reported White-tailed Deer usage of licks increasing from April to May (Weeks and Kirkpatrick 1976; Weeks 1978), May to June (Kennedy *et al.* 1995), and mid-July (Fraser and Hristienko 1981). Weeks and Kirkpatrick (1978) also reported White-tailed Deer use of licks continuing into December with no visits from December to March.

Although several other studies (Cowan and Brink 1949; Carbyn 1975; Fraser and Hristienko 1981; Tankersely and Gasaway 1983) have recorded ungulate use of licks in spring and summer, relatively few studies have looked at lick use year-round (Rea *et al.* 2013a). Snow cover is often assumed to deter ungulate use of licks (Fraser and Hristienko 1981; Jokinen *et al.* 2016), leading to the assumption that licks are not sought out by ungulates in the winter months. However, we recorded Moose excavating licks with their front legs before kneeling to access the material beneath the snowpack during the winter months. Rea *et al.* (2013a) also observed Moose cratering in the snow to access lick soil and water. Because some Moose in our study area do not make seasonal migrations, while others do (Chisholm 2018), there is potential for some animals to use these licks year-round.

Our findings corroborate suggestions by others that peak use of licks occurs in summer with lower use in winter (with February visits being lowest). But we recorded Moose and Elk at licks in every month of the year, and White-tailed Deer in every month but February. Mule Deer were recorded at licks from May to November, after which cameras detected no visits.

The snow may have been too deep for ungulates other than Moose to visit our licks regularly in mid-winter, which may have been the reason only Moose were detected in deep snow in the study by Rea *et al*. (2013a).

Ayotte *et al.* (2006) demonstrated that chemical composition of licks can vary throughout the year. As such, visits to different licks by ungulates throughout the year may be explained by foliage changes (Dalke *et al.* 1965; Carbyn 1975; Weeks 1978; Ayotte *et al.* 2006) and associated changing mineral requirements across different seasons. Chemical data for each of the licks we studied is being determined and will possibly enrich our ability to interpret what is driving ungulate visits.

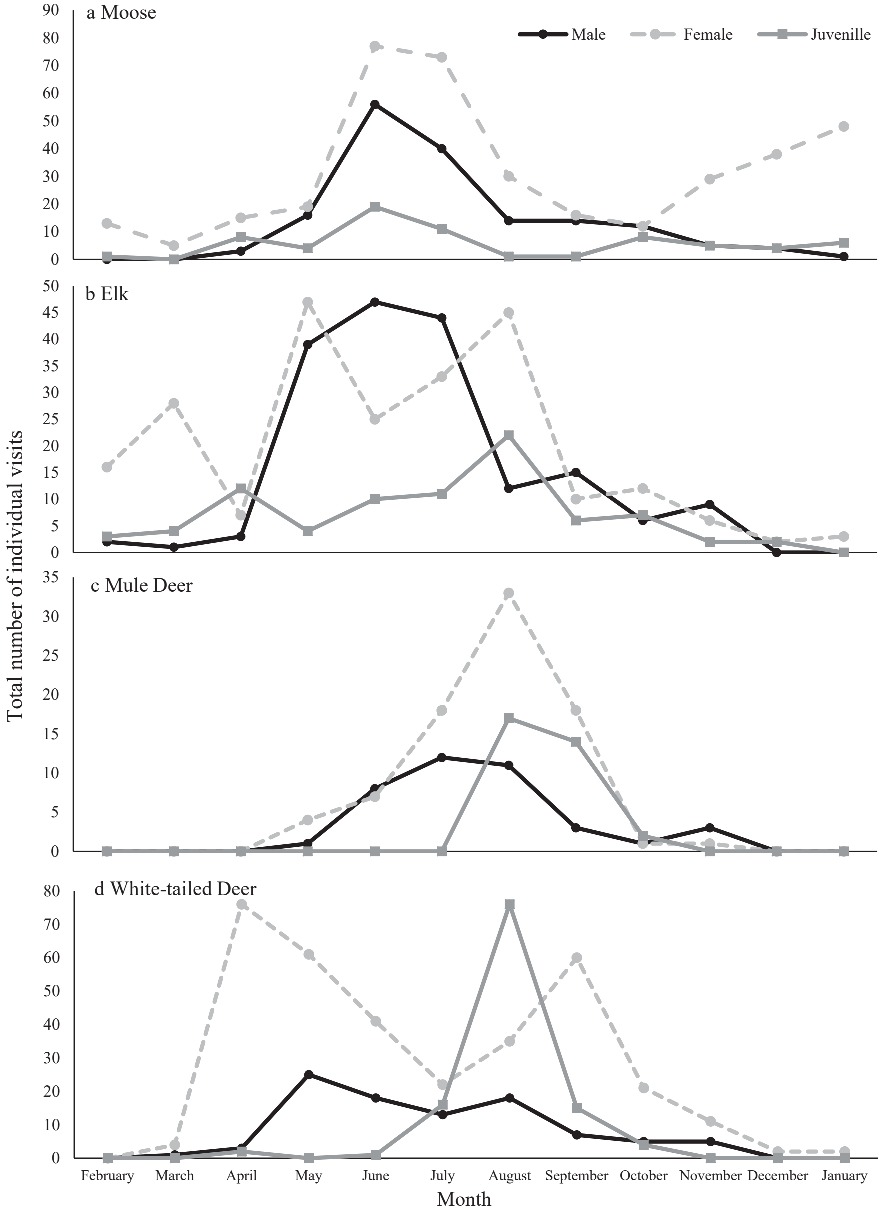

FIGURE 9. Total number of visits by male, female, and juvenile a. Moose (*Alces americanus*), b. Elk (*Cervus canadensis*), c. Mule Deer (*Odocoileus hemionus*), and d. White-tailed Deer (*Odocoileus virginianus*) pooled across all five licks in the John Prince Research Forest (JPRF) in north-central British Columbia, Canada from the beginning of February 2017 to the end of January 2018.

Time-of-day trends

Pooled visits to licks by all ungulate species revealed that peak visitations were during the morning and evening hours with fewer visits in the late afternoon and in the late night/early morning hours after midnight. This pattern was evident when data from all months of the study were combined and held true for the low-use season (October to April), albeit there were fewer visits to licks in the fall to spring months. These diurnal patterns varied by species, with Moose and Elk using licks more in the evening and morning hours while deer concentrated their use at midday. Concentrated use of licks by Moose and Elk in the evening and morning hours has been found by others (Fraser and Hristienko 1981; Tankersley and Gasaway 1983; Ayotte 2005; Rea *et al.* 2013a), although not all have found similar patterns (Carbyn 1975; Jokinen *et al.* 2016).

Mid-day peaks in lick use by deer have been found by others (Carbyn 1975; Fraser and Hristienko 1981), while some suggest deer visit licks throughout the day, but more during the morning hours (Jokinen *et al.* 2016) and after sunset (Wiles and Weeks 1986). The use of licks by different species may be partially attributable to which species are using the lick and whether or not interspecific interactions may modulate that use (Dalke *et al.* 1965; Fraser and Hristienko 1981). Although we detected no distinct patterns of use by one species being dependent on the presence of another, our cameras did record some species being chased out of licks by other species and suspect with more data collection and cameras adjusted to take longer videos, such patterns may emerge with further study.

Length of stay

On average, ungulates spent 15 min at licks per visit. Although Elk visits were on average significantly longer, visit times by Moose and deer were similar. There was a significant difference in the length of visits among licks for Moose and Elk, but not for deer. The average length of stays we found for Moose and Mule Deer were similar to averages found by Jokinen *et al.* (2016), but our average visit lengths for Elk and White-tailed Deer were nearly double those they found. A more detailed examination of the video data from cameras (including more years of video recordings) could perhaps reveal that the longer average visit lengths are an artifact of most visits being made by solitary animals, which might spend more time being vigilant as singletons, than if part of a group.

Ayotte *et al.* (2008) also reported that Elk made shorter visits to remote wilderness licks in comparison to Moose, Stone Sheep (*Ovis dalli stonei*), and Mountain Goat (*Oreamnos americanus*) and that the average length of stay for Moose was always >40 min; the longer length of stay for Moose was not attributed to bedding down near licks. Tankersley and Gasaway (1983) recorded average Moose visits as 15 min in one year of their study and 19 min in the next. Stepanova *et al.* (2017) reported that, on average, moose spent approximately 9 min engaged in geophagy while visiting licks. Wiles and Weeks (1986) found that the average length of stays for White-tailed Deer ranged from 20 to 25 min, whereas Fraser and Hristienko (1981) reported ~13 min. Black (1955) reported an average of 18 min spent at lick sites by Mule Deer.

Moose, Elk, and Mule Deer had longer visits to licks in the evening and White-tailed Deer spent more time at licks in the morning, which differed from findings by Jokinen *et al.* (2016), who reported Elk spending less time at licks in the afternoon but staying longer during the morning. Tankersley and Gasaway (1983) recorded longer visits by Moose between 2100–0459 with peaks around midnight and shorter visits at midday. Ayotte *et al.* (2008) found that Elk and Moose visit times were shorter in the morning than those during the day or evening. Moose and Elk spent less time at licks in the morning. Mule and White-tailed Deer spent less time at licks in the afternoon, which is interesting given deer visits to licks were most frequent in the afternoon, but actual time spent at licks during this period was lowest for both species.

Much of our results on length of stay differed from findings by Jokinen *et al.* (2016), who reported Elk as spending less time at licks in the afternoon but staying longer during the morning. Tankersley and Gasaway (1983) recorded longer visits by Moose between 2100 and 0459 with peaks around midnight and shorter visits at midday. Ayotte *et al.* (2008) found that Elk and Moose visit times were shorter in the morning than those during the day or evening. Several other studies (Carbyn 1975; Weeks 1978; Wiles and Weeks 1986; Rea *et al.* 2013a) provided information on how often ungulates visited during the day, but did not report length of stay. Dalke *et al.* (1965) and Atwood and Weeks (2002) report social interactions being sometimes responsible for the length of time spent at licks, that a more detailed examination of videos might reveal.

Pooled visit times suggest that the longest visits occurred in April and the shortest in January. Moose visits to licks were longest in February and March and shortest in December. Longer stays in February and March corresponded to times of the year when collared cow Moose in our study area began to move less (Scheideman 2018), suggesting they may have been less inclined to range far from licks that were used repeatedly. Videos of Moose recorded at the lick also suggest that Moose were forced to crater through snow to reach the lick and were bedding down near licks more frequently in February and March than at other times of the year.

Elk visits were longest in June and shortest in March. Mule Deer and White-tailed Deer visits were longest in July and April, respectively, with both deer species having the shortest visits in October. Variation in visit times by month have been described by others. Ayotte *et al.* (2008) recorded longer visits by Elk in late May and early June and variable visit lengths by Moose from spring into summer. Fraser and Hristienko (1981) also found that Moose visit lengths would vary at different times of the year, with shorter visits from July to October and longer visits in May and June. However, other studies have found that average visit lengths did not vary among months for Moose (Tankersley and Gasaway 1983) or White-tailed Deer (Wiles and Weeks 1986).

Explaining differences in lengths of stay for different species (or even different individuals) is difficult and could be related to several factors such as weather or predation risks (Carbyn 1975), social interactions (Dalke *et al.* 1965; Atwood and Weeks 2002), human activities (Dormaar and Walker 1996), or overall ungulate health (Tankersley and Gasaway 1983; Ayotte *et al.* 2008; Rea *et al.* 2013a). A more detailed analysis of various behaviours captured by the cameras may help address some of these questions, but would require increasing the length of the videos and the number of cameras at each lick. Combining camera data with collar data could also help to answer how seasonal migrations may factor into differential lick use.

Sex and age classes

The number of adult female ungulates we recorded visiting mineral licks was on average over three times the number of juveniles and twice the number of adult male ungulates. For all ungulates combined there were 29 juveniles and 46.5 males per 100 female ungulates. These patterns may be due in part to a differential need for females to obtain minerals from licks that are not required by males or juveniles but are most likely driven by differences in background sex and age class ratios on the landscape that are a result of hunting regulations that favour males. From census data collected in our study area, 35 juveniles and 26 adult male Moose were recorded per 100 females in 2017 (Klaczek *et al.* 2017), which compares poorly with our ratios of 18 juveniles and 45 males per 100 female Moose from our video records. The relative abundance of Elk, Mule, and White-tailed Deer were only recorded as "low" in the JPRF by Kuzyk *et al.* (2018), so demographic comparisons for these other ungulates cannot be made.

As our findings indicate, female Moose have been recorded visiting licks more often in the early summer to mid/late summer (Ayotte *et al.* 2008), primarily in June (Fraser and Hristienko 1981) and early July (Parker and Ayotte 2004). Adult male Moose visited our licks in nearly every month of the study (except March), and tended to visit licks earlier in the summer than females as has previously been found by others (Fraser and Hristienko 1981; Tankersley and Gasaway 1983; Rea *et al.* 2013a). Parker and Ayotte (2004) recorded a larger number of male Moose visits to licks in early July. Juvenile Moose were not recorded visiting licks during April and May (Rea *et al.* 2013a) or until the middle (Ayotte 2005) to end of June (Tankersley and Gasaway 1983).

Female Elk visits peaked in May and August, with Elk visiting licks the least in December. Ayotte *et al.* (2008) reported female Elk visits increasing in late May and peaking in late June for both males and females. Elk of all sex and age classes in our study increased visits to licks in May, but without a steep June peak, as reported by Ayotte *et al.* (2008). Differences in peak calving time and how lick use is tied to parturition and lactation demands can vary among regions (Dalke *et al.* 1965; Carbyn 1975; Parker and Ayotte 2004) and may help to explain differences in use, not only for Elk but for all species we recorded using licks.

We also detected differences in visitations between juvenile and male and female deer in our study as did Buss and Harbert (1950), Black (1955), Weeks and Kirkpatrick (1976), Weeks (1978), Kennedy *et al.* (1995), and Atwood and Weeks (2002). However, as with Elk, knowing the background sex and age class ratios of all species visiting licks is required before any attempt is made to attribute reasons to why there may be differences in visitation patterns between sex and age classes.

Conclusions

Our camera traps revealed that mineral licks were used by four species of ungulates year-round, use varied among lick sites, and ungulates using licks did so in different ways, allowing us to reject our null hypothesis that all ungulates used all licks equally and that time of day and season of use would not vary among species. Specifically, our cameras recorded differences in seasonal and daily patterns of use by different ungulates that all spent different amounts of time at various licks. Visits by different sex and age classes also varied among licks which may be attributed to differences in mineral requirements among adult males, adult females, and juveniles but was also likely influenced by background differences in the ratios of these sex and age classes due to fall hunting regulations that favour male harvest.

Why some licks were used more often and for longer periods by certain species remains unknown. Reasons for differential use of licks by species may include both site and landscape level factors such as the presence, density and quality of food and cover, the level of disturbance, the timing of parturition, the presence of other species (including predators) as well as the attributes of the lick itself (Dalke *et al.* 1965; Carbyn 1975; Atwood and Weeks 2002; Jokinen *et al.* 2016). The licks in our study do have slightly different mineral contents and concentrations (D.P.H. unpubl. data) which may help explain differential use by ungulates at different times of the year (Fraser and Hristienko 1981; Tankersley and Gasaway 1983; Atwood and Weeks 2002; Ayotte 2005; Ayotte *et al.* 2008), but requires further study.

The role of mineral licks in the physiological ecology of ungulates remains understudied. Data captured by our cameras, however, showed that mineral licks are important to at least four species of ungulates in north-central BC. A more detailed study of ungulate behaviour recorded by video at licks combined with data from collared animals could be used to study ungulate interactions within and among species at licks, help determine if some of the seasonal use patterns are due to seasonal migrations, and the importance of mineral licks for ungulates. The importance, seasonal use, and reasons for use of licks by ungulates are needed by land managers planning development activities such as forest harvesting in areas where licks are known to occur (Rea *et al.* 2004).

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Note

Introduction of Southern White River Crayfish (*Procambarus zonangulus*) to New Brunswick

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Abstract

Southern White River Crayfish (*Procambarus zonangulus*), an aquatic, potentially invasive species, is documented from New Brunswick for the first time. It was found in a small, privately owned, lake in the Saint John River system that was apparently stocked for recreational purposes with non-native fish and the crayfish. *Procambarus zonangulus* has successfully overwintered at the site for at least a year and, more likely, for several years. This is the third species of non-native crayfish recorded in New Brunswick, joining Spiny-cheeked Crayfish (*Faxonius limosus*) and Virile Crayfish (*Faxonius virilis*). This is also the first persisting introduction for the genus *Procambarus* in Canada of which we are aware.

Key words: Aquatic invasive species; introduced species; Maritime Canada; *Procambarus zonangulus*; Southern White River Crayfish

Although Bell (1859) was the earliest to remark on the presence of crayfish in the Maritimes, Ganong (1887, 1898) was the first to report at length on the presence of the only crayfish native to the Maritimes, Appalachian Brook Crayfish (*Cambarus bartonii*). The species is widely distributed in New Brunswick freshwaters, but is absent from Nova Scotia and Prince Edward Island. More recently, two species of non-native crayfishes, Spiny-cheeked Crayfish (*Faxonius limosus*) and Virile Crayfish (*Faxonius virilis*; both formerly genus *Orconectes*), have been documented as established in New Brunswick (McAlpine *et al.* 1991, 1999). *Faxonius limosus* is restricted to the St. Croix River and tributaries, while *F. virilis* has been reported in the upper Saint John River of western New Brunswick and the Black River along the eastern coast of the province (McAlpine *et al.* 2007). *Faxonius virilis* has also been introduced into Cape Breton Highlands National Park, Nova Scotia (Lambert *et al.* 2007). Here we report the presence of a third non-native crayfish, Southern White River Crayfish (*Procambarus zonangulus*), in New Brunswick and the first occurrence of a persisting introduction for the genus *Procambarus* in Canada.

On the basis of reports first received in February 2019 of the presence of non-native Largemouth Bass (*Micropterus salmoides*), Black Crappie (*Pomoxis nigromaculatus*), and Walleye (*Sander vitreus*) in privately owned Big Lake (46.131910°N, 67.226059°W, 156 m above sea level), York County, New Brunswick, about 49 km north-northwest of Fredericton (2.3 km west of Millville), C.B.C. and P.D.S. set a fyke net at the lake on 4 July 2019. Two adult female crayfish were captured (New Brunswick Museum accession numbers: NBM 11441.1, NBM 11441.2; telson–tail length 101.9 mm and 111.8 mm; Figure 1). Efforts in September 2019 (12 baited minnow traps set for 4 h during daylight, wading, and dip netting) and June 2020 (daylight electrofishing) to collect additional material were unsuccessful.

Specimens were initially identified as *Procambarus* sp. using Pflieger (1996), Swecker *et al.* (2019), and the collections of the New Brunswick Museum. A single claw from NBM 11441.1 was then sent to the

Figure 1. a. Big Lake, York County, New Brunswick, site of a population of the non-native Southern White River Crayfish (*Procambarus zonangulus*). b. Female specimen of *P. zonangulus*, Big Lake, New Brunswick, Canada (NBM 11441.1). Photos: D.F. McAlpine.

Canadian Centre for DNA Barcoding, University of Guelph, Guelph, Ontario, Canada. A full-length DNA barcode of 558 base pairs was generated and compared with records in the species sequence reference library in the Barcode of Life Data System (BOLD) available at http://www.boldsystems.org/. The recovered sequence was a 99.64–98.92% match with multiple BOLD reference records representing *P. zonangulus*.

Although *Procambarus* is a large genus with at least 128 species native to North America (Thomas 2016; Crandall and De Grave 2017), none of the species is native to Canada. No *Procambarus* species have been recorded previously as introduced to Canada, although Red Swamp Crayfish (*Procambarus clarkii*) is now one of the mostly widely introduced crayfish species in the world (Loureiro *et al*. 2015). Although proposed as a likely eventual introduction to Ontario (Hamr 1998), little of the Great Lakes region would appear to provide suitable habitat for *P. clarkii* (Egly *et al.* 2019). First form males are required to differentiate *P. zonangulus* morphologically from the naturally more northern ranging White River Crayfish (*Procambarus acutus*; Swecker *et al.* 2019), hence the DNA barcoding reported above.

The native range of *P. zonangulus* is confined to the coastal plains of the Gulf of Mexico, but it is poorly understood, perhaps in part because this species was formerly grouped with *P. acutus,* a species with a wide distribution across the United States (Hobbs and Hobbs 1990; Taylor *et al.* 2007). Simon (2011) reports the native range for *P. zonangulus* as Alabama, Louisiana, Mississippi, Texas, and Virginia, with introductions in Maryland and West Virginia. However, Durland Donahou (2018) reports the native range as the Gulf Coast Plains of Texas and Louisiana and perhaps parts of southern Arkansas, with introductions in Maryland and West Virginia and probably Alabama, Louisiana, and Mississippi. The species is economically important in aquaculture (Taylor and Schuster 2004), and, with a taxonomic history confused with *P. acutus*, both species may have native and introduced ranges that are larger—or smaller, if *P. acutus* is determined to consist of a complex of species—than reported (Walls 2009).

Big Lake is 340 m at its greatest length by 140 m at its greatest width (area 3.4 ha) and has a maximum depth of about 8 m. The lake is surrounded by industrial woodland and is drained via a circuitous route through wetlands to the Nashwaak River, a tributary of the Saint John River system. A single residence, usually seasonally occupied, is present on the north shore. Unfortunately, the full history of the introduction of *P. zonangulus* to Big Lake is uncertain. The current owner took possession of Big Lake in October 2018. The previous owner, a New England resident, held the property from 2006 to 2018. It was during this latter period of ownership that crayfish (and non-native fishes) are believed to have been introduced into Big Lake, perhaps from aquaculture stock now present in Maryland or West Virginia. *Procambarus zonangulus* does not appear to be abundant in Big Lake, nor is there any indication that the species has expanded outside the confines of the lake. *Procambarus zonangulus* is frequently cultured with *P. clarkii* in many parts of the United States and was part of the aquaculture seed stock introduced into Maryland in the 1980s (Kilian *et al.* 2010). Efforts to contact the previous owner of Big Lake to confirm the details of the New Brunswick introduction have been unsuccessful, but *P. zonangulus* has successfully overwintered at the site for at least a year, and more likely, for several years.

Huner (2002) has reviewed some of the management and conservation issues surrounding the introduction of *Procambarus* (including *P. zonangulus*) outside their native range, noting standing stocks that can reach 1000 kg/ha. Although the persistence of *P. zonangulus* in Big Lake, New Brunswick, may be short-lived, Veselý *et al.* (2015) found that some species of "warm water" crayfish have the potential to become invasive in temperate waters (including *P. clarkii*). Currently, it appears that *P. zonangulus* in New Brunswick is restricted to Big Lake. However, the species' presence in the province over a period of at least a year, combined with the work of Veselý *et al.* (2015), suggests that the introduction of even southern species of crayfish into New Brunswick should be of concern to wetland, species at risk, and fisheries managers in the region.

Author Contributions

Writing – Original Draft: D.F.M.; Writing – Review and Editing: D.F.M., C.B.C., and P.D.S.; Investigation: C.B.C., P.D.S., and D.F.M.; Visualization: D.F.M.

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A tribute to Paul-Michael Brunelle, odonatologist, 1952–2020

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Paul Michael Brunelle (Figure 1), 67-years-old, Atlantic Canadian odonatologist, and notable graphic designer, passed away unexpectedly on 18 January 2020. His frozen body was discovered by his former wife in his cabin-cum-laboratory in rural Middle New Cornwall, Nova Scotia. An autopsy revealed cause of death as heart failure.

Paul was born 7 November 1952 in Halifax, Nova Scotia, the eldest among two sons (the second dying shortly after birth) and a younger sister, the children of Paul Joseph Brunelle (1918–2012) and Gwendolyn Pearl Brunelle (1920–1997; nee Myers). Although for much of his adult life Paul's relationship with his father, a one-time military man, was sometimes strained, they shared a diverting interest in natural history, and he acknowledged his parents support in one of his earlier published journal papers (Brunelle 1997). While the senior Brunelle pursued a retirement passion for the greenhouse culture of cacti and succulents, eventually donating his large collection to Dalhousie University, for the junior Brunelle, the biology of dragonflies and damselflies became so diverting, nigh consuming, that it led to a life of penury, privation, mild alcoholism, considerable accomplishment, and the esteem and affection of scientific colleagues continent-wide.

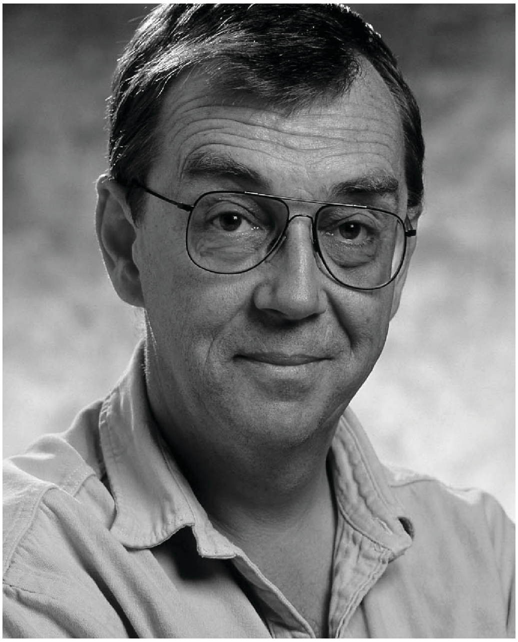

Figure 1. Paul-Michael Brunelle 1952–2020, circa 1990. Photo: George Georgakakos.

Paul graduated from Dartmouth High School in the then city of Dartmouth ("the City of Lakes"), Nova Scotia, since absorbed into the Halifax Regional Municipality. A talented artist, Paul attend the Nova Scotia College of Art and Design (since 2003 NSCAD University) at a period when NSCAD was recognized internationally as "the best art school in North America" (Levine 1973: 15). Opportunities to study aspects of design in England, Scotland, Holland, Germany, and Switzerland broadened his background. Graduating, with a Bachelor of Design in Communication Design in 1976, he founded Graphic Design Associates (GDA) in Halifax, with partner Dereck Day. A variety of significant regional and national design projects followed, including extensive work for Parks Canada, oversight of multi-volume environmental impact statements for Mobil Oil Canada's Venture Development Project and Newfoundland's Hibernia Offshore Development, the design of the Nova Scotia Health card featuring Kejimkujik National Park, and a series of fishing fly stamps for Canada Post. From 1992 to 1994 Paul served as President of the Graphic Designers of Canada (GDC), an organization of design professionals in media and design-related fields and Canada's national certification body for graphic and communication design. He also served as President of the Atlantic chapter of GDC from 1989 to 1990, establishing its organizational structure. The Atlantic Canadian Chapter of the Royal Society for the Encouragement of Arts, Manufactures and Commerce awarded Paul their Silver Medal for 1991 (MacLeod 1992). The category that year was graphic design. In 1999 Paul was awarded designation as a fellow of GDC, a mark of his accomplishments and influence on the design profession in Canada. A first-rate natural history illustrator, Paul was also a member of the Guild of Natural Science Illustrators, a North American organization concerned with communicating and clarifying scientific ideas visually. Among his influences, Paul counted J. Fenwick Lansdowne, Glen Loates, and other commercially successful, contemporary, wildlife artists (Editor 1987).

The late 1980s to early 1990s was a time of tumultuous change in Paul's life. He married Meredith Bell, a fellow graphic designer, and his only child, Michael was born (1991). Remarkably, then in his late 30s, Paul also gradually abandoned what was clearly an outstanding career in graphic design to pursue life as a free-lance odonatologist. Although his marriage was short-lived, ending in 1993, Paul and Meredith remained close for the rest of Paul's life (his cabin was located on Meredith's property, a stones-throw from her home). Nonetheless, it may have been Meredith's gift to Paul of a top-quality dissecting microscope, and his growing obsession with dragonflies, that doomed the union. Life as a free-lance entomologist proved to be a financially precarious one though. So much so, that in the decades that followed it left Paul lurching from debt (much of the time) to occasional plenty (when project or contract money was available). Nonetheless, Paul managed to pay the rent on a small apartment in Halifax and supported a more-than-modest smoking habit with his own rolled, loose leaf tobacco cigarettes and, when times were especially tight, subsisted largely on rice and beans. But by 2017, with contracts scarce and a focus on preparing his magnum opus (*Atlas of the Dragonflies and Damselflies of Acadia* [Maine and the Maritimes]), Paul moved out of the city with his beloved cat Merry to Middle New Cornwall, first into a barn, and eventually into a largely off-grid cabin constructed for him by his son.

Throughout Paul's life he had a passion for natural history and the outdoors, and like so many notable naturalists through the ages, was self-taught. A trip to the Amazon Basin (Manaus, Brazil) in ~1975 to study and acquire neotropical cichlids (Figure 2) led Paul, on his return to Nova Scotia, to expand an aquarium hobby to include local, non-game, fish. His stated goal was the production of an illustrated volume on the fishes of Nova Scotia (Editor 1987). Along the way, he encountered the strikingly large nymphal stage of Dragonhunter (*Hagenius brevistylus*), the adult of which feeds on large insects, including other dragon-

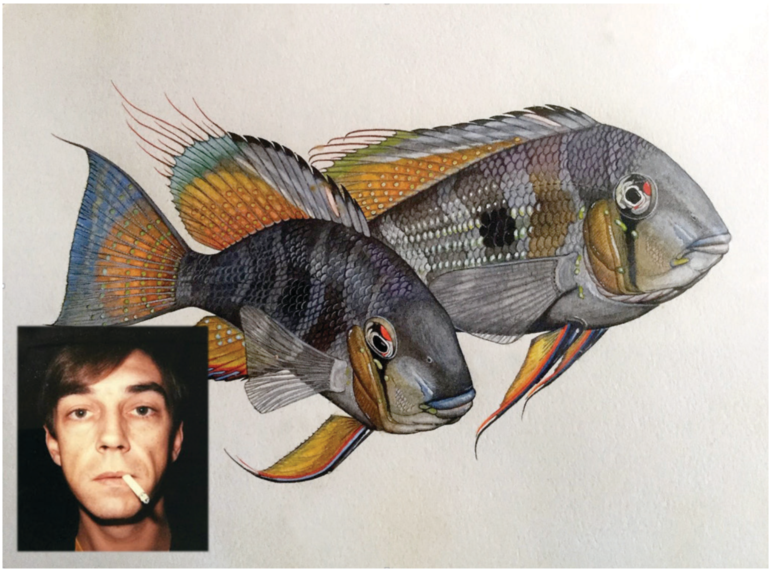

FIGURE 2. A finely executed Brunelle water colour of Threadfin Acara (*Acaricthys heckeleii*) one of a series of paintings of South American cichlids produced circa 1980–1985, which appeared in the Canadian Guild of Natural History Illustrators Newsletter for July 1987 and in the American Cichlid Association journal, Buntbarsche Bulletin. This particular painting graced the cover (sadly, not in colour) of Buntbarsche Bulletin 105 for December 1984. Inset: Paul, about 1978, shortly after he had returned from his Amazonian quest for neotropical cichlids Photo: unknown.

flies (hence the common name). Raised to emergence in one of his living-room fish tanks, a fascination with dragonflies took hold (Steeves 2001).

That fascination led Paul to devote the latter half of his life to the study of the dragonflies and damselflies of the northeast, at the time relatively poorly known (Figure 3). In the years prior to 1990, only about 4700 records of Odonata had accumulated for the entire Acadian region. In 1993, Paul establish the Atlantic Dragonfly Inventory Program (ADIP), an unfunded, volunteer survey to which interested persons were encourage to submit specimens and data to given standards. From 1999 to 2003 Paul was contracted by the State of Maine Department of Inland Fisheries and Wildlife to help co-ordinate (with Wildlife Biologist Dr. Philip deMaynadier) the Maine Damselfly and Dragonfly Survey (MDDS) for the same purpose. At the time of Paul's death, as result of his own efforts, his oversight of organized surveys (undertaken largely by amateurs), and his enthusiastic encouragement of anyone who could hold an insect net, he had meticulously databased in excess of 67 000 records of odonates from the Maritimes and Maine.

Through the early 1990s and until his death, Paul's interest in damselflies and dragonflies never flagged and became his primary vocation. Fortunately, this was a time when both government and public concern for the conservation status of wildlife was beginning to expand to encompass some of the more conspicuous invertebrate groups. Funded by a number of government agencies, commercial contracts, foundations, and species assessments, Paul's insect survey work took him to some of the most remote bogs, streams, and marshes of the Maritimes and the northeastern USA, usually alone, and often at risk of sinking into a quagmire. An early highlight was his 1995 discovery of a new species of dragonfly (Young 1999), Broad-tailed Shadowdragon (*Neurocordulia michaeli*), which he described in the scientific literature and named for his son (Brunelle 2000). A dusk-flying species, Paul discovered larvae in the Canoose, a cool, clear, rocky stream in Charlotte County, New Brunswick (Figure 4). The find was of such significance that it led dragonfly specialists from across the continent to make a trek to southeastern New Brunswick when the 1996 annual meeting

Figure 3. Paul in his Middle New Cornwall, Nova Scotia, cabin-cum-laboratory in September 2017. Inset: Brunelle illustration of Extra-striped Snaketail (*Ophiogomphus anomalus*). Paul drew heavily on his art and graphics skills to illustrate the 80+ papers and reports he produced dealing with dragonflies and damselflies of the northeast. Photo: Bruce Kierstead.

FIGURE 4. Paul at dusk in the Canoose Stream, Charlotte County, New Brunswick in about 2000. This is the site of his discovery of Broad-tailed Shadowdragon (*Neurocordulia michaeli*). Photo: J. Steeves.

of the Dragonfly Society of the Americas was held in St. Stephen. That same year, Paul was awarded the Entomological Society of Canada's Norman Criddle Award, which recognizes the contributions of an outstanding non-professional entomologist to entomology in Canada.

Paul was a teacher without peer who encouraged many others in the study of the flying dragons he found so marvelous. Through 1998–2003 Paul was an annual instructor of speciality courses on odonates delivered at the Humboldt Field Research Institute in Stueben, Maine—until his low tolerance for what he viewed as bureaucratic malfeasance and meddling by officials at the Canada–USA border got the better of him and he simply refused to enter the USA. Wry, opinionated, irreverent, more than occasionally profane, Paul particularly enjoyed working with young people, and they with him. A number of students he took under his wing are now pursuing graduate degrees in the study of insects at Canadian universities. The New Brunswick Museum (NBM) now holds one of the larger dragonfly and damselfly collections in Canada (~100 000 specimens), largely due to Paul's efforts. The scope of the NBM collection reflects not only Paul's decades of field study, but just as important, his huge impact on other naturalists in the region. Paul had a deep understanding of the value of natural history collections and his data collection was meticulous. Most of his collections are housed in the NBM, where Paul held a long-standing appointment as a Research Associate. In fact, Paul was the first NBM Research Associate appointed when the museum established its Research Associate program in 1996. Over the coming decades, Paul became a mainstay of NBM field programs, including those in Protected Natural Areas and a multi-year Community-University Research Alliance program. His customized "odemobile" jeep (Brunelle 1995, also see McAlpine 2020) banged its way over the roughest of tracks and forded washouts in the quest for the next productive wetland, often with some hapless student threatening to vomit out the side window. Paul's deep, baritone voice, well-aged with rum and cigarettes, provided the narration for a 2016 CBC-aired documentary describing some of this biological inventory work and was eventually screened at the United Nations COP13 biodiversity conference in Cancun, Mexico, and later in Croatia through the Canadian embassy there. It is fitting that the fossilized wing of an odonate, recently discovered on the shores of Grand Lake, New Brunswick (an area Paul knew well—see Brunelle [2011]), should be described as new and bear the Brunelle honourific (M. Stimson pers. comm. December 2020).

In the months prior to his death, Paul completed the draft of his *Atlas of the Dragonflies and Damselflies of Acadia*. The 360-page manuscript, written, designed, and replete with illustrations he prepared himself, will hopefully eventually be published, a fitting tribute and legacy to both Paul and the insects he loved.

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The Canadian Field-Naturalist

Book Reviews

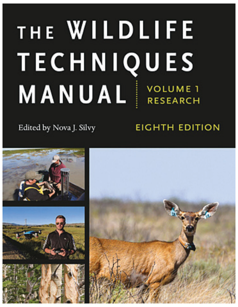
Book Review Editor's Note: *The Canadian Field-Naturalist* is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those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

CONSERVATION AND WILDLIFE

The Wildlife Techniques Manual (Eighth Edition). Volume 1 – Research. Volume 2 – Management

Edited by Nova J. Silvy. 2020. John Hopkins University Press, in association with The Wildlife Society. Volume 1, 759 pages, Volume 2, 614 pages, 174.95 USD, Cloth. Also available as an E-book.



The Wildlife Techniques Manual is a mainstay for many wildlife researchers and managers in North America; I suspect at least one of the various editions has resided on the bookshelves of most government and academic offices of wildlifers during the last 60 years. This edition, the eighth, will require a sturdy bookshelf. Volume 1, on research, is over 700 pages, while Volume 2, which covers management, is nearly as large at over 600 pages. The first edition (1960) was less than 400 pages total and focussed on game species only. Almost every 10 years, The Wildlife Society, which is the main professional organization for wildlife managers in North America, publishes another edition in an attempt to capture an increasing knowledge base, but also to cover the myriad of issues pertinent to wildlife in today's often-complicated management of resources. By the seventh edition (2012), the expanding content warranted the production of a two-volume set, which has been carried over in this latest edition.

The audience for the two books is mainly specialists, rather than people with a general interest in wildlife, such as naturalists and hunters. Although people interested in conservation could benefit from exploring how wildlife managers tackle the often-conflicting values in management (e.g., hunting versus no-hunting, control of 'pest' species in agriculture, re-introductions), and hunters could track how government uses demographic data of harvested animals, most people will find that the books have more technical content than they need. In Volume 1, for example, Chapter 8 is on how to determine the age and gender of over 70 species of game birds and mammals, Chapters 1 and 2 cover statistics and experimental design, Chapters 19 and 20 cover sampling methods for vegetation and nutrition levels in the environment. However, for specialists, *The Wildlife Techniques Manual* is a must have. I use an earlier edition for my university course in wildlife investigation techniques. In addition to researchers and university teachers, Volume 1 is popular with environmental consultants because it contains the standard methodology for such tools as population surveys, habitat assessment, environmental impact assessment, wildlife capture, radio-telemetry, and geo-spatial analyses.

Volume 2 focusses on management strategies that can be applied to real problems; there are chapters on wildlife management in different sectors, such as agriculture, forestry, wetlands, rangeland, and urban environments. There also are chapters on the context of wildlife management, such as the ethical foundations of management, conflict resolution, and communications because, as most managers will agree, wildlife management is often actually people management.

In total, there are 50 chapters, numbered sequentially, with 25 chapters in each volume. Thirteen new chapters were added since the seventh edition; the chapters on nutrition analyses, bio-acoustic monitoring, invasive species, and climate change were oddly absent in the previous addition and are most welcome. Both volumes are edited by Nova Silvy, who dealt with nearly 150 authors for the various chapters. The authors are mainly university academics or government scientists, and each chapter was peer-reviewed.

Notwithstanding the overall worth of *The Wildlife Techniques Manual*, several issues remain. The *Manual*'s contents apply mainly to North America, and most of the species and issues dealt with are a priority more in the United States (US) than in Canada or Mexico. This is not surprising, given the larger US audience, but there is an opportunity to apply lessons learned from international wildlife management cases, particularly regarding wildlife conflicts in impoverished regions. Also, the new chapter on Indigenous Peoples and wildlife management is very focussed on the US, with just a page on Canada. Given that traditional rights to wildlife are legally recognized in Canada, much more content is needed on how nations will accommodate and integrate wildlife management as a shared resource. It is likely that Canada will be a leader in this area, with eventual application to the US. Finally, although minor, it was odd to see some very low-quality figures in some chapters, all of which seem to be carry-overs from older editions that have not held up to higher resolution printing. A figure on bias and accuracy appears in both Chapter 1 and 12. However, these problems do not detract from what is the most comprehensive two-volume set on the methodology used to quantify and understand wildlife populations, and then the application of that information to the management of wildlife in North America.

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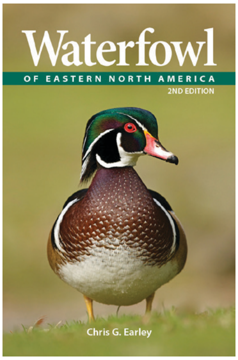
ORNITHOLOGY

Waterfowl of Eastern North America. Second Edition

By Chris G. Earley. 2020. Firefly Books. 159 pages and 400 colour photographs, 19.95 CAD, Paper.



Many bird-lovers would love to see cats skinned because of all the birds these predators kill. Once it is agreed that cats should be skinned, one may have to select from a plethora of ways to do it.

For example, my first reaction upon seeing this book was, "Why another identification guide to the birds of North America?" (i.e., do we need another method for skinning a cat?) There are more than a dozen: Audubon, Bird, Bull, Crossley, Dorling Floyd, Kaufman, Kindersley, National Geographic, National Wildlife Federation, Sibley, Stokes, Vanner, etc. This is not to mention regional guides that treat only part of North America (e.g., a state, province, or groups of these), or guides that treat only a subset of the birds (e.g., this book's "waterfowl").

What does each field guide add to the collective knowledge of bird identification? Very little. The law of diminishing returns applies here. What it may do is present the birds in a different way. My favourite is Peterson's use of arrows in the drawings that correspond to neighbouring italicized text. Earley's specialty is that he has selected birds that "have adapted to swimming for a living" (p. 11). Thus, it includes traditional "waterfowl" (ducks, geese, and swans) and some other swimmers: grebes, Common Gallinule, American Coot, loons, cormorants, and pelicans. Strictly marine species, the shorebirds, and some other swimmers are excluded. It is not always clear why certain birds are included while others are not.

I have trouble with the title *Waterfowl of Eastern North America* for two reasons. Given that it includes more than ducks, geese, and swans (i.e., "waterfowl"), a better term may have been "swimming birds". Limiting the book to eastern North America eliminated only a few western birds, so the book could have treated all North America with little extra effort. This would give us "Swimming Birds of North America".

This book is meant for all birders, be they novices or experts. The front matter includes a page on Wonderful Waterfowl, another two on How to Use this Book, and some other odds and ends. The bulk of the book consists of species accounts. A nice feature is that each species receives one or two two-page spreads. The spreads feature a paragraph focussing on something special about the species, and several photos (of generally excellent quality) that attempt to cover all the different plumages: e.g., male, female, eclipse male, floating, and in flight. There are also notes on "listen for", "compare to", and "nature notes". Finally, the map shows the distribution of the species in the New World. Unfortunately, like virtually all guides, it is usually not clear whether the species occurs in the Old World.

The back matter has a section on Vagrants and Southern and Coastal Specialties, a page on What I can do to Help Waterfowl?, a section on comparing species morphology within species groups, and a final section called, A Win for Waterfowl: What Can we Learn from Success?

Which way to skin the cat? There is a lot of choice, but if swimming birds intrigue you, this is the one for you.

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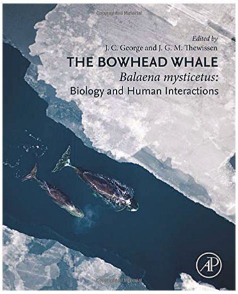
ZOOLOGY

The Bowhead Whale *Balaena mysticetus*: Biology and Human Interactions

Edited by J.C. George and J.G.M. Thewissen. 2020. Academic Press. 516 pages, 120.00 USD, Cloth.



Bowhead Whale (*Balaena mysticetus*) is an iconic Arctic marine mammal. Among baleen whales, and even mammals as a whole, bowheads stand out, and hold the record for many traits. They are the longest living mammal (>200 years old), they have the thickest skull, and they have the thickest blubber. Among whales, they have the longest baleen plates. Bowhead Whale is also one of the few whale species that are still the focus of subsistence hunting and are a cultural keystone in Inuit and other Arctic Indigenous cultures. There are four known stocks or populations of Bowhead Whales: the Bering-Chukchi Beaufort (BCB) stock, the Eastern Canada-West Greenland (ECWG) stock, the East Greenland-Svalbard (EGSB) stock, and the Okhotsk Sea (OKS) stock. All of these stocks were the focus of commercial whaling (mid 1500s to early 1900s), and their numbers were severely depleted. Both the EGSB and OKS stocks remain Endangered, with only a few hundred whales remaining in each stock, whereas both the BCB and ECWG populations have rebounded and are considered Special Concern in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). However, the BCB stock seems to have rebounded the most, and it is perhaps culturally the most important out of all four, as quite a few villages in Alaska hunt this stock every year. The BCB stock also overlaps with increased shipping traffic in the Bering Strait region and has been exposed to wide-spread oil and gas exploration (seismic survey vessels) and extraction activities, and for these reasons it has been the focus of far more research than the other three stocks, particularly in the 1980s and 1990s.

Much of the early research on bowheads culminated in a book called *The Bowhead Whale* (Burns *et al.* 1993), which presented a large amount of research, mainly from the BCB stock, on all aspects of Bowhead Whale biology and ecology. Since the original book was published, there have been large advances in technology and in our understanding of Bowhead Whales, which was the impetus behind this new book with the same title, *The Bowhead Whale,* edited by John George and Hans Thewissen. This new book offers further insights into all four bowhead stocks. Technology has evolved in leaps and bounds since the 1990s. For example, field studies of bowheads used to rely solely on aerial surveys, boat-based and shore-based observations, and fairly limited short-term passive acoustic monitoring. Now, bowheads are studied with advanced satellite telemetry, three-dimensional movement tags, unmanned aerial vehicles, and long-term passive acoustic monitoring. Many lab-based techniques have similarly undergone major advancements, particularly in genetics, which has allowed for interesting perspectives on the differentiation, relatedness, and genetic diversity among the different stocks of bowheads.

Beyond the advances in our knowledge of bowheads, the timing of this book is quite important. The Arctic is warming at twice the rate of the global average, and the ice-covered seas that bowheads are adapted to are undergoing important changes, including physical changes in sea ice and oceanography, and biological changes in the presence and abundance of different species (i.e., a shifting food web). The loss of sea ice is also allowing for increased human access throughout the region. When the original 1993 book was published, warming in the Arctic was less extreme. In fact, most long-term studies of Arctic sea ice and ship traffic compare back to averages in the 1990s, because changes that have occurred over the last three decades are quite drastic. This book therefore provides an update on our knowledge of Bowhead Whales, but also reminds readers of the many threats currently facing bowheads.

The book's structure spans 39 chapters divided into three main themes: 1) basic biology (Chapters 1–24), 2) the bowhead ecosystem (Chapters 25–30), and 3) interactions with humans (Chapters 31–39). The broad themes encompass recent physiological knowledge, evolutionary insights, population sizes, anthropogenic interactions, and future threats to Bowhead Whales. Numerous chapters within each theme provide the reader with a thorough selection of topics discussed by relevant specialists. Closer examination of individual chapters reveals a generally straightforward framework, which facilitates comprehension of the included information. Many specialists have contributed through discussion of their past and current research to this book, which has as well a substantial inclusion of traditional knowledge shared by members of several Indigenous communities. A large amount of detail and references are provided in certain chapters; however, other chapters are more focussed on the authors' personal research and are missing the inclusion of research led by other specialists within a particular field.

In general, this book can be viewed as the "Bowhead Encyclopedia", presenting readers with past and current knowledge in a comprehensive format. If readers desire to dig deeper into a specific topic, numerous references (albeit not exhaustive) are provided within each chapter. There is a great interconnectedness within chapters in this book which lends to some repetition, but also helps to direct readers to specific additional chapters for further information on certain topics. However, all essential information a reader might require, to gain full topic-specific understanding, is provided within each chapter. Thus, individual chapters can be read independently of one another, which is certainly a strength of the book's format and structure. Overall, this book provides knowledge about each of the four unique Bowhead Whale stocks. The greatest amount of information is about the BCB stock, slightly less about the ECWG stock, and very little about the EGSB and OKS stocks. By nature, bowhead research is represented by a strong American focus, and the inclusion of a greater number of non-American authors would have added a beneficial angle of perspective to the book. The addition of non-American authored research, especially from Russia, could greatly reduce the lack of information on the under-represented bowhead populations in this book.

This book is a must-read for researchers, from general marine biologists to specialized cetacean biologists, and undoubtedly to the dedicated Bowhead Whale investigators. All chapters recognize gaps in our knowledge related to bowheads, and also highlight important topics for future research, which may help many generations of scientists to navigate their explorations. With *The Bowhead Whale* being a relatively detailed description of nearly everything related to this remarkable species, it will be of great interest to both experts and whale or Arctic enthusiasts with some grasp of basic science. It satisfies the reader as an encyclopedic book that marries scientific advances with historical facts and Indigenous knowledge, and people with interest in whaling history or in Indigenous Arctic culture will find several of the chapters (31–34) quite insightful. *The Bowhead Whale* covers the entire spectrum of the iconic species' history: from 10 million years ago when Bowhead and Right Whale lineages split, to the cultural ties between whales and Indigenous Arctic communities dating from at least a thousand years ago, to their almost extirpation by commercial whaling in the 19th century, reaching the threats bowheads face in 2020. Despite the extensive slaughtering the species underwent from commercial whalers for 400 years, the current recovery of at least two stocks (the BCB and ECWG) remains a rare and remarkable conservation success story meant to inspire managers, administrators, scientists, and advocates to continue and focus their conservation battles.

There is probably no other species of baleen whale of such critical importance to a human society. Bowheads have been a prominent resource, culturally and nutritionally, for Inuit and Yupik, sustaining the survival of many Indigenous communities. *The Bowhead Whale* devotes considerable space to the traditional and Indigenous knowledge emerging from the intertwined history of humans and bowheads, and highlights the significance of this knowledge to science and conservation efforts today. An entire chapter (31) focusses on anecdotal stories by Indigenous people who share powerful emotions and personal experiences from traditional bowhead hunts. Indigenous whaling never posed a threat to the sustainability of the whale stocks, but instead stems from respect to the animals and reinforces the health of the bowhead populations. The traditional bowhead hunt is very hard work, but it creates a unique social glue for the community that works together to catch the animal and share the meat within the community. The hunt's success is based on trust, partnership, collaboration, coordination, and teamwork. The same practices have been key to the communal understanding of bowhead ecology and biology, and to the conservation of the Arctic ecosystem.

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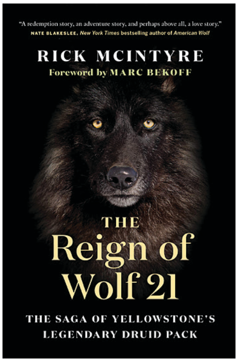
The Reign of Wolf 21: The Saga of Yellowstone's Legendary Druid Pack

By Rick McIntyre. 2020. Greystone Books. 272 pages, 34.95 CAN, 26.95 USD, Cloth.



I was ecstatic to have the opportunity to read *The Reign of Wolf 21* after having reviewed McIntyre's first book in the Alpha Wolves of Yellowstone series, *The Rise of Wolf 8*, last year (Way 2019). In that book, Wolf 21 played a prominent role alongside his step-father, Wolf 8. McIntyre described 21 as being loyal and faithful to 8, as well as being a provider and protector of the pups in the pack. When 21 left his natal Rose Creek pack in fall 1997 at 2.5 years of age, he soon became the dominant male of the adjacent Druid Peak pack. There, 21 reigned not by an iron fist but rather by a caring touch, treating all pack members with dignity and respect, and having a unique, very playful personality which was especially unique for an alpha male. In fact, play behaviour was documented throughout the first book (Way 2019) as well as this one (e.g., pp. 12, 46–47, 125). 21 was never known to have killed rival wolves, always letting them go after only pinning and biting them, including a non-fatal confrontation with his step-father, Wolf 8 (pp. 158, 184). He was recognized as having empathy for other wolves by helping pack members when they were injured or weak (pp. 84, 90).

The Reign of Wolf 21 picks up in the year 2000, where the last book left off. There is some necessary repeated information between the two books so Volume 2 can function as a stand-alone version. It follows the saga of the Yellowstone wolves for five years, through the year 2004 until 21's ultimate demise in June–July of that year. Wolf 21 and his longtime mate, 42, are at the core of this story. The incredible detail in the book on individual pack dynamics and interactions can be summed up in a way that I never expected I would ever write about a wildlife species: a love story. The bond that those two wolves had literally transformed the northeastern part of Yellowstone for generations. The affection ascribed to the couple was repeatedly documented in intimate detail throughout the book (e.g., pp. 10, 46, 125, 203). However, before this love story could fully blossom there was a major impediment in their way: 42's domineering sister Wolf 40, the alpha female of the Druid Pack. Following 42's repeated harsh treatment by 40, documented through much of the original book (McIntyre 2019), 42 and two other packmates killed 40 on an early May 2000 night when it appeared that 40 might kill 42's pups for a suspected third year in a row (pp. 16, 21–25). The next morning McIntyre and his associates saw 40 mortally injured on the side of the road in Lamar Valley, and assumed she was hit by a car. 40 died soon after she was found and the biologists discovered dozens of bite-marks, indicating that 40 was killed by other wolves in a rare instance of intra-pack aggression.

After that event, McIntyre documented Wolf 42 and other females in the pack merging all of four of the pack's litters to the main den, something that never happened when 40 ruled the pack (pp. 28–30). 42 had a similar compassionate personality to 21's, and McIntyre thought that was why they worked so well as leaders of the pack for over six years, a full two-thirds of their lives and longer than the average age of a wolf in the wild (p. 203). She even allowed other adult female wolves to peacefully live with her, breed, and raise pups in the same territory, something 40 never permitted. During summer 2000, the pack of just seven adults raised an astonishing 20 of 21 pups through their first year (p. 49). McIntyre was mightily impressed by the pack's cooperation (p. 50), with 21 being the workhorse of the pack ensuring that everybody was well fed (p. 37) while 42 led when moving pups from den and rendezvous sites (p. 38) and when the pack travelled (p. 111). We learned of 42's intelligence, foresight, and pattern recognition, all signs of advanced intelligence in a species, when she chose to den near where Elk, their favourite prey, were going to be in the future (p. 68). There were multiple accounts of 42 using sticks to get pups to follow her across rivers and to new areas (pp. 38, 178). This was truly a time of legends, a golden age for wolves in the park (p. 42). The year 2001 was historic—37 Druid Pack wolves were observed together on August 29 at their main rendezvous site, while one pup was away but later joined them (pp. 78–79). Those 37–38 wolves are still believed to be a record known pack size for wolves anywhere (p. 79).

The second half of the book documents the Druid super-pack and its travels, which stretched about 40 km (25 miles) from east to west in the most prey-rich part of the park. Eventually wolves dispersed from the large family and, instead of going far and wide, most subdivided their natal home range, eventually forming five stable packs and up to seven packs in total in the original super-territory (pp. 140, 218). McIntyre does an admiral job of explaining all these packs without getting too bogged down in the details of the individuals involved. Sections in some chapters have slightly abrupt or awkward transitions from one scene to the next, but that is to be expected because this book is the first of its kind to document wolves from multiple packs in such incredible, personalized detail. A lot was happening at the time and there was no easier way to explain it than McIntyre did.

To help with organizing the timeline of all of the events taking place, the book is divided into five parts, with each major section being a year from 2000 to 2004. Each section of three to six chapters begins with a map of the pack territories for that year as well as genealogies of each pack, including individual members of each social unit, which really helped in laying a foundation and providing visual organization. McIntyre's books are written in such remarkable detail that the reader can easily get caught up in graphic descriptions of the many individual wild wolves and their families. The level of canine insight that we were privy to witness was amazing. It is remarkable to think that one man could know so much about all of those wolves. Fortunately, the 14-page Index allows one to look up any individual wolf and go back to specific passages when needed.

The last third of the book features 21's main nemesis, Wolf 302, who repeatedly entered the Druid Pack's territory to court and mate with many of 21's daughters, ultimately fathering numerous pups that 21 helped raise. 302 was a much different wolf than 21; he would run off from other wolves and not fight to save himself or his companions (e.g., pp. 163, 191) while 21 was the ultimate defender of his domain, having once run into and forced the retreat of eight Nez Perce wolves, which would forever define 21 for McIntyre (p. 83). 302 did show dogged determination, however, and would regularly make an 80-km (50-mile) roundtrip between his natal territory and 21's family to check in on the pups he fathered, often using the park roads for travelling (pp. 164, 176, 186). 21 would constantly chase 302 away, even forcefully pinning him on occasion, yet 302 would always return. This special wolf's attempt to claim the Druid territory at the end of the book (p. 229) foreshadows McIntyre's third book in the Alpha Wolves of Yellowstone series.

The Reign of Wolf 21 concludes with the heartbreaking account of 21 not knowing that his longtime mate, 42, was killed by other wolves, just shy of her ninth birthday (p. 206). We read a couple of tear-jerking chapters of 21 and the Druid Pack looking for but apparently never finding 42's remains. This wore on 21, who aged quickly, becoming thin and even more grey (p. 226), before ultimately leaving the pack on 11–12 June 2004, ironically on McIntyre's four-year anniversary of being in the park everyday (p. 228; McIntyre extended that streak to over 15 years [Way 2019]). In July 2004, 21's remains were found in a very secluded and sacred part of his pack's territory, almost like he wished to spend his last moments in a favoured area, probably thinking of his longtime love, 42, whom he often cuddled next to and groomed. Having studied canids myself for two decades, it was a treat to read the amazing level of detail of these famous places where 21 and 42 spent time, and I encourage readers to do likewise.

Given that his surname means "son of the land" in Scottish culture, which is tied directly to wolves (p. 203), it is almost like McIntyre was predestined to be in Yellowstone to document the lives of these now world-famous wolves. But it is important to recognize that these wolves are so popular today because of the efforts of people like McIntyre who spent (and continues to spend) so much time studying their nearly every move.

I enthusiastically recommend this book for fans of Yellowstone or wolves, as well as people who enjoy nature, carnivores, and wildlife in general. Animal behaviourists, wildlife biologists, and other professionals should be inspired with the level of detail provided on a wild species which, I hope, will revolutionize our views of wolves. These sentient, intelligent, and ecologically important beings should be treated with much more respect than allowed by the current long hunting seasons that they experience in the Rocky Mountain states surrounding Yellowstone. As I wrote at the end of my review *The Rise of Wolf 8* (Way 2019), I eagerly await the next edition of the Yellowstone wolf saga.

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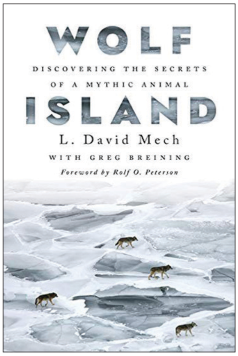
Wolf Island: Discovering the Secrets of a Mythic Animal

By L. David Mech and Greg Breining. 2020. University of Minnesota Press. 202 pages, 24.95 USD, Cloth.



Wolf Island is a fascinating account of Dave Mech's graduate school years, from 1958 to 1961, when he led the first study of wolves on Isle Royale National Park. I have read many of Mech's books over the years including *The Wolf: The Ecology and Behavior of an Endangered Species* (1970; 1981, University of Minnesota Press edition), *The Way of the Wolf* (1991, Voyageur Press), *The Arctic Wolf: Ten Years with the Pack* (1997, Voyageur Press), *The Wolves of Denali* (1998, University of Minnesota Press), *Wolves: Behavior, Ecology, and Conservation* (2003, University of Chicago Press), and *Wolves on the Hunt: The Behavior of Wolves Hunting Wild Prey* (2015, University of Chicago Press), so it was an amazing experience to come full circle with Mech's formative research years 60 years ago as he became the world's foremost authority of wolves.

Isle Royale is a 210 square mile (544 km^2) island national park in the middle of Lake Superior (p. 29). It is technically a part of the state of Michigan but is closer to the Canadian shoreline. Formerly, Caribou, Coyote, and lynx inhabited the island, but they disappeared while Moose in the early 1900s (probably by swimming) and wolves by 1949 (likely by travelling across winter ice) colonized the island (pp. 29–31, 119). This simplified ecosystem, lacking other competitors for both species, such as bears, Bobcats, skunks, and the aforementioned creatures (p. 32), made for an ideal study for the team.

We are taken back to Mech's first days discovering the park; we metaphorically travel with him as he explores the island by foot in the summer, often travelling like a wolf by hiking 32 km (20 miles) a day to collect scats (pp. 25–26), which was a main objective of the study (p. 18). He rarely saw wolves, with his record summer (1959) being when he saw three wolves all field season (pp. 75, 82). Collecting scats provided real info of diet (pp. 72–73) while finding wolf tracks and making those rare sightings was exciting for Mech but didn't really tell him much other than wolves seemed to travel in small groups in the summer (p. 75). The winter field season involved flying over the park in a small plane and counting Moose and wolves as well as observing their interactions.

Mech quickly realized that the core of his research findings would be related to aerially tracking wolves in the winter. He frequently observed them from up in the sky; in fact, in winter 1960 alone he saw wolves for 35 hours and saw 33 hunts involving 66 Moose (p. 108)! He discovered that the big pack of 15 wolves on the island would kill one Moose every three days (p. 108). These extensive sightings made Mech the world's authority by default, as he noted throughout the book, because no one else was really studying them at the time (e.g., p. 81). There are fascinating accounts of wolf behaviour and wolves travelling on the island. I especially liked reading about the large pack scenting a cow and two calves 2.4 km (1.5 miles) away, sniffing the air while wagging their tails and then going straight toward them (p. 88). I had read about this encounter previously in a couple of his other books (e.g., pp. 15, 197 in *The Wolf*; p. 31 in *Wolves on the Hunt*). Even though this memoir came well after those other publications, it felt more personal given that we were essentially reading Mech's original field notes which was provided in more detail than the other sources. I also liked reading about Mech getting dropped off by his pilot, Don Murray, to investigate a wolf-killed Moose against his recommendations for fear that wolves might attack him (pp. 2–4, 6). As Mech snowshoed to and approached the kill, he lifted his park service issued pistol instead of his camera; the wolves instantly ran away and Mech—60 years later—still regrets that decision (p. 89)!

There were some comical stories throughout the book, such as Mech surviving on road-kill as a "starving" undergrad (pp. 14, 116) and his exotic taste for many wild species including Muskrat, Raccoon, Opossum, beaver, and bear, some of which died during research endeavours (p. 150). There were also many accounts of a frontier-like lifestyle where he would chop ice from the thawing Lake Superior and store it in sawdust for use in early refrigerators, something I had never even thought about doing given modern living—I especially like the glossy picture of ice chunks in his small boat! There are also great descriptions of him living in rustic cabins with his wife and young children at the edge of the Isle Royale wilderness, next to the last of the commercial fisherman of a bygone era. And something completely new to my understanding about the man was Mech's disenchantment with religion and politics (pp. 151–152) and how he almost left the wildlife career, spending a year in a doctorate program in American Studies (p. 156) before leaving there for financial reasons (i.e., he had a family to support). Somewhat fortuitous, he found a postdoc position working on radio-tracking research in its infantile stage, right across the street at the Museum of Natural History in Minneapolis (p. 157). That jump started his career that many of us now know much about given his many publications.

The most important finding in Mech's early research was that wolves failed much more than they succeeded in killing Moose, with a <8% success rate when they managed to get a Moose to run; standing Moose were basically immune to wolf attacks (p. 154). This has been confirmed time and again in future work that Mech and his collaborators have performed on a myriad of prey species which are documented in the aforementioned publications. One big change from Mech's grad school research to current knowledge was the illusion that wolves and Moose reached equilibrium at populations of 21–22 wolves and ~600 Moose on the island (p. 161). After Mech's work on Isle Royale, subsequent investigators discovered Moose going up to 2400 individuals and wolves all the way to 50, before both populations subsequently crashed (pp. 161–162). In short, there was no mythical 'balance of nature'; instead, weather—especially winter snow fall—climate change, and disease influenced populations (pp. 162–163).

The last chapter of the book brought us to modern times, nicely summing up the past 60 years of Mech's research findings at his various study sites, including Superior National Forest in Minnesota, Alaska's Denali National Park, Yellowstone National Park, and Canada's Ellesmere Island in the high Arctic (pp. 163–164). One of his most important discoveries, after an amazingly long and productive career, was that weather trumps all else in determining whether animals live or die (p. 165). Wolves typically do better in more severe winters because prey become more weakened. Mech concludes with a discussion of how wolf recovery has exceeded all expectations, with over 6000 wolves now living in the Lower 48 with some populations expanding and still being discovered in new areas (p. 167). We also come full circle on Isle Royale where wolves were dying out on the island after ~70 years of inbreeding with only two non-reproducing, related wolves remaining on the island in 2016 (p. 171). Mech originally did not want the park service to intervene but once he saw the population's inevitable demise he had a change of heart and supported wolves being reintroduced from nearby source populations (p. 172). As of early 2020, 12–14 restored wolves call the island home, providing a unique opportunity to study the success of wolf translocation (p. 174).

Writer Greg Breining did an admiral job combing through Mech's original and highly detailed field notes, his early publications, as well as extensively interviewing him to put together a highly engaging account that wolf aficionados, lovers of wilderness and national parks, and people that enjoy wildlife biology and natural history stories will appreciate. It was exciting to go back 60 years to when wolf research was in its early stages; there are even 16 pages of glossy colour pictures to bring the story to life. It is an easy read and follows Mech's graduate years in order of summer and winter field seasons. Numerous anecdotes bring his experience to real life and allowed me to appreciate the context of all of his other books a little more. There was a map at the beginning of the book (pp. xii–xiii) which I found crucial for locating place names frequently mentioned throughout the text; most locations (e.g., lakes, bays, coves, cabins) were there but some were not, such as Crow Point (pp. 52, 119), Hat Island (p. 102), Island Mine Trail (p. 106), and Gull Rocks (p. 132). It would have been helpful to have a few more detailed maps within some of the chapters, such as the account from 4 March 1960 when he observed multiple chases of wolves on Moose during his seven hours in the air (pp. 99–101). Other than that minor quibble, I wholeheartedly recommend this book. It is well worth the read!

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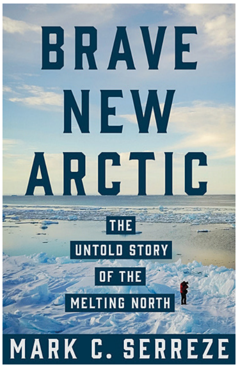
OTHER

Brave New Arctic: The Untold Story of the Melting North

By Mark C. Serreze. 2018. Princeton University Press. 264 pages, 24.95 USD, Cloth, 272 pages, 17.95 USD, Paper.



Climate change is happening at twice the rate in the Arctic compared with the global average. Air temperature is increasing and coverage by glaciers and sea ice is decreasing every year. The physical changes then have cascading impacts on the people and animals that live in the Arctic. *Brave New Arctic* lays out much of the evidence showing how the Arctic climate has been changing over the last 50 years (and beyond), including the mechanisms behind that change. The author, Mark Serreze, has been studying Arctic climate for decades, and is a global expert on climate change in the Arctic.

A really interesting aspect of this book is that it focusses on the history of Arctic climate science. Serreze began his studies of the Arctic climate in the late 1970s, and has experienced much of this history firsthand. Earlier in the century, scientists had detected a cooling trend, and early during his career, the evidence supporting widespread climate change in the Arctic seemed weak. However, in the 1990s and onwards, particularly at the turn of the century, evidence of climate change, and in particular, human-caused climate change, began piling up. The book also delves into many of the social repercussions and politics around evidence of climate change in the Arctic.

Overall, I wholeheartedly recommend this book. It provides accessible and easily digestible information on climate change in the Arctic. The book also relies on personal anecdotes from the author, which add an interesting element to the history. Any naturalist interested in climate change should be especially interested in this book, which details climate change in the region being most impacted.

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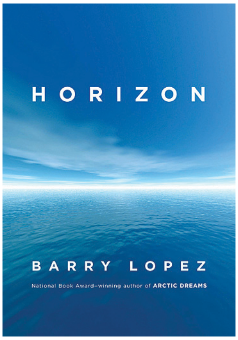
Horizon

By Barry Lopez. 2019. Vintage Canada. 572 pages, 21.00 CAD, Paper, 13.99 CAD, E-book.



The evening has arrived, you pour a glass of your preferred beverage, mine is aged rum, throw another log on the fire, and settle into a comfortable chair to delve into a book that takes you places that make you pause, reflect, and consider events that shape your place in this world and the horizon that lies ahead. Lopez has spent a lifetime of travelling, questioning, and reflecting on our world and humans' place in it historically, currently, and in the future. *Horizon* might be described as Lopez's thesis pulling together a life's work.

Horizon has a prologue and introduction that establish the relatively serious and reflective tone of the book's six chapters, each with a particular narrative. Chapter 1, Cape Foulweather on the Coast of Oregon, discusses Captain Cook's ocean voyages of discovery. Chapter 2, Skraeling Island in Nunavut, the archaeology of hardy Thule culture, now extinct. Chapter 3, Puerto Ayora in the Galápagos Islands, considers Darwin's insights of an evolving world. Chapter 4, Jackal Camp in Kenya, the archaeology of early humans. Chapter 5, Port Arthur to Botany Bay in Australia, reflects on how humans treat each other, examining the United Kingdom's repugnant export of criminals and colonization's contempt of Indigenous cultures. Chapter 6, Graves Nunataks to Port Famine Road in Antarctica, reminds us of the endless horizon of what remains to be discovered. These are places Lopez has visited one or more times and which he has thought about deeply and broadly in terms of their physical and biological histories and trajectories and how humanity is embedded within these.

Horizon is a testament to Lopez having kept detailed and copious notes and drawings over the course of his life. His descriptions of places and events from decades ago are mesmerizing: you can feel the wind and rain, see the foggy coastline, hear the waves, and feel the mood evoked by the impending storm. The stories draw you in, conjuring up analogous memories of places, events, and encounters, exhorting you to pause and reflect on the complex thoughts and ideas Lopez places before you. The book it is not, therefore, a jolly travel story providing a superficial discourse of the people and places Lopez has visited. If you want a fun and easy read, try one of Bill Bryson's books, such as *A Walk in the Woods* (1998, Broadway Books).

"The whitecaps on a windy day collapse, the ships' wakes disappear, the skittering takeoff track of a seabird fades out, leaving no record of its having been there" (p. 83). These words evoke memories for me of a chilly September day standing in a palsa bog in a remote area of the Hudson Bay lowlands near Hawley Lake. The terrain was open, with short, narrow Black Spruce; I was facing the orange sun emitting a little warmth far off on the horizon. A movement on the spruce beside me caught my eye: a small black spider moved around the narrow trunk, placing itself strategically to catch the last of sun's heat. These are singular moments in time, when the physical and biological world of the universe near and far merge in a singular horizon. And over the years I return to that memory and wonder is the palsa bog still there, are the hummocks collapsing as climate change melts the ice lenses, and did the spider survive the winter to produce progeny that continue to survive in a changing environment?

Given Lopez's sensitivity to his fellow humans, I was surprised he largely uses the male gender when referring to humanity. So as not to be annoyed by every occurrence, and there are many, I merely read phrases such as "all of mankind" as "all of humankind" and "him" as "her" or "them". Also, although *Horizon* is science-based, it is frustrating that imperial measure is used without metric equivalents, meaning you may need to remind yourself how cold minus 20° Fahrenheit is. If you enjoy a book that sends you searching for definitions of the words used, Lopez will not disappoint. For example, while I could visualize "bumptious overweight Americans" (p. 232), the first adjective was not in my vocabulary, nor were "stygian imps" (p. 226); "the adumbration of something quite new" (p. 301); "His forehead, cheeks and chin are neatly ribbed with small cicatrices" (p. 320); or "committing to the eschatology of an organized religion" (p. 256). The list is so long I sometimes wished the book had a glossary, for cantus, lebensraum, plosive, susurration, etc.

As stories unfold in *Horizon*, simple, profound, and impartial statements of fact convey weighty lessons. For example, we think of *Australopithecus* species, which emerged four to five million years ago, as our ancestors; however, the more relevant period of human evolution is the emergence of culturally complex *Homo sapiens* in the Horn of Africa around 55 000 years B.P. Within a very short evolutionary period, these more recent ancestors proliferated globally, displacing all hominid competitors and much of everything else on the planet. What is to become of our evolutionary tree—will our branch be as long as that of our *Australopithecus* ancestors or a short twig?

Horizon considers elders Lopez has encountered around the globe. Elders are typically held in high regard within traditional cultures and "Their feelings toward all life around them are more tender, their capacity for empathy greater" (p. 312). Are these the qualities of today's 'leaders' who inspire economic growth and wealth? Can we not see where they are leading humankind? But there is hope with leaders, such as New Zealand's Jacinda Ardern, who show genuine human empathy and real concern for our planet. There is a recurrent theme in *Horizon*, does humankind have the wisdom, the imagination, and the intelligence to dismantle the apparatuses that are leading us into a frightening future of continued habitat destruction, climate change, and a rising tide of human suffering? Lopez leaves us questioning the shared horizon of humans in the 21st century, the challenges and the hope we ourselves create. Frighteningly, the horizon critically important to our survival, is insignificant, even trivial, within the wider horizon of our planet evolving within an expanding universe.

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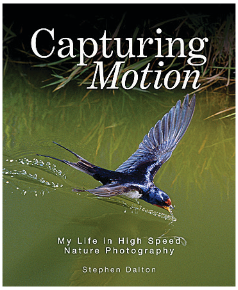
BOOKS IN BRIEF

Strange Sea Creatures. By Erich Hoyt. 2020. Firefly Books. 192 pages and 80 colour photographs, 35.00 CAD, Cloth.

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



The visions and ambitions of photographers, amateur and professional, are limitless. The exponential rate of technological advances on several different fronts has enabled those with the creative ideas and ambition to bring them increasingly to fruition. The two books discussed here each, in their different ways, underscore the point. On the face of it, these books are similar—both are, in the best sense, large-size picture books; both reveal aspects of the natural world that are unavailable to most of us; both seek not only to enhance awareness of that world, but to encourage us to engage in it, to appreciate it, simply to learn about it, in new ways.

The two books differ in several ways as well. Erich Hoyt's *Strange Sea Creatures* is almost purely photographic, with almost every page containing a large view of some usually tiny, exotic, never-seen-before (by most of us, I mean) creature that is given a name—when known—and brief description. Hoyt provides the expert commentary, half-a-dozen photographers the wonderful photos. These alien deep sea creatures are presented mostly on their own, against black backdrops, in three sections: The Blackwater Vertical Migrators, Masters of the Language of Light, and The Bottom Dwellers. Our role is primarily as viewers, marvelling at their strangeness and beauty.

In contrast, Stephen Dalton's *Capturing Motion* presents a lifetime engaged in a process he pretty much invented: taking photos of animals—insects, birds, reptiles, and amphibians—in motion, often in flight, freeze-framing them in clean, crisp, stop-action shots that were impossible to make until he diligently and systematically developed the methods. In three introductory sections, Dalton recounts how he developed early on an interest in nature and photography, the daunting technical challenges of equipping himself for action photography long before the ease of digital cameras, and practical notes for photographers. The bulk of the book is six themed chapters charting his interests over time and place. Dalton's incredible photos and the stories behind them are shown in two-page spreads. The images throughout, taken from the 1970s through 2019, are amazing as technical achievements and studies of animal-in-motion behaviours. We can only marvel at both the techniques and the results.

While Dalton takes us on a solo voyage, Hoyt presents the work of others. He is a Whale and Dolphin Conservation research fellow who has spent most of his life studying, learning, and writing about these large animals. The photographers whose work is featured in *Strange Sea Creatures* are also divers who travel the oceans to work with researchers such as Hoyt and expeditions mounted by organizations such as National Geographic and David Attenborough's Blue Planet. Hoyt has written 24 books—and some 600 scientific papers—from academic monographs to books for children and young adults, including a couple similar to this one. The unseen locations are exotic—Russia's White Sea and Sea of Okhotsk, the waters of Komodo National Park in Indonesia, or Scotland's Loch Duich—and familiar, such as the gulfs of Maine or Mexico. Place is less important for Dalton, who very often brings his subjects to the studio, filled with complex equipment and gear designed for the sole purpose of catching them in motion. And catch them he did—and does—for, like Hoyt, he is still at it. Each author continues to open up through photography new fields of experience for armchair observers. In both books we see things that most of us cannot observe any other way. The authors share the hope that not all of us will stay in our armchairs but be inspired to follow their pioneering trails and become, wherever we are, ambitious students of the natural world around us.

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NEW TITLES

Prepared by Barry Cottam

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BOTANY

Anatomy of Flowering Plants: An Introduction to Structure and Development. Fourth Edition. By Paula J. Rudall. 2020. Cambridge University Press. 139 pages and 73 black and white photos and illustrations, 39.95 CAD, Paper.

Bark: A Field Guide to Trees of the Northeast. By Michael Wotech. Foreword by Tom Wessels. 2020. Brandeis University Press. 280 pages, 283 colour plates, 151 halftones, and 65 maps, 29.95 USD, Paper.

***Flora of Oregon. Volume 1: Pteridophytes, Gymnosperms, and Monocots**. Edited by Stephen C. Myers, Thea Jaster, Katie E. Mitchell, and Linda K. Hardiston. 2015. OregonFlora, Oregon State University, and Botanical Research Institute of Texas. 608 pages, 520 black and white figures and maps, and 73 landscape colour photos, 75.00 USD, Cloth.

***Flora of Oregon. Volume 2: Dicots A-F**. Edited by Stephen C. Myers, Thea Jaster, Katie E. Mitchell, Tanya Harvey, and Linda K. Hardiston. 2020. OregonFlora, Oregon State University, and Botanical Research Institute of Texas. 880 pages, 785 black and white figures and maps, and 96 landscape colour photos, 85.00 USD, Cloth.

***Herbarium: The Quest to Preserve and Classify the World's Plants**. By Barbara M. Thiers. 2020. Timber Press. 304 pages, 40.00 USD, Cloth, 30.05 USD, E-book.

Remarkable Trees. By Christina Harrison and Tony Kirkham. 2019. UCP. 256 pages and 225 colour plates, 32.50 USD, Cloth.

The Curious World of Seaweed. By Josie Iselin. 2019. Heyday Books. 256 pages and 350 photographs and images, 35.00 USD, Cloth or E-book.

The Wardian Case: How a Simple Box Moved Plants and Changed the World. By Luke Keogh. 2020. Royal Botanic Gardens, Kew. 288 pages, 19 colour plates, and 40 halftones, 35.00 USD, Cloth. Also available as an E-book.

CLIMATE CHANGE AND CONSERVATION

Cataclysms: An Environmental History of Humanity. By Laurent Testot. Translated by Katharine Throssell. 2020. University of Chicago Press. 480 pages, 35.00 USD, Cloth or E-book.

Chocolate Crisis: Climate Change and Other Threats to the Future of Cacao. By Dale Walters. 2021. University of Florida Press. 230 pages, 40.00 USD, Cloth. Also available as an E-book.

Climate in Motion: Science, Empire, and the Problem of Scale. By Deborah R. Coen. 2020. University of Chicago Press. 464 pages, 40.00 USD, Cloth, 30.00 USD, Paper. Also available as an E-book.

Foresters, Borders, and Bark Beetles: The Future of Europe's Last Primeval Forest. By Eunice Blavascunas. 2020. Indiana University Press. 236 pages, 75.00 USD, Cloth, 24.00 USD, Paper or E-book.

†Fossilized: Environmental Policy in Canada's Petro-Provinces. By Angela V. Carter. 2020. UBC Press. 244 pages, 75.00 CAD, Cloth, 32.95 CAD, E-book.

Habitat Ecology and Analysis. By Joseph A. Veech. 2021. Oxford University Press. 240 pages and 47 colour illustrations, 100.00 CAD, Cloth, 49.95 CAD, Paper. Also available as an E-book.

Marine Conservation: People, Ideas and Action. By Bob Earll. 2018. Pelagic Publishing. 314 pages, 43.17 CAD, Paper.

Standing between Life and Extinction: Ethics and Ecology of Conserving Aquatic Species in North American Deserts. Edited by David Propst, Jack Williams, Kevin Bestgen, and Christopher Hoagstrom. Foreword by Senator Tom Udall. 2021. UCP. 496 pages, 90 color plates, and 22 halftones, 150.00 Cloth, 65.00 Paper. Also available as an E-book.

The Citizen's Guide to Climate Success: Overcoming Myths that Hinder Progress. By Mark Jaccard. 2020. Cambridge University Press. 304 pages, 68.95 CAD, Cloth, 22.95 CAD, Paper. Also available as an E-book.

There Is No Planet B: A Handbook for the Make or Break Years. Updated Edition. By Mike Berners-Lee. 2021. Cambridge University Press. 336 pages, 14.95 USD, Paper.

Woodland Survey Handbook: Collecting Data for Conservation in British Woodland. By Keith Kirby and Jeanette Hall. 2019. Pelagic Publishing. 220 pages, 51.80 CAD, Paper.

ENTOMOLOGY AND ARACHNOLOGY

Diptera: An Introduction to Flies. By Nikita Vikhrev. 2020. Privately Published. 160 pages, with colour photos, 14.99 GBP, Cloth. First published in Russian in 2019; English version substantially extended and revised by the author and editors. Available through NHBS, Natural History Book Service, https://www.nhbs.com/publisher/nikita-vikhrev-privately-published.

Ecological and Economic Entomology: A Global Synthesis. By Brian Freeman. 2020. CABI. 784 pages, 275.00 USD, Cloth, 90.00 USD, EPDF, 75.00 USD, E-book.

Les insectes du Québec et autres arthropodes terrestres. Par Étienne Normandin. 2020. Les Presses de l'Université de Montréal. 612 pages et plus de 3300 photos couleur, 49.95 CAD, Papier.

†Lyme Disease, Ticks and You: A Guide to Navigating Tick Bites, Lyme Disease and Other Tick-Borne Infections. By Shelley Ball. 2021. Firefly Books. 128 pages, 19.95 CAD, Paper.

Mosquitoes of the World, Volumes 1 and 2. By Richard C. Wilkerson, Yvonne-Marie Linton, and Daniel Strickman. 2021. Johns Hopkins University Press. 1332 pages, 199 line drawings, and 168 colour plates, 195.00 USD, Cloth or E-book.

Papillons de nuit et chenilles du Québec et des Maritimes. Séri Guides Nature Quintin. Par Stéphane Le Tirant et Michel Leboeuf. 2018. Éditions Nature Quintin. 336 pages, 39.95 CAD, Papier.

Pollinators & Pollination: Nature and Society. By Jeff Ollerton. 2021. Pelagic Publishing. 300 pages and 78 colour illustrations, 43.54 CAD, Paper.

Spider Webs: Behavior, Function, and Evolution. By William G. Eberhard. 2020. University of Chicago Press. 816 pages, 195 colour photos, and 97 line drawings, 75.00 USD, Cloth. Also available as an E-book.

HERPETOLOGY

Galapagos Giant Tortoises. Biodiversity of the World: Conservation from Genes to Landscapes Series. Edited by James Gibbs, Linda Cayot, and Washington Tapia A. 2020. Elsevier Academic Press. 536 pages, 90.00 USD, Cloth or E-book, 120.00 USD, Cloth and E-book.

Turtle. By Louise M. Pryke. 2021. Reaktion Books. 200 pages and 100 illustrations, 12.95 GBP, Paper.

ORNITHOLOGY

Bird Senses: How and What Birds See, Hear, Smell, Taste, and Feel. By Graham R. Martin. 2020. Pelagic Publishing. 270 pages, 50.98 CAD, Paper.

Birds: An Anthology. Edited by Jaqueline Mitchell. 2020. Bodleian Library, University of Oxford. 272 pages, 25 halftones, 25.00 USD, Cloth.

Fragile: Birds, Eggs and Habitats. By Colin Prior. 2020. Merrell Publishers. 240 pages, 130.00 AUD, Cloth.

European Breeding Bird Atlas 2: Distribution, Abundance and Change. By Verena Keller, Sergi Herrando, Petr Voříšek, Martí Rodríguez-Franch, Marina Kipson, Pietro Milanesi, David Martí, Marc Anton, Alena Klvanová, Mikhail V. Kalyakin, Hans-Günther Bauer, and Ruud P.B. Foppen. 2020. Lynx Edicions. 90.00 EUR, Cloth.

The Art of Birds: Grace and Motion in the Wild. By Jim Miller. 2021. University Press of Florida. 208 pages and 120 colour photos, 49.95 CAD, Cloth.

†The Bird-Friendly City: Creating Safe Urban Habitats. By Timothy Beatley. 2020. Island Press. 272 pages, 35.00 USD, Cloth or E-book.

The Largest Avian Radiation: The Evolution of Perching Birds, or the Order Passeriformes. Edited by Jon Fjeldså, Les Christidis, and Per G.P. Ericson. 2020. Lynx Edicions. 345 pages, 80.00 EUR, Cloth.

The Swallow: A Biography. By Stephen Moss. 2020. Square Peg. 195 pages, 27.99 CAD, Cloth.

What Is a Bird? An Exploration of Anatomy, Physiology, Behavior, and Ecology. Edited by Tony D. Williams. 2020. Princeton University Press. 368 pages and 400 colour photos and illustrations, 35.00 USD, Cloth. Also available as an E-book.

ZOOLOGY

Bears of the World: Ecology, Conservation and Management. Edited by Vincenzo Penteriani and Mario Melletti. Foreword by Tim Clutton-Brock. 2021. Cambridge University Press. 388 pages, 166.95 CAD, Cloth, 116.00 USD, E-book.

Birds and Mammals of the Galapagos. Lynx and BirdLife International Field Guides. By Dušan M. Brinkhuizen and Jonas Nilsson. 2020. Lynx Edicions. 660 pages and 110 colour maps, 35.50 EUR, Cloth, 29.95 EUR, Flexibound.

Felids and Hyenas of the World: Wild Cats, Panthers, Lynx, Pumas, Ocelots, Caracals, and Relatives. Princeton Field Guides Series. By José R. Castelló. Foreword by Alexander Sliwa and Andrew C. Kitchener. 2020. Princeton University Press. 280 pages, 79.95 USD, Cloth, 29.95 USD, Paper.

Freshwater Fishes of North America, Volume 2: Characidae to Poeciliidae. Edited by Melvin L. Warren, Jr., and Brooks M. Burr with Anthony A. Echelle, Bernard R. Kuhajda, and Stephen T. Ross. Illustrated by Joseph R. Tomelleri. 2020. Johns Hopkins University Press. 150.00 USD, Cloth or E-book.

Shark Biology and Conservation: Essentials for Educators, Students, and Enthusiasts. By Daniel C. Abel and R. Dean Grubbs, with contribution from Tristan Gutteridge. Illustrated by Elise Pullen and Marc Dando. 2020. Johns Hopkins University Press. 424 pages and 255 photos and illustrations, 49.95 USD, Cloth or E-book.

OTHER

A Biologist Abroad. By Rory Putman. 2021. Barnes & Noble. 148 pages, 22.95 USD, Paper.

A Series of Fortunate Events: Chance and the Making of the Planet, Life, and You. By Sean B. Carroll. 2020. Princeton University Press. 224 pages, 22.95 USD, Cloth. Also available as an E-book.

Accidental Wilderness: The Origins and Ecology of Toronto's Tommy Thompson Park. By Walter H. Kehm. Photography by Robert Burley. 2020. Aevo UTP. 176 pages and 100 illustrations, 32.47 CAD, Cloth or E-book.

†**Becoming a Wildlife Professional**. Edited by Scott E. Henke and Paul R. Krausman. 2020. Johns Hopkins University Press. 232 pages, 59.95 USD, Cloth or E-book.

Biostatistics with R: An Introductory Guide for Field Biologists. By Jan Lepš and Petr Šmilauer. 2020. Cambridge University Press. 382 pages, 102.95 CAD, Cloth, 39.95 CAD, Paper, 28.00 CAD, E-book.

Dancing with Bees: A Journey Back to Nature. By Brigit Strawbridge Howard. 2020. Chelsea Green Publishing. 304 pages, 17.95 USD, Paper.

Ecology of Freshwaters: Earth's Bloodstream. Fifth Edition. By Brian R. Moss. 2018. Wiley. 560 pages, 110.24 CAD, Paper, 88.99 CAD, E-book.

†**Game Theory in Biology: Concepts and Frontiers**. By John M. McNamara and Olof Leimar. 2020. Oxford University Press. 352 pages, 95.00 CAD, Cloth, 45.95 CAD, Paper. Also available as an E-book.

Life in Extreme Environments: Insights in Biological Capability. Ecological Reviews Series. Edited by Guido di Prisco, Howell G.M. Edwards, Josef Elster, and Ad H.L. Huiskes. 2020. Cambridge University Press. 396 pages, 130.00 USD, Cloth, 49.99 USD, Paper, 40.00 USD, E-book.

Making Modern Science. Second Edition. By Peter J. Bowler and Iwan Rhys Morus. 2020. University of Chicago Press. 608 pages, 35.00 USD, Paper. Also available as an E-book.

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The Genesis Quest: The Geniuses and Eccentrics on a Journey to Uncover the Origin of Life on Earth. By Michael Marshall. 2020. University of Chicago Press. 368 pages, 26.00 USD, Cloth or E-book.

The Pelagic Dictionary of Natural History of the British Isles: Descriptions of all Species with a Common Name. By Peter Jarvis. 2020. Pelagic Publishing. 549 pages, 60.44 CAD, Cloth.

The Reindeer Chronicles and Other Inspiring Stories of Working with Nature to Heal the Earth. By Judith D. Schwartz. 2020. Chelsea Green Publishing. 256 pages, 17.95 USD, Paper.

***The World in a Grain: The Story of Sand and How It Transformed Civilization**. By Vince Beiser. 2019. Riverhead Books. 304 pages, 17.00 USD, Paper, 4.99 USD, E-book (2018).

Timefulness: How Thinking Like a Geologist Can Help Save the World. By Marcia Bjornerud. 2020. Princeton University Press. 224 pages, 24.95 USD, Cloth, 16.95 USD, Paper. Also available as an E-book.

Wetland, Woodland, Wildland: A Guide to the Natural Communities of Vermont. Second Edition. By Elizabeth H. Thompson, Eric R. Sorenson, and Robert J. Zaino. 2019. Chelsea Green Publishing. 256 pages, 17.95 USD, Paper.

What Is Life? Five Great Ideas in Biology. By Paul Nurse. 2021. W.W. Norton. 160 pages, 20.00 USD, Cloth.

The Canadian Field-Naturalist

News and Comment

Compiled by Amanda E. Martin

Upcoming Meetings and Workshops

Entomological Society of America, Eastern Branch Meeting

The annual Eastern Branch Meeting of the Entomological Society of America to be held as an online meeting 22–24 March 2021. Registration for this event is free for members. More information is available at https://www.entsoc.org/eastern/2021-branch-meeting.

Alberta Chapter of The Wildlife Society Conference

The Alberta Chapter of The Wildlife Society Conference to be held as an online meeting 22–26 March 2021. The theme of the conference is: 'Species on the Move'. Registration is currently open. More information is available at https://www.actws.ca/conference/.

Entomological Society of America, Southeastern Branch Meeting

The annual Southeastern Branch Meeting of the Entomological Society of America to be held as an online meeting 29–31 March 2021. Registration for this event is free for members. More information is available at https://www.entsoc.org/southeastern/2021-branch-meeting.

Entomological Society of America, Pacific Branch Meeting

The annual Pacific Branch Meeting of the Entomological Society of America to be held as an online meeting 5–7 April 2021. Registration for this event is free for members. More information is available at https://www.entsoc.org/pacific/2021-branch-meeting.

International Association for Landscape Ecology, North America Regional Chapter Annual Meeting

The annual meeting of the North America Regional Chapter of the International Association for Landscape Ecology to be held as an online meeting 12–16 April 2021. Registration is currently open. More information is available at http://www.ialena.org/annual-meeting.html.

Entomological Society of America, International Branch Virtual Symposium

The International Branch Virtual Symposium of the Entomological Society of America to be held as an online meeting 26–28 April 2021. More information is available at https://www.entsoc.org/international/2021-virtual-symposium.

North American Caribou Workshop

The 18th North American Caribou Workshop to be held as an online meeting 3–6 May 2021. Registration is currently open. More information is available at https://www.uqar.ca/recherche/la-recherche-a-l-uqar/unites-de-recherche/18th-north-american-caribou-workshop-2021/nacw-2021/.

Ontario Ecology, Ethology, and Evolution Colloquium

The 51st annual Ontario Ecology, Ethology, and Evolution Colloquium to be held as an online meeting 13–14 May 2021. More information is available at https://oe3c.com/.

International Association of Great Lakes Research Conference

The 64th annual Conference on Great Lakes Research, hosted by Michigan Technological University, to be held as an online meeting 17–21 May 2021. The theme of the conference is: 'Bridging: Knowledges • Seven Generations • Land to Lake'. More information is available at http://iaglr.org/iaglr2021/.

Society for Freshwater Science Annual Meeting

The annual meeting of the Society for Freshwater Science to be held as an online meeting 23–27 May 2021. Registration is currently open. Registration is currently open. More information is available at https://sfsannualmeeting.org/.

Carolyn Callaghan—stop stepping down!

Carolyn Callaghan served "exceptionally" as Editor-in-Chief of *The Canadian Field-Naturalist* (CFN) from 2011 (vol. 125(1)) to 2016 (vol. 130(2)). She was cautious, sensitive, and a very hard worker. In recognition of her outstanding editorial work, she received the Ottawa Field-Naturalists' Club (OFNC) President's Prize (Trail & Landscape 51(2): 55). During her tenure she was very interested in involving youth and went out of her way to help younger people with their analysis and writing. She encouraged students to contribute to CFN, accepting and publishing two articles written by high school students. She also applied practices that supported gender diversity and inclusion in the peer review process. She brought some of the complaints of authors to the OFNC Publications Committee meetings and argued successfully on their behalf. She also updated the instructions to contributors and we initiated the online version of CFN while she was editor. During the early part of her editorial work she much appreciated the help of previous editor Francis Cook. She enjoyed getting to know authors, reviewers, Associate Editors, and journal staff. Carolyn noted that: "A well-functioning peer-review publication requires a community of dedicated individuals. I deeply appreciated the dedication I saw on a daily basis editing the journal".

Carolyn did not stop helping OFNC when she stepped down as Editor-in-Chief, but let us pause for a moment. CFN has not had a great many editors and we know a good deal about many of them. It often happens though that we do not know the wonderful people around us as well as we would like to. Just in case you did not know Carolyn as well as we did, she grew up near the Carolinian forest of the Niagara escarpment in Hamilton. Her Ph.D. in Zoology was completed at the University of Guelph in 2002. Her thesis was entitled "The ecology of gray wolf (*Canis lupus*), habitat use, survival, and persistence in the Central Canadian Rockies"; it was in Banff that her path crossed with the current Editor-in-Chief. She has done significant work on a great variety of subject areas, including environmental law, agricultural landscape diversity, neo-nicotinoid insecticides, Arctic Caribou, climate change, and Species at Risk. She has helped numerous organizations including University of Ottawa, University of Calgary, Agriculture Canada, Canadian Wildlife Service, and Environment and Climate Change Canada, and has mentored many students. She has organized world symposia on the ecology and protection of wolves.

Members of the Publications Committee recall some meetings we had at Carolyn's home in the upper Ottawa Valley where we enjoyed adventurous hikes and great food, and met her wonderful family (all of whom have spent weeks on safari in Africa).

In 2021 Carolyn had to step down again, this time as Associate CFN Editor for large mammals. This was a great loss because she is widely respected as a world expert in mammal ecology. She truly excelled in this area and was able to provide very helpful reviews and to inspire authors to improve their work. Although Carolyn had to leave some OFNC posts, she is continuing as a member of the Publications Committee, and we hope that she will be able to continue with us for a long time. Carolyn brings a great deal of experience to the committee and to the Club, now as a Senior Conservation Biologist with the Canadian Nature Federation.

PAUL CATLING
OFNC Publications Committee

Dan Brunton steps down from the Ottawa Field Naturalists' Club Publications Committee after many years of service

Dan Brunton, Honourary Member of the Ottawa Field-Naturalists' Club (OFNC; Canadian Field-Naturalist 124: 183–184), has been a long-standing and valued member of the OFNC Publications Committee, including serving in the role of committee Chair from 2011 to 2014. Dan has been a long-time champion of the Club's role in disseminating knowledge to the community, and is a passionate supporter of the Club's publications, *Trail & Landscape* (T&L) and *The Canadian Field-Naturalist* (CFN). His enthusiasm for club activities and deep knowledge of the history of the OFNC and its publications were among his many valuable contributions as a member of the Publications Committee. Dan has also worked to raise awareness of the significant contributions of Canada's field naturalists, and he played a key role in the development of CFN's "Great Canadian Field-Naturalists" initiative, designed to formally recognize individuals who have made significant contributions to our knowledge of natural history in Canada (Canadian Field-Naturalist 131: 280–283).

In addition to his contributions to the OFNC Publications Committee, Dan is an active contributor to T&L and CFN, writing and reviewing research articles, reviewing books, and crafting tributes.

Dan stepped down from the OFNC Publications Committee in early 2021. We thank Dan for his years of exemplary service to the Publications Committee. He will be missed at our OFNC Publications Committee meetings. However, we look forward to his future contributions to both T&L and CFN.

Amanda E. Martin
OFNC Publications Committee

In Memoriam: Ronald E. Bedford (26 June 1930–3 November 2020)

Ron Bedford, active member of the Ottawa Field-Naturalists' Club (OFNC) and Honorary Member (since 2010; OFNC 2011), died in Ottawa, at age 90 (Ottawa Citizen 2020). He was a distinguished scientist at the National Research Council of Canada, in Ottawa for 40 years before retiring in 1995. He earned his Ph.D. in physics in 1955 from the University of British Columbia. He also served on the OFNC Publications Committee for 32 years, including as Chair. A full tribute is planned for an upcoming issue of *The Canadian Field-Naturalist.*

Literature Cited

OFNC (Ottawa Field-Naturalists' Club). 2011. Ronald E. Bedford – 2010 Honorary Member. Accessed 4 February 2021. https:/ofnc.ca/wp-content/uploads/2017/09/2010HonoraryMember_RonBedford.pdf.

Ottawa Citizen. 2020. Obituary: Bedford, Ronald Ernest June 26, 1930 – November 3, 2020. Accessed 4 February 2021. https://ottawacitizenremembering.ca/obituary/ronald-bedford-1080816364.

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

In Memoriam: Donald A. Smith (29 August 1930–13 November 2020)

Don Smith, long-time Ottawa Field-Naturalists' Club (OFNC) member, Council Member, Vice-President, Recording Secretary, and events speaker, died at his family home near Stittsville, Ontario, at age 90. He was the first Interpretation Specialist at E.C. Manning Provincial Park, British Columbia, hired by R. Yorke Edwards, whose tribute was published in the previous issue of *The Canadian Field-Naturalist* (CFN; Cannings *et al.* 2020). He was a professor in biology at Carleton University and curator of the Museum of Zoology (1957–1995), having completed his Ph.D. at University of Toronto in 1957. He also served as the Assistant Editor of CFN (1972–1981). A full tribute is planned for an upcoming issue of CFN.

Acknowledgements

Thanks to Fenja Brodo for sharing Don's obituary from *The Ottawa Citizen* and her tribute to Don expected to be published in an upcoming issue of *Trail & Landscape*, the Ottawa regional OFNC publication.

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Cannings, R.A., T. Goward, and W. J. Merilees. 2020. Tribute to R. Yorke Edwards, 1924–2011. Canadian Field-Naturalist 134: 270–294. https://doi.org/10.22621/cfn.v134i3.2657

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

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Compiled by William Halliday

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