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COVER: *Polyergus bicolor*, a slave-making ant, was recently discovered for the first time in Alberta, a substantial range expansion for the species. It was found parasitizing *Formica podzolica*, a new host for the species. See note in this issue by Christine Sosiak *et al.*, pages 309–312. Photo: C. Sosiak, 21 July 2017, near Sylvan Lake, Alberta.

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Note

A successfully breeding, partially leucistic American Robin (*Turdus migratorius*)

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Abstract
American Robin (*Turdus migratorius*) is the most abundant and broadly distributed thrush in North America. Both sexes likely engage in mate choice, and there is some evidence of assortative mating based on breast colour in this species. Over two breeding seasons, we documented a case of partial leucism, primarily of the breast feathers, in a male American Robin in London, Ontario, Canada. We report evidence that the leucistic robin was capable of successful breeding. How the fitness of leucistic versus normal robins compares and how leucism influences mate choice in this and other species remain to be explored.

Key words: Ornithology; colouration; leucism; sexual selection; fitness; breeding; American Robin; *Turdus migratorius*

The colouration of birds is a result of light interacting with either the nanostructure of the integument or cellular pigments, and sometimes a combination of the two (Prum 2006). In birds, melanin is the most common pigment. A variety of feather and skin colour is attributable to two forms of melanin, eumelanin (grey to black colours) and phaeomelanin (some yellows and reds, and browns by admixture of eumelanin). The other major source of pigments in birds is carotenoids derived from their diet. Melanins are not derived from food but are produced by animals endogenously. Early in embryonic development, neural crest-derived melanoblasts migrate to the skin and the newly forming feathers. The melanoblasts differentiate into melanocytes and begin synthesizing melanin by the end of the first week of development (Bharti *et al.* 2006; McGraw 2006).

A multitude of mutations can cause white feathers where there should be feathers coloured by pigments, and there is much confusion in the literature and among birders about the correct names for such colour aberrations. We follow van Grouw (2006, 2013), who provided a summary of the most frequently occurring colour aberrations and a much-needed guide to standardize their naming. Leucism is defined as the partial or total lack of both melanins in feathers and skin as a result of the heritable failure of melanoblasts to migrate to the proper area of the body. Melanocytes and the resulting colours are absent in those areas, and the feathers appear white. Birds may be partially leucistic, with only some white feathers, or totally leucistic, with all white feathers. Importantly, melanocytes and eye pigment cells differ in their embryological origin and leucistic birds have normally coloured eyes (Bharti *et al.* 2006; van Grouw 2013).

Wild birds with leucism may face a number of challenges; however, evidence of a detrimental effect of leucism is inconclusive. In one study, the mortality of leucistic young was double that of young with normal plumage (Reese 1980). In another, a leucistic adult was not accepted into a conspecific group (Corrêa *et al.* 2017). In contrast, a leucistic adult was frequently accompanied by conspecifics in another study (Cestari and Vernaschi Vieira da Costa 2007). Several studies report no evidence that leucism affects adult breeding performance (Owen and Skimmings 1992; Forrest and Naveen 2000).

American Robin (*Turdus migratorius*) is North America's largest, most abundant, and widely distributed thrush. Typically, adult male American Robins have deep greyish to dark-brown upper parts, a blackish head, white crescents above and below the eye, white undertail coverts, and, in most eastern populations, white tips on the outer retrices. The under

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parts and breast are a rich rufous colour (Vanderhoff *et al.* 2016; Figure 1a,b). Females appear similar but with a paler grey crown and mantle, more white on the ventrum, and a paler breast (Figure 1a,b). Adult plumages vary little throughout the year; however, males have darker crowns, less white on the ventrum, and darker breasts in spring compared with autumn (Vanderhoff *et al.* 2016).

There is great interest in documenting the behaviour of leucistic birds to further understand the effects of aberrant plumages and the diverse roles plumage colouration plays in the lives of birds. Here we present evidence of a partially leucistic male American Robin successfully breeding on a ~0.2-ha private property in northwest London, Ontario (43.00°N, 81.29°W) during the 2016 and 2017 breeding seasons.

FIGURE 1. American Robin (*Turdus migratorius*). a,b. Male (top) and female specimens showing normal plumage colouration, collected in Strathroy, Ontario, 1932, Western University Zoological Collections: a. dorso-lateral view; b. ventral view. c–e. Partially leucistic male American Robin, London, Ontario: c. 30 June 2016, d. 27 May 2017, e. 5 June 2017. f. American Robin embryo, below nest site of partially leucistic robin, 18 June 2017. Photos: Nina M. Zitani.

Beginning in late spring 2016, a male American Robin with aberrant white feathers and normal eye colouration was observed multiple times. A photo of the robin was taken on 30 June 2016 (Figure 1c). Later in the summer, the leucistic robin was observed mating with a female of normal plumage and subsequently feeding a fledgling on a lawn. In 2017, the leucistic robin was first observed on 23 April. Over the course of the spring, the robin was observed repeatedly, and photos were taken on 27 May 2017 (Figure 1d) and 5 June 2017 (Figure 1e). By early June, the leucistic robin and a mate with normal colouration were observed bringing nest materials into a large, woody climbing hydrangea (*Hydrangea* sp.). On 18 June 2017, a nearly fully developed embryo was found smashed on a rock below the nest site (Figure 1f). Throughout the season, several Brown-headed Cowbirds (*Molothrus ater*) were observed in the area. On 5 August 2017 at 2000, the leucistic robin was observed on a lawn 0.25 m from a vocalizing fledgling. Shortly thereafter, the leucistic robin approached and fed the fledgling. On several occasions, the leucistic robin was observed singing normally.

The plumage colouration of this leucistic robin was as follows: the typically greyish upperparts of the body were mixed with patches of white, particularly on the mantle and lesser, median, and greater coverts. There appeared to be a greater-than-normal proportion of white around the eye and throat. The usually rich rufous breast was heavily marked by white feather patches. The eyes of the robin were black. The lack of colouration in typically pigmented areas that we observed in this bird and normally coloured eyes are characteristic of partial leucism (van Grouw 2006, 2013). Because of the characteristic markings of this bird, we were confident in all cases that our observations were of the same individual (Figure 1c–e).

The occurrence of leucism in natural populations of wild birds rarely exceeds 1% (Bensch *et al.* 2000). Gross (1965) reported that American Robin had the highest rate (8.2%) of "albinism" among North American birds he surveyed; his tally included not only leucism but all forms of pale aberrations. When strictly defined, leucism in American Robin has been reported less often than albinism and melanism (Vanderhoff *et al.* 2016).

Plumage colouration has long been associated with sexual selection (Darwin 1871), with females typically preferring brightly coloured males (e.g., Safran *et al.* 2005), likely because plumage is often condition-dependent (Hamilton and Zuk 1982). Leucistic birds may appear duller or less attractive to prospective mates and, consequently, may have lower reproductive success and overall fitness compared with normally-coloured individuals, especially those with brightly coloured plumage.

In species where the sexes share the same traits (e.g., breast colour in American Robin), mutual sexual selection can occur if both sexes benefit from discriminating among potential mates based on these traits (Rowe and Weatherhead 2011). The partially leucistic male robin we observed had a large proportion (~40–50% of breast area) of white feathers on his breast. To our knowledge, there are no data on how leucism might influence mate preference in American Robin; however, because robins apparently exhibit positive assortative mating with respect to breast colour (Rowe and Weatherhead 2011), we expect this leucistic male would be more likely to mate with a paler female.

In conclusion, our report documents a rare case of partial leucism in American Robin, and provides evidence that leucistic robins are capable of successful breeding. How the fitness of leucistic versus normal robins compares remains to be explored. Given the mixed results in the literature on the impacts of leucism, more studies are needed to understand the maintenance of leucism in natural populations and the impacts of this plumage abnormality on wild birds.

Author Contributions

Writing – Original Draft: N.Z. and L.G.; Writing – Review & Editing: N.Z., L.G., and R.G.T.; Conceptualization: N.Z.; Investigation: N.Z and R.G.T.

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Occurrence of anthropogenic litter in nestling Tree Swallows (*Tachycineta bicolor*)

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Abstract

While undertaking a study of the effects of strontium-90 on Tree Swallow (*Tachycineta bicolor*) near Chalk River, Ontario, we noticed the presence of anthropogenic litter (pieces of metal, glass, and plastic, and paper, plastic, and foil wrappers, >1 mm in size) in the nestlings. Although combustible litter (pieces of plastic and wrappers) were not quantified before the nestlings were incinerated in 2014 and 2015, gizzards were dissected in 2016. Litter (>1 mm diameter) was found in 30% of the 74 nestlings examined. This material is most likely provided to nestlings, along with food (insects) and natural grit (sand, stones, and mollusc shells), which we also found, by parent birds; however, it could lead to internal injuries and/or harmful substances being absorbed by the young birds.

Key words: Tree Swallow; *Tachycineta bicolor*; nestling; grit; environmental impact; anthropogenic litter; metal; glass; plastic; paper

Introduction

Insoluble and soluble natural grit (sand, stones, and mollusc shells) is an important component of many avian diets, as it improves the process of grinding foods, such as seeds, plant material, and insects, in the gizzard (Barrentine 1980; Best and Gionfriddo 1991; Gionfriddo and Best 1995). In atricial species, grit is provided by parents. The amount and size of grit consumed by a species is believed to depend on the specific diet of the bird (Gionfriddo and Best 1995). Tree Swallow (*Tachycineta bicolor*), an insectivorous species, requires grit for efficient digestion (Mayoh and Zach 1986), and adults have been found to feed grit to nestlings as young as three days of age (Mayoh and Zach 1986).

If anthropogenic litter (e.g., pieces of metal, glass, and plastic as well as paper, plastic, and foil wrappers) is present near nesting locations, it too could be fed to nestlings. However, ingested anthropogenic litter could lead to internal injury, and/or harmful substances from the materials could be absorbed by the nestlings (Bellrose 1975; Trost 1981; Azzarellow and Van Vleet 1987; Fry *et al.* 1987; Laist 1987; Colabuono *et al.* 2010). Herein, we report on the ingestion of anthropogenic litter by Tree Swallow nestlings near Chalk River, Ontario, Canada.

Methods

In preparation for a strontium-90 (Sr-90) study described in Lee *et al.* (2019), nest boxes were installed on the 4000-ha property of the Canadian Nuclear Laboratories' Chalk River Laboratories (46.052578°N, 77.360890°W; Figure 1) in suitable Tree Swallow nesting habitats (wetland and shoreline; De Steven 1980; Robertson and Rendell 1990). Tree Swallows will readily inhabit nest boxes and tolerate human disturbances, making them an ideal bird for biomonitoring and research (De Steven 1980; Mayoh and Zach 1986; Robertson and Rendell 1990).

Monitoring of the nest boxes began in late April or early May of each year, and observations of nesting, egg laying, clutch size, hatchings, nestling growth, and fledging were documented. When nestlings were 12 days old (as determined from known hatch dates), one nestling from each nest box with at least four young was collected (on average a nest box would contain six nestlings). In all, 74 12-day-old nestlings

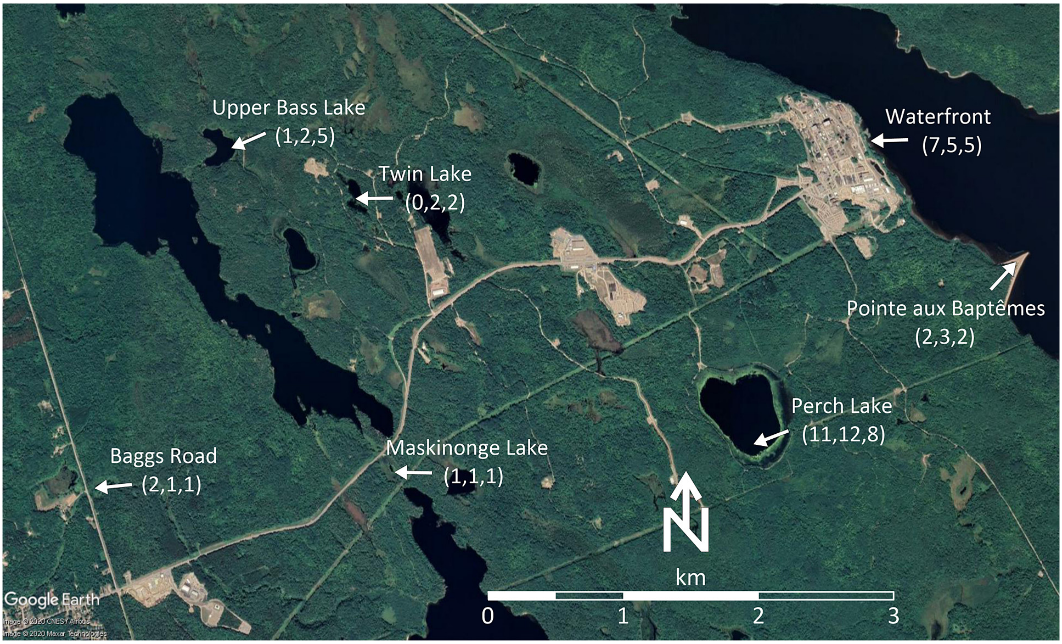

FIGURE 1. Number of Tree Swallow (*Tachycineta bicolor*) nestlings (2014, 2015, 2016) collected at each location on the Canadian Nuclear Laboratories' Chalk River property. Source: Chalk River Laboratories, Chalk River, Ontario, Canada. 46°03′00.2″N, 77°21′51.7″W. Google Earth Imagery date: 20 August 2019. Data providers: DigitalGlobe 2019. Accessed: November 2019.

were taken, euthanized, their external surfaces verified clean, and frozen.

In 2013, carcasses were incinerated for the determination of Sr-90 (Lee *et al.* 2019). Frozen carcasses were thawed overnight in a refrigerator, then dehydrated overnight in an oven, at 105°C. After cooling to room temperature, carcasses were heated to 250°C for 2 h and to 450°C for 16 h, with the 16 h incineration performed a second time to ensure complete ashing. After incineration, samples were cooled to room temperature. The ash was gently milled using a spatula, and any material (i.e., stone, glass, and metal fragments) larger than about 1 mm in diameter was removed. Beginning in 2014, natural grit materials and anthropogenic litter larger than about 1 mm in diameter observed in the ashes were noted and photographed.

In 2016, on thawing of the carcasses, the gizzard contents of each bird were examined visually for materials (e.g., insects, shells, plastic items) that would be incinerated during the ashing process. Observations were noted and the material was returned to the carcass before each carcass was dried and incinerated as above; non-combustible materials larger than about 1 mm in diameter were removed and photographed after the ashing process. Although the general type of litter was noted, pieces were not measured.

Results

In addition to small stones, metal, and/or glass fragments were found in five of 24 nestlings in 2014 and in 10 of 26 nestlings in 2015 (Table 1). Because the gizzards of nestlings collected in 2014 and 2015 were not examined before the nestlings were incinerated, results for combustible materials, such as plastic, are not available. In 2016, the gizzards were examined prior to incineration and we observed flying insects mixed with small stones, sand, grass, and mollusc shells, as well as anthropogenic materials, including pieces of metal and glass, sections of wrappers (most often pieces of shiny cigarette and chewing gum wrappers up to ~1 cm wide) in seven of 24 birds (Table 1). Figures 2 and 3 provide examples of litter collected from nestlings sampled in 2014–2016.

The presence of anthropogenic material in the nestlings occurred most often along the Ottawa River shoreline and around Perch Lake, where human activities are more prominent (Figure 1; Tables 2 and 3). Such material was seldom found in nestlings collected from more remote areas.

In 2016, no significant differences (t-test, $t_9 = 1.146$, $P = 0.281$) were found between the weights of 12-day-old nestlings with (average 21.0 g, range 19.5–22.2 g) and without (21.8 g, 20.5–22.8 g) anthropogenic litter in their gizzards.

TABLE 1. Types of litter (>1 mm diameter) found in nestling Tree Swallows (*Tachycineta bicolor*), 2014–2016.

Year	No. nestlings	% nestlings containing fragments			
		Metal	Glass	Wrapper	Plastic
2014	24	12.5	4.2	n/a*	n/a
2015	26	30.8	11.5	n/a	n/a
2016	24	12.5	20.8	4.2	4.2

*n/a = not available because these materials would have been incinerated.

FIGURE 2. Examples of metal turnings found in the whole body ashes of a Tree Swallow (*Tachycineta bicolor*) nestling. Photo: Jennifer Haughton.

FIGURE 3. Examples of glass fragments found in the whole body ashes of a Tree Swallow (*Tachycineta bicolor*) nestling. Photo: Jennifer Haughton.

TABLE 2. Locations of nestling Tree Swallows (*Tachycineta bicolor*) with anthropogenic litter (>1 mm diameter) in their gizzards, 2016.

Location	No. nestlings	No. nestlings containing anthropogenic fragments			
		Metal	Glass	Wrapper	Plastic
Baggs Road	1	0	0	0	0
Maskinonge Lake	1	1	0	0	0
Upper Bass Lake	5	0	1	0	0
Twin Lake	2	0	0	0	0
Perch Lake	8	0	2	0	0
Pointe aux Baptemes	2	1	0	0	1
Waterfront	5	1*	1	1*	0

*Both fragment types were in the same nestling.

TABLE 3. Locations of nestling Tree Swallows (*Tachycineta bicolor*) containing glass and metal pieces (>1 mm diameter) in 2014 and 2015.

Location	No. nestlings	No. nestlings containing anthropogenic fragments	
		Metal	Glass
Baggs Road	3	0	0
Maskinonge Lake	2	0	0
Upper Bass Lake	3	0	0
Twin Lake	2	0	0
Perch Lake	23	4	2
Pointe aux Baptemes	5	3	1
Waterfront	12	4*	1*

*Both fragment types were found in one nestling.

Discussion

Anthropogenic litter was found in 30% of 74 nestling Tree Swallows collected in 2014–2016 near Chalk River, Ontario. We consider this to be an underestimate, because it does not include litter fragments <1 mm in diameter or combustible litter for two of the three years of the study.

Barrentine (1980) reported grit in 80% of Barn Swallow (*Hirundo rustica*) nestlings sampled, providing evidence that grit is an important dietary factor during the growth of swallow nestlings and a cause for concern for birds that nest in areas where grit-like anthropogenic material may be present.

Mayoh and Zach (1986) found that Tree Swallows had a greater percentage of anthropogenic litter in their "stomachs" than did House Wrens (*Troglodytes* *aedon*) at the same age. This may be because swallows forage along shorelines and nearby roads (in a ~400 m feeding radius during the nestling period), where greater amounts of anthropogenic litter are generally found. Barrentine (1980) showed that while swallows consumed grit of various colours, sizes, and compositions, they have a clear preference for light-coloured objects between 1 and 3 mm in size. Considering metals are generally light in colour, and glass, plastic, and wrapper materials can also be a light colour, swallows could be intentionally choosing human-made materials over natural grit.

Anthropogenic litter can be domestic or industrial. The presence of metal turnings in Tree Swallow nestlings was a unique finding that is particularly relevant to industrial areas.

The potential detrimental effects of anthropogenic materials on birds are well known. For example, the ingestion of metal pieces by waterfowl can result in lead poisoning (Bellrose 1975; Trost 1981), and the occurrence and impacts of plastic ingestion by bird species, especially marine birds, are prevalent (see for example Provencher *et al.* 2014). Reported adverse health effects include: proventricular impactions, ulcerative lesions (Azzarellow and Van Vleet 1987; Fry *et al.* 1987); digestive tract blockages, stomach lining damage, appetite suppression (Azzarellow and Van Vleet 1987; Laist 1987); exposure to polychlorinated biphenyls and organochlorine pesticides (Colabuono *et al.* 2010); and lowered steroid hormone levels, delayed ovulation, and reproductive failure (Azzarellow and Van Vleet 1987).

We have documented the presence of anthropogenic litter in young Tree Swallows, in an environment previously considered to be relatively litter free. While we observed that the ingestion of litter did not significantly impact the weights of the nestlings, potential risks of ingestion of anthropogenic litter on Tree Swallow nestlings remain to be investigated.

Author Contributions

Writing – Original Draft Preparation: S.W.; Writing – Review & Editing: L.B., A.F., I.G., J.H., D.L., M.S., and S.W.; Methodology: D.L. and M.S.; Investigation: L.B., A.F., I.G., and J.H.; Resources: L.B.; Data analysis: A.F. and I.G.; Visualization: L.B.; Project Administration: M.S.; Supervision: D.L. and M.S.

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Note

First record and new host record of the obligate dulotic ant, *Polyergus bicolor* (Hymenoptera: Formicidae), in Alberta, Canada

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Abstract

We describe the discovery of *Polyergus bicolor*, an obligate slave-making ant species, as a new provincial record in Alberta. This species was previously known mostly from eastern Canada and the northeastern United States and has been sparsely collected: only once in the past 50 years. *Polyergus bicolor* was discovered parasitizing *Formica podzolica*, which is also a new host for the species. This discovery marks a significant expansion of both range and host for *P. bicolor*.

Key words: *Polyergus bicolor*; dulotic parasitism; range expansion; host expansion; Alberta; *Formica podzolica*

Polyergus (Latreille 1804) is a predominantly holarctic genus of ants that contains 14 species, 11 of which are present in North America (Trager 2013). All *Polyergus* display obligate dulotic behaviour (slave-making), making them a remarkable genus that has received a good deal of research interest.

Colony foundation occurs when a mated *Polyergus* queen enters a *Formica* nest, kills the queen, and usurps her role, with *Formica* workers taking care of her and her brood (Hölldobler and Wilson 1990). To maintain *Formica* worker populations in the colony, *Polyergus* workers locate a host nest, and then raid it for pupae, prepupae, and occasionally last-instar larvae. When the *Formica* pupae mature to adults in the *Polyergus* nest, they accept that nest as their own, and perform the majority of tasks within the colony (Trager 2013). Host *Formica* species vary, depending on the *Polyergus* species: some *Polyergus* will parasitize only one *Formica* species, while others are capable of parasitizing multiple species. Generally, the host species is from the *Formica fusca* group or the *Formica pallidefulva* group (Trager 2013).

In western North America, *Polyergus* is overwhelmingly represented by *Polyergus mexicanus* (Trager 2013; Glasier *et al.* 2016); in Idaho, *P. breviceps* is also present (Wheeler 1917; Smith 1947; Trager 2013). (Note: there are generally no accepted common names for ants.) *Polyergus bicolor* was previously reported as restricted to eastern North America: Ontario to Illinois (Smith 1947; Wheeler 1968; Trager 2013). It was reported as far west as Saskatchewan and Montana by Wheeler (1917) as *Polyergus rufescens bicolor*. It was only confirmed as far west as the Dakotas by Trager (2013), who raised it to the status of species. Trager noted that he was unable to collect any *P. bicolor* during the course of his study within its historical range, save for one collection made in Wisconsin. In the last 50 years, he had found no *P. bicolor* collection records from its historical range (Trager 2013).

We first found *P. bicolor* in Alberta in summer 2017. We collected two colonies in Jarvis Bay Provincial Park, on Sylvan Lake, while collecting and observing *Formica* colony behaviour. Jarvis Bay Provincial Park is a drywood boreal forest characterized by mostly deciduous stands dominated by Trembling Aspen (*Populus tremuloides* Michaux), Balsam Poplar (*Populus balsamifera* L.), Black Spruce (*Picea mariana* (Miller) Britton, Sterns and Poggenburgh), and White Spruce (*Picea glauca* (Moench) Voss); prior records of *P. bicolor* note that it nests mostly in mesic forest, generally in rotten

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stumps or fallen logs, thus habitat similar to Jarvis Bay (Trager 2013).

The specimens were collected by hand around the provincial park campsite after mistaking them for a species of the *Formica rufa* or *Formica sanguinea* species groups. They were found in domed dirt and debris mounds with the host species *Formica podzolica*, identified using published keys (Francoeur 1973; Glasier *et al.* 2013). Our *Polyergus* specimens were identified using Trager's revised key to global *Polyergus* species (Trager 2013). They differ from *P. mexicanus*, the other known *Polyergus* species in the area, by the degree of dark colouration on the abdomen and a complete lack of pilosity on both the vertex of the petiole and the pronotum (Glasier *et al.* 2013; Trager 2013).

A second collection occurred in July 2018 near Hay Lakes, Alberta, an area dominated by mixed deciduous woodlands (Trembling Aspen and Balsam Poplar) similar to Sylvan Lake. They were collected from a rounded mound within a grass meadow and were also using *F. podzolica* as a host. *Polyergus bicolor* has been formally recorded parasitizing both *Formica neorufibarbis* and *Formica subaenescens*, but not *F. podzolica*. The mounds in which we found *P. bicolor* were unlike their normal reported nesting sites, but this could be the result of their using a different host species.

This discovery represents a significant expansion of *P. bicolor*'s previously known range, although it supports Wheeler's (1917) reports of *P. bicolor* in Saskatchewan as *P. r. bicolor*. Although the habitat where we found *P. bicolor* in Alberta is similar to the type of habitat from which it was previously known, the climate of Alberta is distinct from that of southern Ontario and the northeastern United States. The expansion of host species to include *F. podzolica* is also notable; *Polyergus* may use one or several hosts species but tends to show high fidelity to one host for a given population. Within a *Polyergus* species, if different populations are using different hosts, they are often highly specialized to their own host species. Populations show distinct chemical and genetic divergence from one another, perhaps reflecting incipient speciation (Torres *et al.* 2018). Because newly mated *Polyergus* queens typically stay with the host species of their parent colony, this fidelity is passed down from generation to generation (Hölldobler and Wilson 1990). *Formica podzolica* is widespread throughout North America and its range overlaps with that of *P. bicolor* in the northeastern United States (Wheeler and Kannowski 1994; Ellison *et al.* 2007); thus, it is difficult to say where host expansion took place. Further genetic work would shed light on potential divergence between *P. bicolor* populations in western and eastern North America, contingent on their host species.

Voucher specimens

Canada, Alberta: Sylvan Lake Jarvis Bay, 52.347°N, 114.091°W and 52.345°N, 114.089°W, hand collected, 21 July 2017, C. Sosiak (Figure 1, personal collections of Christine Sosiak and Mari West).

Canada, Alberta: 4 km SE of Hay Lakes, Aspen Parkland, 53.165°N, 113.014°W, hand collected, with *F. podzolica,* 27 July 2018, J.R.N. Glasier (Strickland Museum and personal collection of J.R.N. Glasier). Strickland Museum accession numbers: *P. bicolor* specimens UASM396245, UASM396246; *F. podzolica* specimens UASM396247, UASM396248.

Author Contributions

Writing – Original Draft: C.E.S.; Writing – Review & Editing: C.E.S., M.W., and J.R.N.G.; Species Collection: C.E.S., M.W., and J.R.N.G.; Species Identification: C.E.S. and J.R.N.G.; Funding Acquisition: M.W.

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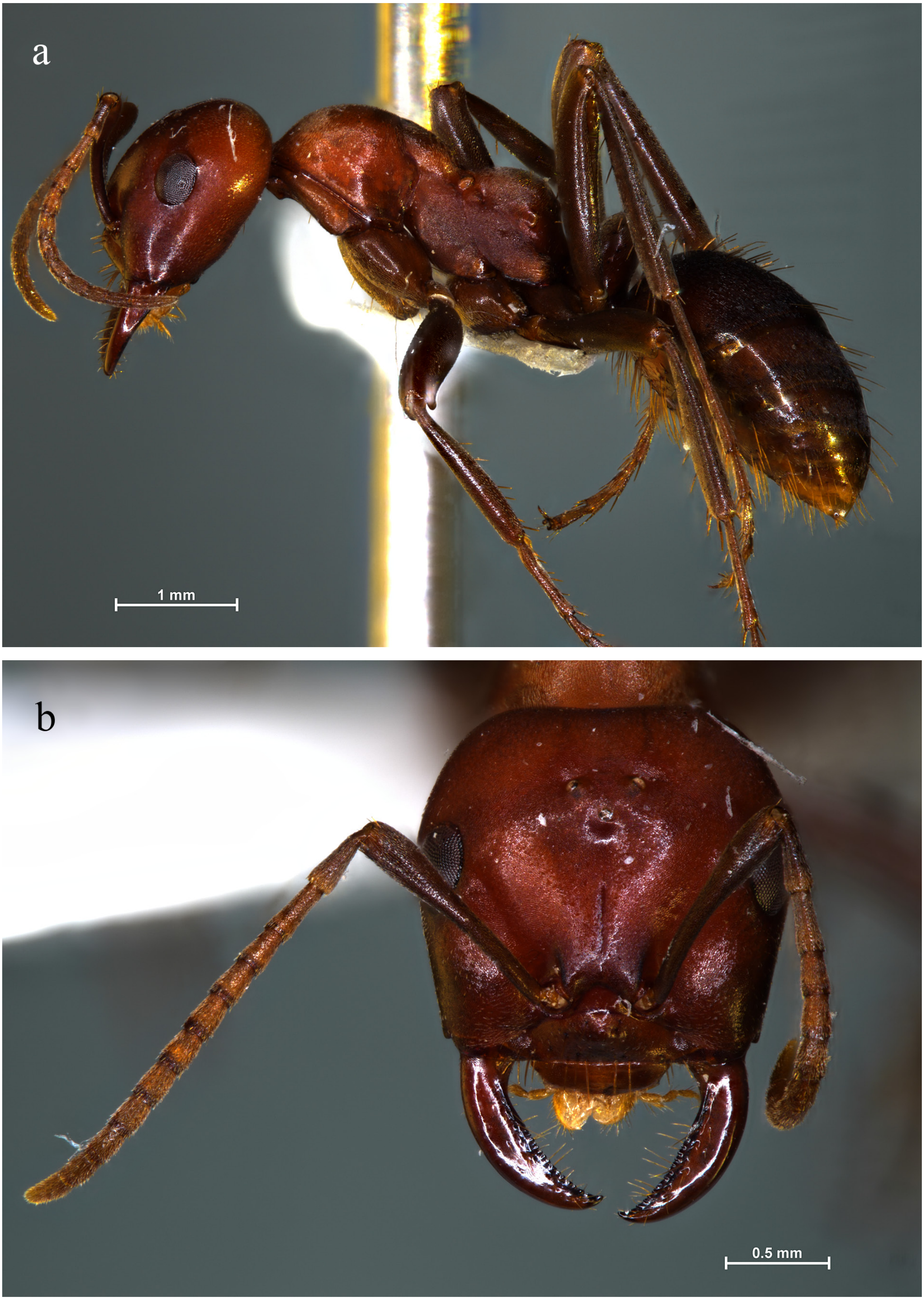

Figure 1. Lateral a. and frontal b. views of a *Polyergus bicolor* specimen collected in Jarvis Bay Provincial Park, Sylvan Lake. Photos: Christine Sosiak.

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Tall grass prairie ecosystem management—a gastropod perspective

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Abstract

Less than 5% of the original tall grass prairie in North America remains. A portion of this remnant, composed of wetland, grassland and forest, is protected by the Nature Conservancy of Canada (NCC) in southern Manitoba. This heterogeneous ecosystem has rich biodiversity; however, gastropods have not been surveyed in Canada's tall grass prairie. We studied gastropods in Prairie, Wet Meadow, Forest, and Wet Forest habitats of the Manitoba Tall Grass Prairie Preserve that vary with respect to land management practices (prescribed burning, grazing by cattle). Gastropod community composition was unique in the Prairie where mounds of grass litter form permanently moist cavities harbouring aquatic species, while dry-habitat species colonized the upper parts of these mounds. Gastropod communities in Prairie habitats were negatively affected by grazing and burning that occurred in the five years prior to our survey. Unburned Forest patches included both forest gastropod species and edge effect influenced open-habitat species and harboured the most diverse gastropod communities. These unburned Forest patches potentially provide a species pool for post-burn prairie recolonization. The gastropod community of Wet Meadows was not affected by grazing and was composed mainly of aquatic species. In this gastropod survey five species were recorded from Manitoba for the first time. The rare Blade Vertigo (*Vertigo milium*) is also reported.

Key words: Fire; grazing; freshwater snails; terrestrial snails and slugs; protected area; rare species; Manitoba

Introduction

Tall grass prairie once covered 68 million ha of North America before conversion to urban areas or cropland in the United States and Canada—less than 5% remains (Sampson and Knopf 1994). Tall grass prairie harbours a diversity of terrestrial and aquatic plants and animals within a mosaic of grassland, pothole-forming wetland/grassland systems, and shrubby/wooded areas. Ecosystem services that include nutrient cycling, water retention, aquifer recharge, the storage of atmospheric carbon, as well as enhanced water infiltration and improved runoff water quality are all of great ecological and economic importance (Glaser 2012). As a result of human activity, prairies are the most highly impacted of any of the continent's terrestrial ecosystems. Current threats to the biodiversity and ecological functioning of the remaining tall grass prairie include: habitat fragmentation, loss by conversion to cropland, incompatible grazing practices, undesirable habitat changes due to fire and fire exclusion, spread of invasive plant species, and stream degradation due to incompatible land management practices and soil erosion (Glaser 2012).

The biodiversity of northern tall grass prairie has been poorly explored, especially that of soil related functional animal groups, such as terrestrial gastropods. Terrestrial gastropods are generally under-surveyed in most of Canada and are usually absent from management strategies for protected areas. Being a significant component of biodiversity among ground dwelling species, terrestrial gastropods are globally declining (Lydeard *et al.* 2004) and play a crucial role in ecological processes (Jordan and Black 2012) by aiding in decomposition, nutrient cycling and soil building processes, and by providing food and essential nutrients to wildlife. Also, terrestrial gastropod abundance and diversity can be used as ecological indicators at the litter-soil interface, such as for logging practice management in forests (British Columbia Ministry of Forests 2008). Previously, only a few terrestrial gastropod surveys have occurred in Manitoba, e.g., by the Manitoba Museum and by Nekola (2005), and none of these targetted the community in the tall grass prairie.

Humans have long used fire to influence North American ecosystems, including First Nations who

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used fire to create large areas of grassland in the Great Plains regions (Pyne 1983; Botkin 1990). While First Nations used fire to promote a habitat mosaic and a resource diversity that provided greater stability to their lives, later European settlers used burns to create uniformity in ecosystems (Lewis 1985). Prescribed fire has become an important management tool for prairie and forest conservation in North America (Gottesfeld 1994; Williams 2000), and is used to limit the spread of invasive plants (Brooks and Lusk 2008), promote growth and reproduction in native prairie vegetation (Towne and Owensby 1984), and improve and expand habitat for grassland and parkland birds (e.g., Burkman 1993; Madden *et al.* 1999; Davis *et al.* 2000; Ludwick and Murphy 2006; Vierling and Lentile 2006; Buehler *et al.* 2007; Grant *et al.* 2010; Klaus *et al.* 2010; Austin and Buhl 2013) and rare prairie plants (e.g., Becker 1989; Bleho *et al.* 2015). Some authors have expressed concern about the detrimental impacts of prescribed burns on prairie that include providing optimal germinating conditions for invasive plant seedlings by opening the vegetation canopy (Ohrtman *et al.* 2011), and negative direct and indirect effects on the abundance of small mammals (Kaufman *et al.* 1990), birds (Reinking 2005), arthropods (Swengel 1996; Harper *et al.* 2000), and terrestrial gastropods (Nekola 2002; reviewed by Saestedt and Ramundo 1990; Knapp *et al.* 2009).

In addition to structural modification by fire, tall grass prairie has also been intermittently grazed by large ungulates, i.e., Bison (*Bison bison*; Knapp *et al.* 1999). Domestic Cattle (*Bos taurus*) are now the dominant grazers at most prairie sites. Grazing can enhance plant diversity by encouraging the growth of some prairie species (Damhoureyeh and Hartnett 1997, 2002). The effect on prairie fauna is also selective; birds (Sliwinski 2012 as cited in Glaser 2012), arthropods (van Klink *et al.* 2015), and terrestrial gastropods (Baur *et al.* 2007) respond differently to grazing regimes, defined by stocking rate, grazing frequency, and livestock type.

One of the largest remaining tall grass prairie complexes in Manitoba is protected by the Nature Conservancy of Canada (NCC) and partners as part of the Manitoba Tall Grass Prairie Preserve (MTGPP). As part of an effort to preserve tall grass prairie biodiversity and the ecosystem services it provides, managers need to understand how management practices influence the gastropod community in the MTGPP. Currently, the NCC uses rotational prescribed burning and grazing by cattle to maintain a spatial and structural mosaic of grassland, wetland, and forest within the tall grass prairie system. For managers of protected prairie habitat, such as the NCC, the question of which management strategy to apply remains an ongoing challenge. The goal is to identify the appropriate regime of prescribed burns and grazing required to maintain a generally rich floral and faunal diversity without negatively affecting the diversity of functional groups, such as gastropods involved in litter-soil processes, or those of conservation concern. To assess the impact of current management practices on the composition of the gastropod community in the MTGPP a gastropod survey was undertaken at variously managed sites (burning or grazing within the past five years) within the preserve.

Study Area

The 4100 ha MTGPP is located in the rural municipality of Stuartburn, in southeastern Manitoba, Canada (Figure 1). The majority (>70%) of MTGPP lands are owned by the NCC; the Manitoba Habitat Heritage Corporation and Nature Manitoba own the remainder. Preserve lands are jointly managed through a Management Committee that includes landowners as well as Manitoba Sustainable Development and Environment and Climate Change Canada. The preserve is comprised of dozens of distinct management units, allowing temporal and spatial variation in management practices.

The habitats comprise two grassland types (Prairie and Wet Meadow) and two woodland patches (Forest and Wet Forest). The two woodland types range from small groves to larger forest areas and provide mostly edge habitat, but also include humid microhabitats under logs and drier microhabitats on the surface of logs and on branches. The habitat types (classification based on Minnesota Department of Natural Resources 2005) differ in vegetation composition and structure as well as in seasonal cycle of flooding as follows:

Prairie (P)

Tall grass prairie communities dominated by tall and mid-height graminoid species up to 1.50 m tall. Big Bluestem (*Andropogon gerardi* Vitman), Prairie Dropseed (*Sporobolus heterolepis* (A. Gray) A. Gray), Little Bluestem (*Schizachyrium scoparium* (Michaux) Nash), Yellow Indiangrass (*Sorghastrum nutans* (L.) Nash), and Plains Porcupine Grass (*Hesperostipa spartea* (Trinius) Barkworth) are most common. Not flooded but forming very humid microhabitats of roots and decaying grass leaves in the upper soil layer between mounds of grass.

Wet Meadow (WM)

Meadow dominated by graminoid species up to 0.50 m tall. Broad-leaved species such as Slim-stemmed Reedgrass (*Calamagrostis stricta* (Timm) Koeler), Prairie Cordgrass (*Sporobolus michauxianus* (Hitchcock) P.M. Peterson & Saarela), Sartwell's Sedge (*Carex sartwellii* Dewey), and Woolly Sedge

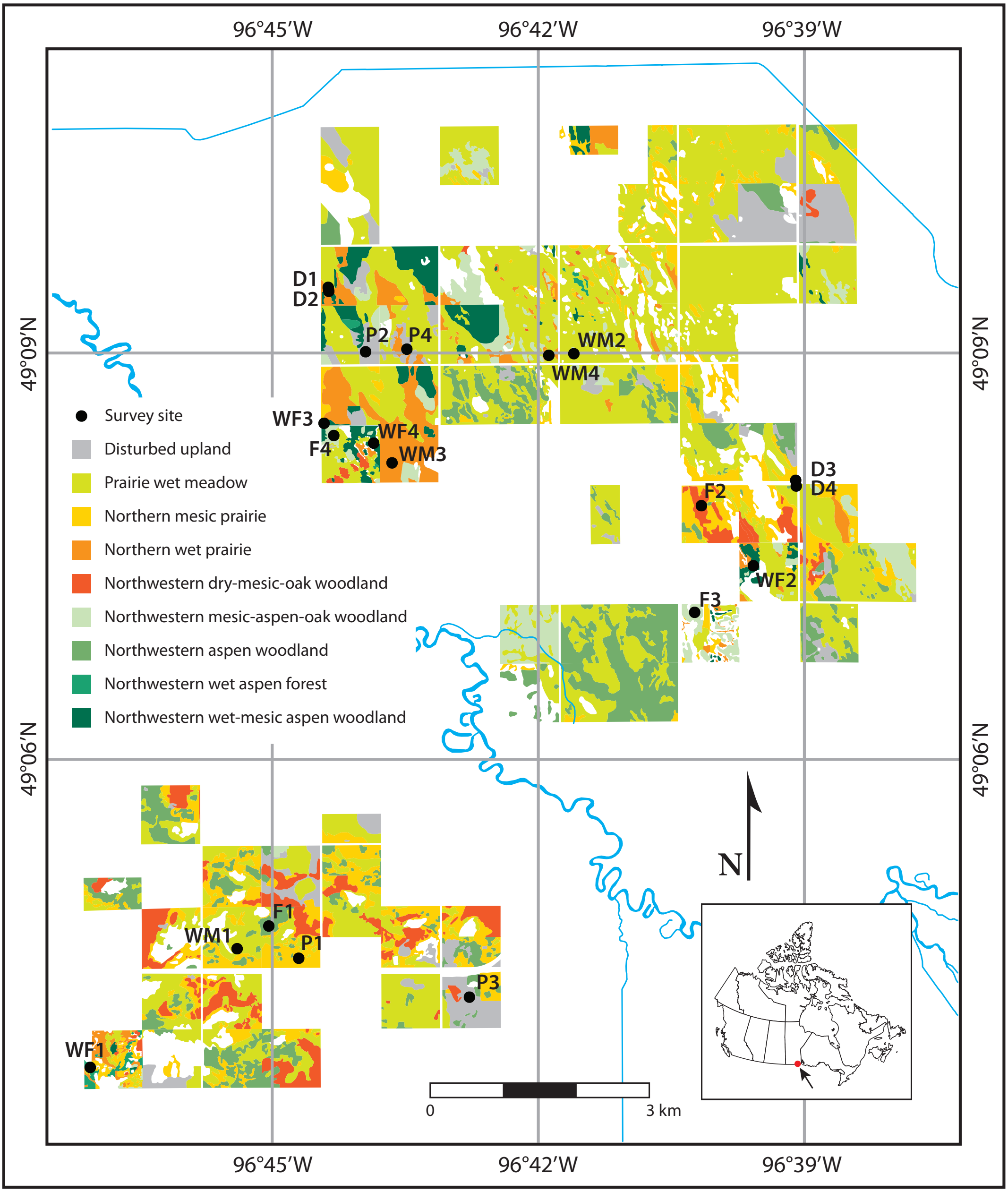

FIGURE 1. Phytosociology classification in the Manitoba Tall Grass Prairie Preserve and gastropod survey sites: F = Forest, WF = Wet Forest, P = Prairie, WM = Wet Meadow. Two drainage sites have also been analyzed, D1/D2 and D3/D4, with sampling points on each side of the road.

(*Carex pellita* Muhlenberg ex Willdenow) are typical, with Tussock Sedge (*Carex stricta* Lamarck) an occasional dominant. Habitat is subjected to moderate inundation by standing water following spring thaw and heavy rains, and to periodic drawdowns during the summer.

Forest (F)

Forest patches within the grassland that are not flooded and are dominated by trees and herbaceous species. Herbaceous plant cover commonly includes: Wild Lily-of-the-valley (*Maianthemum canadense* Desfontaines), Northern Bedstraw (*Galium boreale*

L.), Wild Sarsaparilla (*Aralia nudicaulis* L.), American Vetch (*Vicia americana* Muhlenberg ex Willdenow), and Lindley's Aster (*Symphyotrichum ciliolatum* (Lindley) Á. Löve & D. Löve). Bur Oak (*Quercus macrocarpa* Michaux) and Trembling Aspen (*Populus tremuloides* Michaux) are dominant tree species.

Wet Forest (WF)

Forest patches dominated by trees and herbaceous species that are subjected to the same inundation regime as Wet Meadow sites. Herbaceous cover commonly includes: Star-flowered False Solomon's Seal (*Maianthemum stellatum* (L.) Link), Wild Strawberry (*Fragaria virginiana* Miller), Northern Bedstraw (*G. boreale*), Calico Aster (*Symphyotrichum lateriflorum* (L.) Á. Löve & D. Löve), and Dwarf Raspberry (*Rubus pubescens* Rafinesque). Trembling Aspen (*Populus tremuloides*), Balsam Poplar (*Populus balsamifera* L.), or Black Ash (*Fraxinus nigra* Marshall) are the most important tree species.

Historical and recent fire and grazing management on MTGPP property is highly diverse; there is no specific information on the historical frequency of grazing or burning for this area. Long-term management plans include prescribed burns once every five years, typically in spring or fall. In the year prior to prescribed fire, properties are not grazed. However, the interval between fires can be variable due to occasional wildfires and seasonal weather conditions not conducive to the use of prescribed fire (Bleho *et al.* 2015). A twice-over rotational grazing system is used at the MTGPP but is individually managed by cattle owners. Information on frequency and intensity of grazing and fire was not available. Timing of fire and grazing (Table 1) was based on best available information.

Sites within historically human-built drains are also part of the MTGPP ecosystem, and potentially could serve as a source for post-management recolonization by gastropods. Drainage wells were therefore also investigated for richness and abundance of aquatic gastropods that might be available to colonize wet and flooded grassland or forest habitat.

Methods

All sites (*n* = 16) examined within the MTGPP had been managed either by burning or grazing (exclusively cattle) within the last five years (*n* = 10) or had received no active management over the past five years or more (*n* = 6). Although we were able to sample recently managed (<5 years) and unmanaged (≥5 years) sites for both woodland and grassland habitat types, we were unable to find any Wet Forest that had been subject to both grazing and burning in the previous five years (Table 1).

In September 2013, a visual search and hand collection of gastropods occurred in the litter and the uppermost soil layer using six 0.2 × 0.2 m plots per site (Figure 1). The plots were separated by a distance of at least 20 m on a random, non-linear transect to sample different microhabitats within the same vegetation zone (= site). Additionally, four drainage-well sites of 10 × 10 m were searched during 30 min each for aquatic gastropod species to establish the full gastropod species list in the MTGPP.

Gastropods were identified by A.N. and R.G.F. Vouchers of all species have been deposited in the Manitoba Museum (Catalogue numbers: MM65991 to MM65999 and MM66178 to MM66311). Live gastropods were stored as wet samples at the Biodiversity Institute of Ontario (BIO), Guelph, Ontario, and incorporated into the BOLD database under field sample numbers ANi039 to ANi056 and under the BIO collection numbers BIOUG09921-C08 to -C09 and BIOUG09922-B10, -C02, -C05 to -C07, -C10 to -C12, -D01 to -D07, -E01, -E03 to -E12, and -F02. Individuals of each species were counted to determine abundance/m^2 for each site.

Due to the diversity of management combinations, it was not possible to assemble a set of replicates, so we used an exploratory approach in our multivariate analysis. Species richness was compared among habitat types using an adjusted *t*-test (Welch) and one-way analysis of variance (ANOVA). The gastropod community composition was analysed with nonmetric multidimensional scaling (NMDS) with Euclidean distance similarity coefficient applied to

Table 1. Management history of the sites in the Tall Grass Prairie Preserve, Manitoba, prior to the 2013 sampling year. Information about grazing was available since 1993 and about fire since 1992. F = Forest, WF = Wet Forest, P = Prairie, WM = Wet Meadow.

Habitat	Sites	Years since last grazing	Years since last fire
Woodland	F1	5	2
	F2	1	10
	F3	<20	<21
	F4	<20	<21
	WF1	<20	2
	WF2	1	<21
	WF3	<20	<21
	WF4	<20	<21
Grassland	P1	5	2
	P2	2	<21
	P3	5	<21
	P4	<20	<21
	WM1	5	2
	WM2	1	<21
	WM3	<20	<21
	WM4	<20	7

abundance data (N/m^2) based on the normalized minimal threshold density (Legendre and Legendre 2007; Ramette 2007). The stress coefficient indicates the badness-of-fit, this is the quality of the NMDS (S < 0.10: good). Mann-Whitney and Kruskal-Wallis tests were used on scores of the axes to analyse gastropod community differences between habitat types. Hierarchical clustering was performed with the centroid method on a Euclidean distance matrix calculated on the abundance of gastropods (N/m^2). Approximately unbiased P-values were computed by multiscale bootstrap resampling, n = 1000 (Shimodaira 2004). Spatial autocorrelation of community composition was analysed with the Mantel test using Euclidean distance and n = 1000 permutations. Moran's I was calculated for species richness on an inverse distance matrix. All analyses were conducted with the software R 2.8.0 (R Core Team 2008).

Results

The forest and grassland communities formed by terrestrial and aquatic species are distinguishable on the NMDS model (Figure 2) by scores on the first axis (Mann-Whitney, W = 55, n = 16, P = 0.01) and on the third axis (Mann-Whitney, W = 53, n = 16, P = 0.03), but not on the second axis (Mann-Whitney, W = 41, n = 16, P = 0.38). Species richness (Table 2) did not differ between forest and grassland communities (t-test, $t_{11.93}$ = 0.88, P = 0.39). Likewise, species composition (measured as scores on the three NMDS axes; Figure 2) and species richness (Table 2) were not significantly different among Forest, Wet Forest (forest communities), Prairie and Wet Meadow (grassland communities; axis 1: Kruskal-Wallis, χ^2_3 = 6.9, P = 0.07; axis 2: Kruskal-Wallis, χ^2_3 = 1.3, P = 0.73; axis 3: Kruskal-Wallis, χ^2_3 = 5.1, P = 0.16; species richness: ANOVA, $F_{1,12}$ = 0.27, P = 0.84). Nevertheless, nine of 23 gastropod species showed habitat preference based on presence in a single habitat type (Table 2). Among aquatic gastropods, six of nine species are characterized as vernal species (Clarke 1981), being generally restricted to periodically flooded terrestrial habitats (Table 2). Only two of the vernal species were absent from the drainage well sites (with permanent water). Some typically open-habitat species, such as Costate Vallonia (*Vallonia costata* (O.F. Müller, 1774)) and Trumpet Vallonia (*Vallonia parvula* Sterki, 1893), were only observed at the forest edge. Glossy Pillar (*Cochlicopa lubrica* (O.F. Müller, 1774)), Small Spot (*Punctum minutissimum* (I. Lea, 1841)), and *V. parvula* were only found in the dry, unflooded, Forest, while Tapered Vertigo (*Vertigo elatior* Sterki, 1894), a species preferring very wet habitats (Nekola and Coles 2010), only occurred in the Wet Forest. Blade Vertigo (*Vertigo milium* (Gould, 1840)), a wet grassland species (Nekola and Coles 2010), was only recorded in Prairie sites while Multirib Vallonia (*Vallonia gracilicosta* Reinhardt, 1883) occurred only in Wet Meadow. Marsh Hive (*Euconulus* cf. *praticola* (Reinhardt, 1883); = *E. alderi* (Gray, 1840), see Forsyth and Oldham 2016), also a wet grassland species (Forsyth 2004, 2005), occurred in both grassland habitats.

The cluster analysis of the gastropod community composition (Figure 3) based on the distances in the NMDS model (Figure 2) showed three distinctive clusters (cluster P3-P4, cluster WM2-WM4, and a cluster including the remaining sites) that were not explained by spatial autocorrelation (Mantel test, $z = -0.03$, P = 0.50). Moreover, species richness was not spatially autocorrelated (Moran test, $I_{obs} = -0.16$, $I_{exp} = -0.07$, SD = 0.11, P = 0.38). This result indicated that management practices may influence gastropod community composition in some habitats. While, two recently managed Prairie sites, P1 and P2, were not significantly different from most sites (Figures 3 and 4a), P3 and P4, left unmanaged for at least five years, had a unique community composition characterized by high abundance of aquatic species (Figures 3 and 4a). P3 and P4 had deep litter filled holes between mounds of grass, whereas recently burned

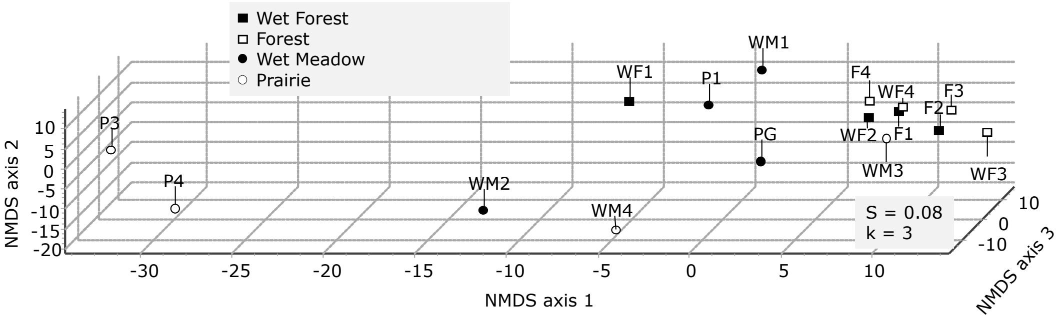

FIGURE 2. NMDS plot of gastropod communities in different habitats occurring in the Tall Grass Prairie. S indicates the stress and k the total number of axes used in the analysis. F = Forest, WF = Wet Forest, P = Prairie, WM = Wet Meadow.

TABLE 2. Frequency and abundance of gastropods in different habitats in the Tall Grass Prairie Preserve, Manitoba (frequency / minimal-maximal abundance per m^2 in four sites per habitat). Species richness is indicated as mean ± SE.

Family	Species	Woodland		Grassland		Drainage
		Forest	Wet Forest	Prairie	Wet Meadow	
Terrestrial gastropods						
Agriolimacidae	*Deroceras laeve*, Meadow Slug	4 / 3–5	4 / 3–5	1 / 3		
Cochlicopidae	*Cochlicopa lubrica*, Glossy Pillar	1 / 3				
Discidae	*Discus whitneyi*, Forest Disc	3 / 3–5	2 / 3–8			
Euconulidae	*Euconulus fulvus*, Brown Hive		1 / 8			
	Euconulus polygyratus, Fat Hive	2 / 3–8	3 / 5–11	2 / 3–24	3 / 5–21	2 / 2–3
	Euconulus cf. *praticola*, Marsh Hive			1 / 3	1 / 24	
Gastrodontidae	*Nesovitrea electrina*, Amber Glass	3 / 8–16	4 / 3–16	3 / 13–37	4 / 8–32	
	Striatura milium, Fine-ribbed Striate		1 / 3			
	Zonitoides arboreus, Quick Gloss	4 / 5–19	2 / 21–27	1 / 3	3 / 3–5	
Punctidae	*Punctum minutissimum*, Small Spot	1 / 3				
Pristilomatidae	*Hawaiia minuscula*, Minute Gem			2 / 5–11	1 / 13	
Succineidae	*Mediappendix* cf. *vermeta*, Suboval Ambersnail	1 / 3	2 / 3–5	2 / 3–11	2 / 5–16	1 / 3
	Novisuccinea ovalis, Oval Ambersnail	2 / 5–11	2 / 3–16		1 / 11	
	Oxyloma sp., an ambersnail		1 / 13	1 / 16		3 / 3–5
Valloniidae	*Vallonia costata*, Costate Vallonia		1 / 3			
	Vallonia gracilicosta, Multirib Vallonia				1 / 3	
	Vallonia parvula, Trumpet Vallonia	1 / 3				
	Vallonia pulchella, Lovely Vallonia	1 / 3		2 / 3–8	1/ 27	
Vertiginidae	*Gastrocopta tappaniana*, White Snaggletooth			1 / 5	1 / 8	
	Vertigo elatior, Tapered Vertigo		1 / 3			
	Vertigo milium, Blade Vertigo			1 / 3		
	Vertigo ovata, Ovate Ambersnail			1 / 3	1 / 8	
Vitrinidae	*Vitrina angelicae*, Eastern Glass-snail	2 / 5–6	1 / 3			
Aquatic gastropods						
Lymnaeidae	*Galba* sp., a fossaria			4 / 13–104	3 / 5–53	2 / 8–9
	Stagnicola elodes, Marsh Pondsnail	1 / 8	1 / 16		3 / 3–11	4 / 3–24
Planorbidae	*Gyraulus circumstriatus*, Disc Gyro					1 / 24
	Gyraulus parvus, Ash Gyro			3 / 3–32	2 / 8–13	
	Planorbella subcrenata, Rough Ramshorn				1 / 8	
	Planorbella trivolvis, Marsh Ramshorn					1 / 5
	Promenetus umbilicatellus, Umbilicate Sprite	1 / 8	1 / 3	3 / 8–19	2 / 48–59	4 / 8–27
Physidae	*Aplexa elongata*, Lance Aplexa	1 / 3	4 / 3–56	3 / 5–48	3 / 5–45	4 / 19–61
	Physella gyrina, Tadpole Physa					2 / 8–21
Species richness		7.0 ± 1.3	7.3 ± 1.3	7.8 ± 1.0	8.3 ± 0.5	6.0 ± 1.1

Prairie (P1, Table 1) had bare soil between small grass mounds over most of the habitat. A recently grazed Prairie (P2, Table 1) had smaller grass mounds and less litter than unmanaged Prairie, but the structure of the vegetation and the grass litter were not quantified. Although P1 and P2 had been managed within the past two years prior to our study, their gastropod community composition was similar to those of Forest and Wet Forest. In the Wet Meadow, the recently grazed (WM2) and unmanaged WM4 formed a cluster distinct from the remaining sites (Figures 2 and 3). WM2 and WM4, sites separated only by a small gravel road, had a higher abundance of aquatic species (Figure 5a) relative to other Wet Meadow sites (WM1 and WM3, Figure 5b).

Discussion

The prairie ecosystem is a patchy assemblage of grassland, groves, and small forests. In general, the different habitats are moist due to periodic flooding, especially in the Wet Forest and Wet Meadow. Species richness and gastropod community composition are driven by climate parameters such as water balance at a large sub-continental scale (Horsák and Chytry 2014) and by soil moisture, temperature, and calcium-content at a local scale (Dvořáková and

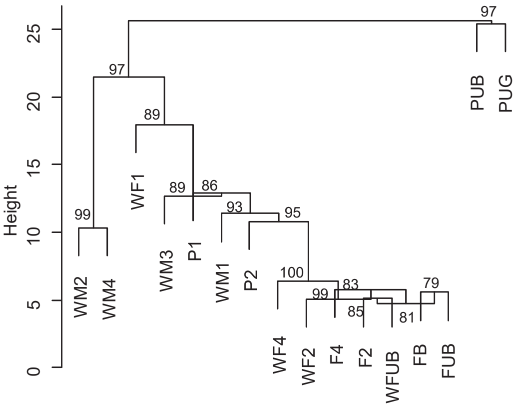

FIGURE 3. Dendrogram of gastropod community clusters in different habitats occurring in the Tall Grass Prairie. Approximately unbiased *P*-value computed by multi-scale bootstrap resampling ($n = 1000$) are indicated on the branches. F = Forest, WF = Wet Forest, P = Prairie, WM = Wet Meadow.

Horsák 2012; Hettenbergerová *et al.* 2013). Because of the small size of the forest patches, most of the forested habitat includes forest edges that are suitable for open land species. Therefore, community composition in general is very similar for most grassland and woodland sites. However, the Prairie sites, when undisturbed by human activity, host a very particular gastropod community, characterized by the presence of vernal species, such as Lance Aplexa (*Aplexa elongata* (Say, 1821)) and Umbilicate Sprite (*Promenetus umbilicatellus* (Cockerell, 1887)), and the presence of dry-habitat species, such as Lovely Vallonia (*Vallonia pulchella* (O.F. Müller, 1774)) and *V. gracilicosta*. Dead vegetation accumulates in prairie habitat over years to form mounds of grass litter. Within these mounds, cavities retain water permanently. This permanent water availability allows aquatic species to colonize the cavities within mounds of grass litter, while upper parts of the mounds are exposed to drying and are suitable for dry-habitat species. Burning

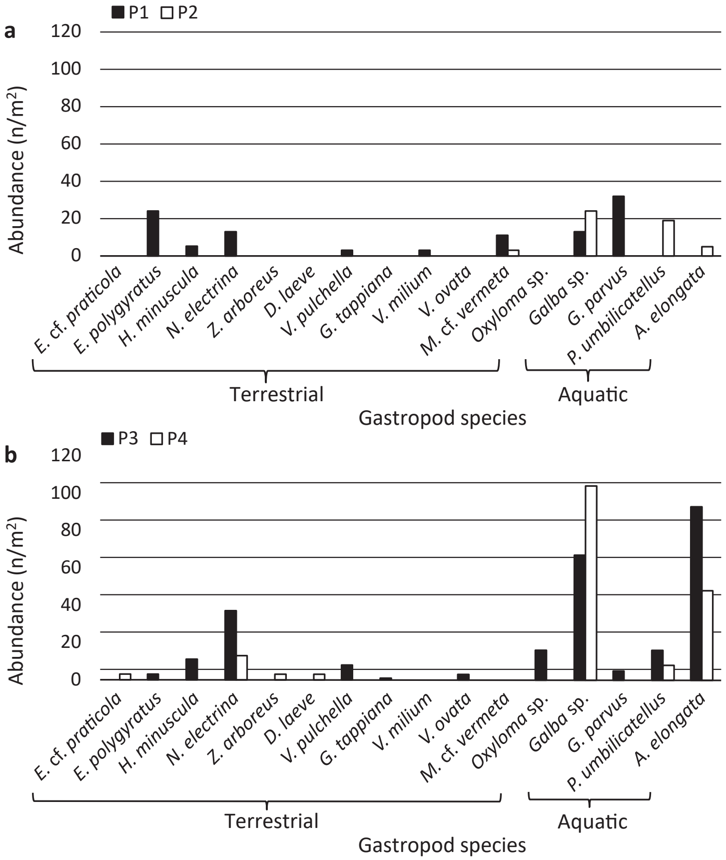

FIGURE 4. Abundance of gastropod species in a. recently burned (P1) and grazed (P2) Prairies, and in b. Prairies where the last management was at least five years ago, in the Tall Grass Prairie Preserve in Manitoba. P3 and P4 form a distinct cluster in the NMDS model (see Figures 2 and 3). Pooled species richness for P1 and P2 is six terrestrial and four aquatic gastropod species, and for P3 and P4 is 10 terrestrial and four aquatic gastropod species. See Table 2 for full species names.

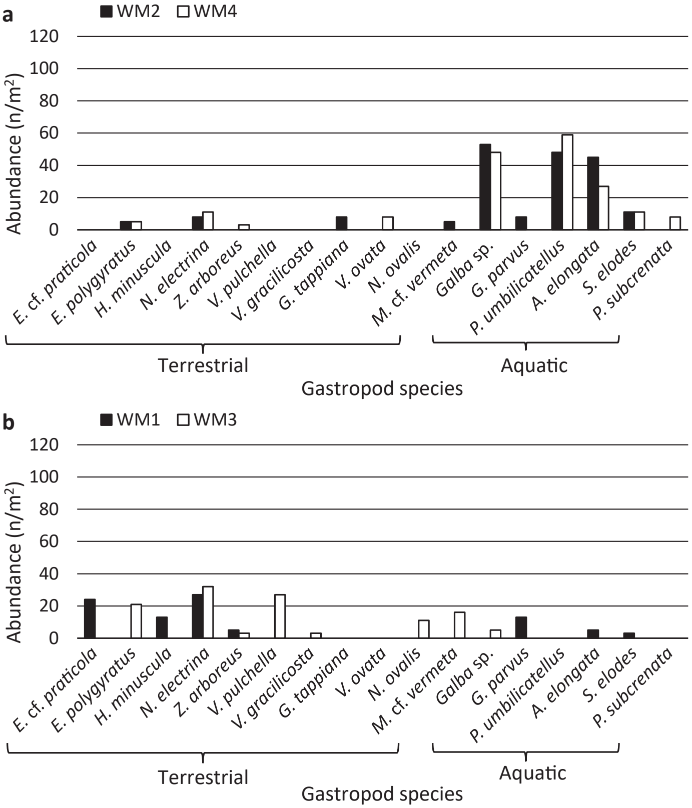

FIGURE 5. Abundance of gastropod species in a. recently grazed Wet Meadow (WM2) and in a Wet Meadow where the last management was at least five years ago (WM4), and in b. recently burned Wet Meadow (WM1) and in a Wet Meadow where the last management was at least five years ago (WM3), in the Tall Grass Prairie Preserve in Manitoba. WM2 and WM4 form a distinct cluster in the NMDS model (see Figures 2 and 3). Pooled species richness for WM1 and WM3 is nine terrestrial and four aquatic gastropod species, and for WM2 and WM4 is six terrestrial and six aquatic gastropod species. See Table 2 for full species names.

and grazing, as well as trampling by cattle, may reduce the mounds of grass litter and impact the aquatic micro-habitat. For this reason, only undisturbed Prairie sites are unique, harbouring a gastropod community composed of both aquatic and dry habitat species. However, our characterization of sites as "undisturbed" or "unmanaged" only means that they have not be subject to grazing or burning in recent years. All sites sampled had a prior history of burning and grazing, with the rotation of these land management practices over time and space nonetheless responsible for this unique faunal assemblage. Without fire at some point, these sites would all have transitioned to Forest or Wet Forest, and thus harbour a different gastropod community. Short term declines in gastropod diversity or abundance that result from management measures may be an essential part of ensuring the long term maintenance of both grassland and the gastropod species dependent on open habitats.

Nekola (2002) indicates that frequent prescribed burns represent a significant threat to the diversity of grassland snail communities, directly and indirectly affecting snail survival. Snails in the upper litter layer die from exposure to high heat during burning (Nekola 2002). Post-burn mortality of snails is also high due to desiccation, due to the loss of shelter and micro-habitats (Ray and Bergey 2015). Fire destroys that part of the soil habitat upon which most litter-soil organisms depend and is therefore the most important factor affecting survival (Bellido 1987). In prairie habitat this means the loss of mounds of grass litter forming moist cavities. At the recently burned Prairie sites soil was bare between the re-establishing mounds of grass litter, but moist cavities were absent. Therefore, aquatic species were negatively affected by the loss of micro-habitat. Burning may be beneficial for forest/grassland species, such as *V. milium* (only observed in the burned Prairie site in our study), which can exploit open-burned habitat close to the forest edge. Similarly, in the

Mediterranean region Santos *et al.* (2012) only found gastropods of the family Geomitridae: Montserrat Heath Snail (*Xerocrassa montserratensis* (Hidalgo, 1870)) and Striped Heath Snail (*Xerocrassa penchinati* (Bourguignat, 1868)), two endemic open-habitat species, in burned sites. The availability of cryptic refuges within these Mediterranean forest patches (Kiss and Magnin 2003, 2006) presumably facilitates the survival of open-habitat snail populations (Santos *et al.* 2012). Likewise, in the tall grass prairie system, the manner in which fire spreads through burn units varies depending on habitat and weather conditions. Skips, or 'refugia', within the burn extent are common (Sveinson Pelc 2013). The resulting patchy consumption of litter layer and exposure of mineral soil allows recolonization from unburned areas. The result is that most sites recently burned (<2 years) had gastropod composition similar to unmanaged sites, demonstrating rapid recolonization in this patchy ecosystem. Ray and Bergey (2015) showed that in favourable weather conditions snail communities in post-burn habitats that include leaf litter showed growth rate increases due to higher soil pH following fire. In Prairie habitat once reestablishment of the litter layer is underway, recolonization from adjacent sites such as Wet Forest patches or drainage sites (especially by aquatic species) can be rapid.

Grazing also contributes to the preservation of the prairie ecosystem mosaic by limiting the spread of woody species and the expansion of forest. In the Tall Grass Prairie Preserve grazing had a significant effect on snail community composition only at Prairie sites where vegetation structure was destroyed. At other sites, grazing intensity (frequency, number of animals, length of grazing period, and their combinations) may be low enough to keep disturbance below a threshold and to maintain snail species composition. When formerly managed grassland was abandoned in Romania, open-habitat gastropod species decreased (Cremene *et al.* 2005). However, grazing intensity negatively influenced the snail fauna in Swiss grasslands, independent of livestock species (Boschi and Baur 2007). Different mechanisms involved in grazing may affect the snail community. The choice of food plants by livestock may impact seed dispersal and therefore plant composition, affecting food sources and micro-habitat for snails. Also, trampling may affect snail survival directly, or indirectly by destroying micro-habitat (Fischer *et al.* 1996; Rook *et al.* 2004). In the Tall Grass Prairie Preserve the structure of mounds of grass litter in Wet Meadow is less important than in Prairie sites. Aquatic species might take more advantage of long periods of flooding in the former. Also, drainages are usually wet and provide a species pool for colonizing wet meadows after periods of drought. Dry-habitat species were absent from the Wet Meadow, however some terrestrial gastropods, such as Fat Hive (*Euconulus polygyratus* (Pilsbry, 1899)) and Amber Glass (*Nesovitrea electrina* (Gould, 1841)) are adapted to both moist and dry habitats and, were present, in Wet Meadow. Two Wet Meadow sites were distinct from all others due to a high abundance of aquatic species which may be the result of a particular flooding regime.

Management recommendations for grasslands in general include low intensity burns that preserve the organic litter layer. Intervals between burns of >5 years (Kiss and Magnin 2006) and >15 years (Nekola 2002) have been recommended to allow for restoration of the gastropod community. However, it is not clear if an interval >15 years would apply in the MTGPP system, where fire rotation historically has ranged 3–6 years (Hamel *et al.* 2006) and is currently 5–6 years. Unfortunately, the gastropod community composition prior to this management strategy is unknown. First Nation fire management was also frequent (<5 years; Lewis 1985). Our observations suggest that short burn intervals have low impact when habitat is patchy, and gastropods can easily recolonize from adjacent unburned areas. In European grasslands, Boschi and Baur (2007) advise extensive grazing. Independent of livestock species, the number of livestock present and the duration of grazing has an impact on the gastropod community. Because there can be an interaction between different management methods (Damhoureyeh and Hartnett 1997), it is difficult to predict the effect of the highly diverse fire-grazing management combinations on gastropod communities in the different habitats of the tall grass prairie system.

Mounds and leaf litter seem to be important for populations of gastropods to recover after burns. Leaf litter supplementation may be a management option.

The gastropod fauna of Manitoba is poorly known and there is little information on the terrestrial molluscs of the Canadian prairie ecosystem. This study increases our knowledge concerning the range of *V. parvula*, *P. minutissimum*, Fine-ribbed Striate (*Striatura milium* (Morse, 1859)), *E.* cf. *praticola*, and Suboval Ambersnail (*Mediappendix* cf. *vermeta* (Say, 1829)), all recorded for the first time in Manitoba during our study. *Vertigo milium*, reported previously in Canada only from a few sites in Ontario and one site in Manitoba (Nekola and Coles 2010) is ranked as Nationally Imperilled to Vulnerable (N2N3, CESCC 2016). *Galba* Schrank, 1803 sp. could not be identified to species because of taxonomic issues, and uncommon grassland species/subspecies within the genus, recorded previously in Alberta (Boag and Wishart 1982) are poorly known.

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Batch spawning in five species of minnows (Cyprinidae) from Ontario, Canada

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Abstract

Batch spawning, the act of spawning more than once within a spawning season, is assessed in six species of minnows (Cyprinidae) from Ontario, Canada. The bimodal frequency distribution of egg size in mature specimens suggests that the following species are batch spawners: Blacknose Dace (*Rhinichthys atratulus*), Brassy Minnow (*Hybognathus hankinsoni*), Common Shiner (*Luxilus cornutus*), Creek Chub (*Semotilus atromaculatus*), and Hornyhead Chub (*Nocomis biguttatus*). However, there is no evidence that Northern Pearl Dace (*Margariscus nachtriebi*) is a batch spawner. Thus, we now have evidence that 11 of 39 cyprinid species in Ontario are batch spawners. Knowledge about the reproductive habits of these species should be integrated into the comprehensive standards for the protection of fish habitat in Ontario to ensure the survival of populations.

Key words: Cyprinidae; minnows; spawning; batch; Ontario

Introduction

Batch (or fractional) spawning is widespread among fishes (e.g., Conover 1985). The phenomenon is defined as spawning more than once during a spawning season as opposed to spawning only once in a relatively short period, hereafter, referred to as "conventional" spawning (Conover 1985). Batch spawning presents a problem to fisheries managers because it confounds or renders impossible any attempt to estimate total fecundity (e.g., Conover 1985). Batch spawning has been frequently reported in the minnows (Cyprinidae; e.g., Heins and Rabito 1986).

The objective of this study was to report on the occurrence of batch spawning in some Ontario cyprinids through the examination of ovaries of mature individuals of six species: Blacknose Dace (*Rhinichthys atratulus*), Brassy Minnow (*Hybognathus hankinsoni*), Common Shiner (*Luxilus cornutus*), Creek Chub (*Semotilus atromaculatus*), Hornyhead Chub (*Nocomis biguttatus*), and Northern Pearl Dace (*Margariscus nachtriebi*).

Methods

In 2013–2015, minnows were captured with standard (40 × 20 cm) cylindrical wire traps set overnight from late April (ice out) to 30 June, a period when spawning of these fish is underway. Five of the six species were caught in Clarke Creek (45°06′N, 77°48′W) near Bancroft, Ontario. Hornyhead Chub was caught in an unnamed creek near Madoc, Ontario (44°30′N, 77°39′W).

Standard length and weight of fish were recorded on capture. Ovaries were removed and preserved in 10% buffered formalin. The gonadosomatic index (GSI) was calculated as ovary weight divided by total weight (including ovaries). Cyprinids typically spawn with a GSI of about 10% (e.g., Abiden 1986).

The approach used to determine mode of spawning was based on frequency distribution of the size of eggs in ovaries. Batch spawners in or near spawning condition should show a multimodal distribution of egg sizes. Large, fully mature eggs should be observed in the presence of mid-sized eggs, the latter representing the batch to be spawned at a later date. Conventional, one-batch spawners should show only mature eggs amid a mass of very small "recruitment" eggs (Conover 1985; Powles *et al.* 1992) to be spawned the following year. This approach has been used previously, including with cyprinids (Heins and Rabito 1986; Powles *et al.* 1992; Heins and Baker 1993; Wang *et al.* 2014); as Heins and Baker (1993: 15) state, two separate groups of developing eggs is "a profile typical of fish that produce multiple clutches".

Ovaries from specimens in or near spawning condition, that is, having mature eggs (as described below) were examined to determine the frequency distribution of egg sizes. The fixed ovaries were

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weighed to the nearest 0.01 g. A sample of the ovarian matrix was obtained by cutting out two small pieces, one from each ovary. Herrera and Fernandez-Delgardo (1994) and Al Saleh *et al.* (2012) found that the size of eggs is more or less independent of position in the ovaries of minnows. The samples were weighed (typically 0.05–0.15 g) and placed on a glass slide, covered with a drop of water, and the eggs were spread out with the flat of a scalpel. The sample was then examined under a microscope at 40× magnification and all eggs were counted and sorted into one of three size classes: 0.20–0.60 mm, 0.61–1.00 mm, and >1.00 mm. The slides had an underlying grid to help prevent double counting of eggs, and an ocular micrometer was used to measure eggs when size class was not obvious. The overall colour of eggs in each size class was noted.

The size classes correspond to the three categories in Powles *et al.* (1992) for the minnow Northern Redbelly Dace (*Chrosomus eos*): 1) "immature" ("recruitment" in Conover 1985), white-grey with no yolk; 2) "maturing" (or mid-sized), vitellogenic (accruing yolk) and yellow or orange; and 3) "mature", >1.00 mm and translucent, but with yellow hues. Eggs in the mature category were fully developed (Conover 1985; Powles *et al.* 1992). No mature eggs of any observed species were greater than 1.20 mm; thus, it is assumed that size at development stage of eggs of these species and that of *C. eos* eggs is comparable (Brassy Minnow, an exception, is discussed below). The subsamples typically contained 150–400 eggs. An estimate of total number of eggs and number in the three size categories was made by multiplying the weight of the ovary divided by weight of subsample times eggs counted in the subsample. Mid-sized eggs in the presence of mature eggs were deemed evidence of batch spawning.

To produce more precise frequency distributions for graphic illustration, eggs were counted and measured a second time. The subsample was again placed under the microscope and the diameter of 100 eggs measured with an ocular micrometer. To avoid bias, eggs were measured in the order of appearance in the field of view while the slide traversed the field of view. Distorted and ovoid eggs were quite common, but only round eggs were measured.

Results

Most mature female Creek Chub, Common Shiner, Blacknose Dace, and Hornyhead Chub had hundreds of mid-sized eggs in the presence of mature eggs, supporting the hypothesis that they are batch spawners (Table 1). All Brassy Minnow specimens had relatively small eggs. The 12 Brassy Minnow females (caught between 4 May and 24 June in all three years) had GSI >10% and hundreds of vitellogenic eggs, but none >1.00 mm. However, five females had bimodal frequency distributions of egg size (Figure 1l). Thus, Brassy Minnow appears also to be a batch spawner. Northern Pearl Dace is the anomaly in this group; the four mature females had essentially all eggs in the mature category (Figure 1o,p) with negligible immature or mid-sized eggs. With this limited evidence, Northern Pearl Dace appears to be a conventional spawner.

Figure 1 shows selected frequency distributions of egg size (from the 100 measured eggs per specimen). The histograms were selected as typical of patterns observed for each species. Note that most (except for Northern Pearl Dace) show mid-sized eggs in the presence of mature (>1.00 mm) eggs.

TABLE 1. Gonadosomatic index (GSI) and egg-size distribution in mature females of six Ontario cyprinids.

	No. mature females	Mean standard length, cm	Mean GSI, % body weight	No. (%) of fish with mid-sized eggs	Egg-size distribution, means* (%)
Creek Chub (*Semotilus atromaculatus*)	29	11.05	9.78	29 (100)	2603/959/107 (100/36.8/4.1)
Common Shiner (*Luxilus cornutus*)	22	8.40	10.56	22 (100)	1587/427/480 (100/26.9/30.3)
Blacknose Dace (*Rhinichthys atratulus*)	28	7.46	12.95	25 (89)	1440/245/535 (100/17.0/37.2)
Brassy Minnow (*Hybognathus hankinsoni*)	12	7.74	10.76	—†	3294/0/1028 (100/0/31.2)
Hornyhead Chub (*Nocomis biguttatus*)	8	9.52	14.31	8 (100)	2560/723/850 (100/28.2/33.2)
Northern Pearl Dace (*Margariscus nachtriebi*)	4	7.90	15.87	0	775/757/28 (100/97.7/3.6)

*Means of total no. eggs/mature eggs/mid-sized eggs. Mature eggs >1 mm, mid-sized 0.6–1.0 mm.

†Size categories of eggs of Brassy Minnow are an exception (see text for explanation).

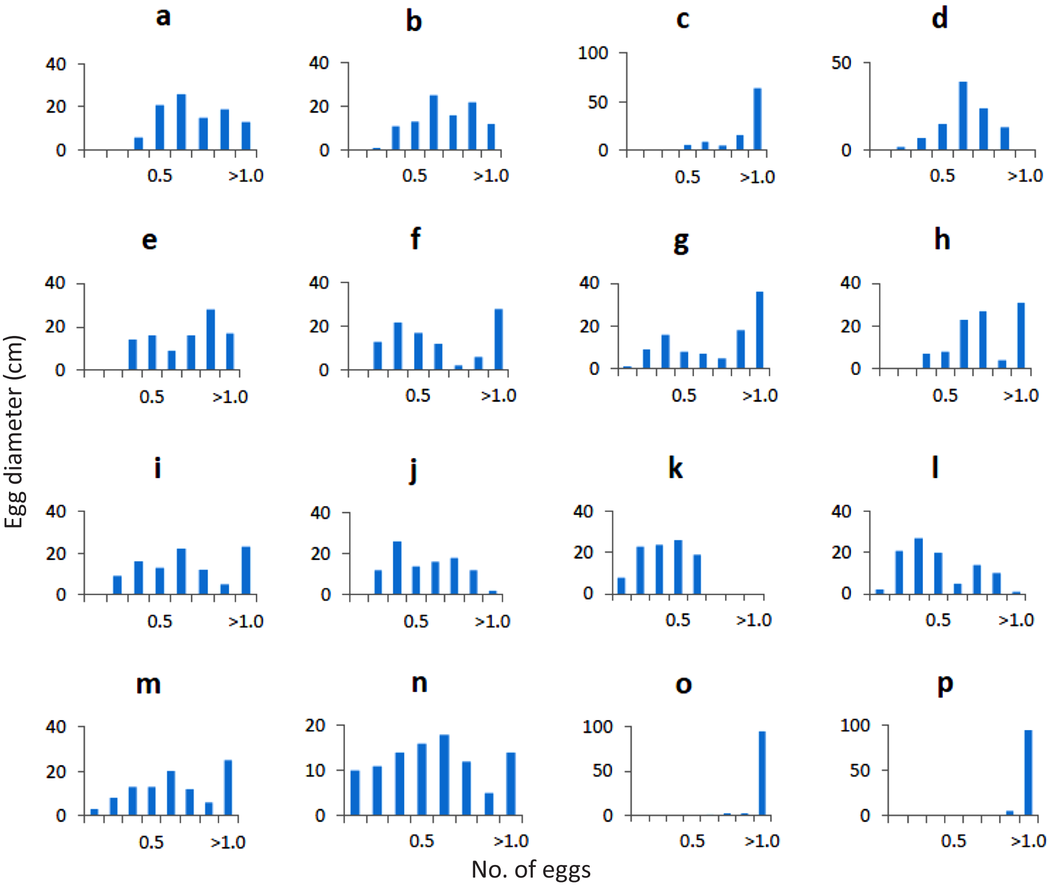

FIGURE 1. Selected egg-size distributions for six Ontario cyprinids. a–d: Creek Chub (*Semotilus atromaculatus*), e–g: Common Shiner (*Luxilus cornutus*), h–j: Blacknose Dace (*Rhinichthys atratulus*), k and l: Brassy Minnow (*Hybognathus hankinsonii*), m and n: Hornyhead Chub (*Nocomis biguttatus*), o and p: Northern Pearl Dace (*Margariscus nachtriebi*).

Discussion

Batch spawning is reported frequently in the Cyprinidae and from locations as disparate as Spain (Herrera and Fernandez-Delgrado 1994), Iraq (Al Saleh *et al.* 2012), and Malaysia (Abiden 1986). Conventional spawning is also occasionally reported (e.g., Wang *et al.* 2014). This study adds five species to the six cyprinid species already documented as batch spawners in Ontario. These other species are: Blacknose Shiner (*Notropis heterolepis*; Roberts *et al.* 2006), Bluntnose Minnow (*Pimephales notatus*; Gale 1983), introduced Common Carp (*Cyprinus carpio*; Ivanov 1976), Fathead Minnow (*Pimephales promelas*; Gale and Buynak 1982), introduced Goldfish (*Carasius auratus*; Ivanov 1971), and Northern Redbelly Dace (Powles *et al.* 1992). Thus, 11 of the 39 Ontario cyprinids have been confirmed to be batch spawners.

This study suggests that Northern Pearl Dace is a conventional spawner. The evidence for batch spawning reported here is indirect because direct observation in the field is difficult (Conover 1985).

Ontario has developed comprehensive standards for the protection of fish habitat (e.g., Anonymous 2006). For example, timing restrictions force work in water away from periods when spawning or egg development may occur (Anonymous 2006). In systems with complex fish communities, this can mean that work is restricted to a few weeks in late summer. However, because of batch spawning, the reproduction of cyprinids may be prolonged; some species, for example, Fathead Minnow, spawn more than 15 times in a season (Gale and Buynak 1982). Such a prolonged spawning period suggests that even late summer restrictions may be inadequate to fully protect cyprinid populations.

The evolution of batch spawning has been interpreted according to three adaptive scenarios or hypotheses. It may be a "bet hedging" life history pattern

(Morrongielo *et al.* 2012), whereby a variable post-hatch environment and consequent unpredictable mortality of young favour a reproductive effort that is spread out temporally, thus increasing the probability of survival of the progeny. Second, Schlosser (1998) and Matthews *et al.* (2001) suggest that fish in confined environments, such as streams, extend reproduction to minimize intraspecific competition for the developing young. Third, Coburn (1986) argues that developmental and ecological factors limit egg size to a certain minimum. Thus, fish with small adult body size, having smaller ovaries, compensate for less output by laying multiple clutches.

More basic research and data on cyprinid reproductive patterns are needed to verify these adaptive hypotheses.

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Note

High reliance on a diet of Moose (*Alces americanus*) by Eastern Coyotes (*Canis latrans* var.) in Cape Breton Highlands National Park, Nova Scotia, Canada

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Abstract

Eastern Coyote (*Canis latrans* var.) scats were collected along transects in Cape Breton Highlands National Park, Nova Scotia, Canada, from May 2012 to August 2013 to determine diet. Based on 294 scats, Moose (*Alces americanus*) remains made up the highest percentage by volume in scats during fall, winter, and spring. During the summer, Moose remains were found in over 30% of scats (18% by volume), although fruit and berries were more commonly found. No other study has documented such high annual use of Moose. As there was no evidence that the consumed Moose were killed by Coyotes, presumably Coyotes scavenged Moose that had died of natural causes.

Key words: Eastern Coyote; *Canis latrans* var.; diet; Moose; *Alces americanus*; Cape Breton Highlands National Park

Eastern Coyotes (*Canis latrans* var.) were first recorded in Cape Breton Highlands National Park (CBHNP; Figure 1), Nova Scotia, Canada, in 1980 (E.M.M. pers. obs.). A high level of coyote–human aggressive encounters, including a human fatality (E.M.M. pers. obs.), resulted in the park initiating a study of the ecology of Coyotes within its boundaries. One aspect of this study was to understand their diet.

Coyotes typically exhibit a generalist diet (Young and Jackson 1951; Bekoff 1977; Prugh 2005; Lukasik and Alexander 2011) adjusting to seasonal availability of prey and other food sources (Patterson *et al.* 1998; Lukasik and Alexander 2011). Food selection ranges from preying on small mammals, such as rodents and lagomorphs, to large ungulates, livestock, or pets, as well as foraging for fruit, eating garbage, and scavenging (i.e., Bowyer *et al.* 1983; Fedriani *et al.* 2001; Lukasik and Alexander 2011). Eastern Coyotes have been known to prey effectively on adult White-tailed Deer (*Odocoileus virginianus*; Parker 1986; Patterson and Messier 2000) and, more recently, they have been documented killing adult Moose (*Alces americanus*) in Ontario (Benson and Patterson 2013). Here, we report on an unusually high reliance on a diet of Moose by Eastern Coyotes year round in CBHNP.

From May 2012 to August 2013, scats were collected every three weeks from 21 2-km-long transects randomly selected along established paths and trails throughout CBHNP (Figure 1). Percentage by volume for each prey remain was determined using the point-frame method (Chamrad and Box 1964) after scats were washed to retain hair and bones and other hard material and dried. A Kruskal-Wallis test (R Studio, version 0.98.490; R version 3.0.2 reports χ^2) was used to test for differences in prey remains among calendar seasons.

In total, 294 Coyote scats were collected along 966 cumulative km of trail transects. Dietary analysis of these scats indicated that Moose, fruit/berries, and Snowshoe Hare (*Lepus americanus*) made up the highest percentage of volume by season (Table 1).

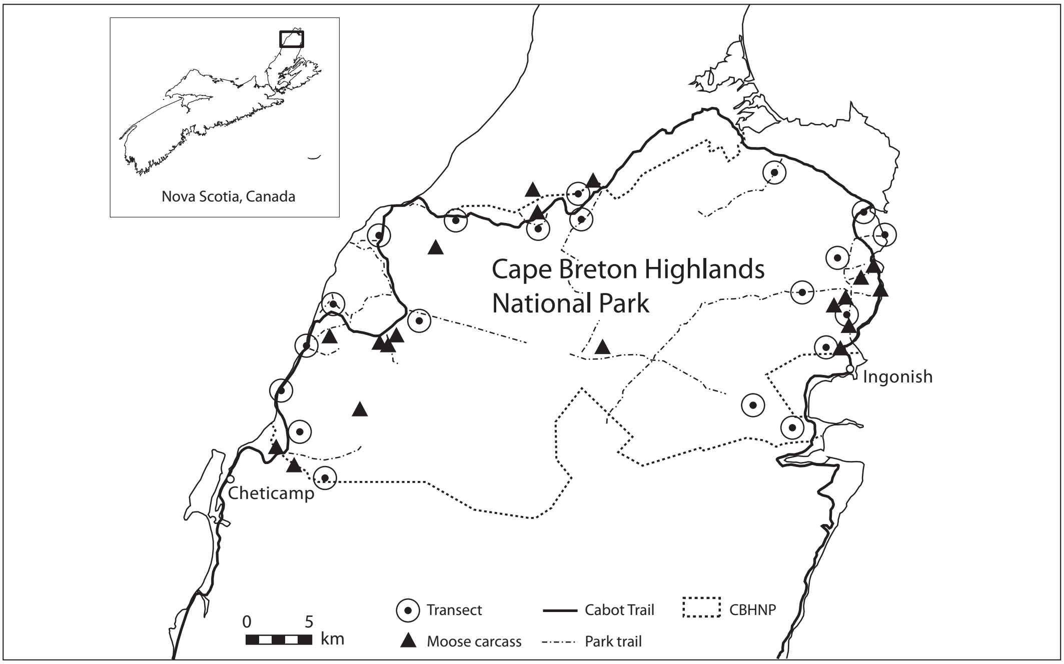

FIGURE 1. Locations of scat transects and Moose (*Alces americanus*) carcasses found between May 2012 and August 2013 in Cape Breton Highlands National Park.

Overall, Moose was the most common food by volume found in Coyote scats (over 70% during spring and winter), followed by fruit/berries (fall 29%, summer 56%) and Snowshoe Hare (winter 25%). Small mammals (23% fall), birds (9% fall), and deer (8% spring) were less common.

While opportunistically back tracking Coyotes (57 tracks for a total of 109 km) in winter, we found 19 Moose carcasses, all female ranging from 1.5 to 10.5 years old (aged by analyzing tooth pattern of lower jaw; Figure 1). None of the carcasses was located on or near scat transects. These carcasses had been scavenged by Coyotes; there was no evidence that Coyotes had killed any of these Moose.

These results indicate that Eastern Coyotes in CBHNP have a generalist diet with a high reliance on Moose. Studies in eastern Maine (Litvaitis and Harrison 1989), northwestern Wyoming (Dowd and Gese 2012), southeastern Quebec (Richer *et al.* 2002), western Maine (Major and Sherburne 1987), and New Brunswick (Dumond *et al.* 2001) have found Moose to make up a smaller proportion of the diet of Coyotes. Only in eastern Quebec did Boisjoly *et al.* (2010) report a high frequency of 51% Moose in scats. Our study documents the highest percentage by volume of Moose in scats of Eastern Coyotes in CBHNP during the winter (71%).

At the time of this study, Moose were likely the

TABLE 1. Analysis of prey remains identified from 294 scats of Eastern Coyote (*Canis latrans* var.) collected on trail transects in Cape Breton Highlands National Park, Nova Scotia, from May 2012 through August 2013.

Dietary remains	% prey by volume (mean ± SD) in each season*				χ^2	*P*
	Fall (*n* = 40)	Winter (*n* = 80)	Spring (*n* = 64)	Summer (*n* = 110)		
Moose (*Alces americanus*)	23.3 ± 39.4	71.2 ± 44.5	70.9 ± 44.5	18.0 ± 35.8	78.98	0.000
White-tailed Deer (*Odocoileus virginianus*)	—	1.2 ± 11.3	7.8 ± 27.0	—	13.99	0.003
Snowshoe Hare (*Lepus americanus*)	16.2 ± 34.6	24.8 ± 42.2	18.1 ± 37.5	11.8 ± 30.4	3.52	0.317
Bird	8.6 ± 24.1	0.9 ± 5.8	1.6 ± 12.5	1.9 ± 6.4	19.76	0.000
Small mammal	22.9 ± 39.6	1.9 ± 12.1	1.6 ± 12.1	12.0 ± 27.6	33.49	0.000
Fruit	29.1 ± 41.9	—	—	56.3 ± 43.1	147.20	0.000

*Fall = 22 September to 20 December, winter = 21 December to 19 March, spring = 20 March to 20 June, summer = 21 June to 21 September.

most biomass-rich food source available to Coyotes, especially in the highlands. Moose density in the highlands of CBHNP is typically high, with well over 1000 individuals in the park (Bridgland *et al.* 2007), although no estimate of Moose density was available during our study period. Gray Wolves (*Canis lupus*) in western Quebec were observed feeding on single Moose carcasses for up to 23 days (Messier and Crête 1985); thus, a Moose carcass could likely sustain a Coyote pack for several weeks as a protein- and energy-rich food source. Furthermore, less energy is likely expended scavenging a Moose carcass during winter and spring months compared with hunting small mammals. Cyclical lows of the Snowshoe Hare population during this study (E.M.M. pers. obs.) may have contributed to the primary occurrence of Moose in Coyote scats. Coyotes in CBHNP may rely on Moose carcasses because of their apparent availability and the lack of other prey, such as Snowshoe Hare, a common food source of Coyotes in other parts of Nova Scotia (Patterson *et al.* 1998).

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A review of the historical and current status of American Beaver (*Castor canadensis*) on Prince Edward Island, Canada

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Abstract

Evidence supporting the native status of American Beaver (*Castor canadensis*) on Prince Edward Island (PEI) before European contact in 1534 has yet to be established; however, the postglacial and archaeological records have not previously been reviewed in this context. We demonstrate the coincidence of a land bridge between the mainland and PEI and the occurrence of beavers in the region dating between 9500 and 5000 BP (before present, with present defined as 1950). We provide an archaeological record of 14 beaver incisors in six locations, deposited between 500 and 1650 AD and also show that beavers could swim to PEI. Based on this evidence, we conclude that beavers were native to the province. The current population, originating via reintroductions from New Brunswick, has populated much of the available habitat and engendered considerable controversy.

Key words: American Beaver; *Castor canadensis*; status; dispersal; Prince Edward Island; history; archaeology

Introduction

The historical status of mammals of Prince Edward Island (PEI) during the early years of European contact and settlement has been extensively researched by Sobey (2007). While admitting that American Beaver (*Castor canadensis*) may have been extirpated from PEI before 1700, he believed that the evidence supporting native status for this species in the province was remarkably weak. In a more recent review of mammal status in the region, the beaver has been described as extirpated from PEI and reintroduced (Forbes *et al*. 2010), but without supporting details. With regard to the existing population, Cameron (1958) noted the reintroduction of beavers to PEI from Algonquin Park, Ontario, in 1908–1910 and Dibblee (1994) found contemporary records of importation by private individuals; however, both efforts were unsuccessful because of unregulated trapping. The current PEI population originated via reintroductions from New Brunswick (NB) after 1940 (Cameron 1958; Dibblee 1994).

It is perhaps the uncertainty about beaver status on PEI that led the Atlantic Salmon Federation to label the beaver a non-native species and to call for its removal from several eastern PEI rivers as part of a conservation strategy for Atlantic Salmon (*Salmo salar*; Guignion 2009). Similarly, Cairns *et al.* (2010) suggested that the beaver's effect on Atlantic Salmon associated with river damming could be classified as (negatively) anthropogenic, rather than natural. However, management decisions about beavers on PEI should be based on a comprehensive understanding of the historical and current status of the species.

When assessing mammal colonization of islands, Mazza *et al.* (2013) suggest considering palaeontological, climate and sea-level evidence, characteristics and behaviour of the species, the historical record, and the primary source of information, the fossil record. To determine whether the beaver is an alien species on PEI or a native mammal that was extirpated and reintroduced, we reassess the historical evidence from Sobey (2007) and others, as well as the post-glaciation history and geography of the province, and archaeological materials. Finally, we present the current status of the beaver in the province.

Methods

We reviewed both historical and scientific literature for references to beavers and beaver habitat on PEI and elsewhere. Our search included local history documents, scientific literature, government reports, archaeological reports, and collections at the Canadian Museum of History and Parks Canada (Halifax). Sobey's (2002, 2006a,b, 2007) wildlife history research covered much of the historical account.

Archaeological field research was undertaken by D.L.K. from 1980 to 2008 and by H.E.K from 2009 to 2018. Dating of beaver teeth from these archaeological studies was based on the site characteristics, cultural associations, and, more specifically, radiocarbon dating of associated charcoal in shell middens at South Lake and Greenwich. An incisor from MacMillan's Point was radiocarbon dated through accelerator mass spectrometry at Beta Analytic Testing Laboratory (Miami, Florida, USA). Dr. Frances Stewart, a peer-recognized leading zooarchaeologist for eastern Canada with an extensive reference collection of skeletons, determined the species identity of bones at George Island.

The distance beavers may have swum or rafted to get to islands was calculated using Google Earth (Keyhole, Inc., Mountain View, California, USA). Where island hopping was possible, the longest open-water swim using islands was calculated, as well as the straight-line distance through water.

Monitoring of beaver populations from 1972 to 2007 was conducted by R.L.D. while employed by the PEI government. Areas of beaver-influenced wetlands were delineated and measured on aerial photos from 1990, 2000, and 2010 captured at a 1:17 500 scale (PEICLUI 2010). Beaver dams and the triangular flooded areas behind them are readily recognized at this scale. Wetland sizes ranged from 0.1 to 240 ha.

In 1990 and 2000, coverage of PEI included the use of infrared photography. Both active and inactive beaver dams were delineated on the 1990 photographs. Each photo was overlain with a same-scale transparent map showing roads and streams. These lines were then transferred to the map and digitized to create the first vector-based PEI wetland inventory. In 2000, the analog film was then scanned and the resultant imagery used to create complete orthorectified imagery of PEI. Using the orthomaps and existing digital 1990 inventory, the 2000 PEI wetland inventory, including beaver dams, was incorporated into a province-wide digital land use inventory.

In 2010, digital imagery was acquired in both colour and colour-infrared with 40-cm resolution. Softcopy photogrammetry was used to generate the PEI 2010 Land Use Inventory in which the same interpretation parameters were applied.

Results

Historical evidence of Castor canadensis

Cameron (1958: 45) listed the beaver as a native mammal in PEI, taking as proof "the presence of beaver tooth marks on sticks found in peat bogs", but presented no further details. Sobey (2007) acknowledged no firsthand account of beavers in the PEI historical record since French settlement in 1721. There are two early French reports. In 1721, Denys de La Ronde stated that there were no beavers in Ile Saint-Jean (as it was then named; Sobey 2007). However, footnoted evidence reveals that Père René-Charles Breslay, who lived in Ile Saint-Jean from 1721 to 1723, took eight beaver skins to France (Sobey 2006a). Beavers were included in an 1802 shipment of pelts and an 1808 list of pelt prices from PEI. It is notable that credible mammal listers (e.g., Johnston 1822; MacGregor 1828) in the early 1800s failed to include the beaver for the island. Peter Sinott emigrated to PEI in 1821 and stated in 1876 that the beaver had been present when he was younger (Sobey 2006b), whereas, in the late 19th century, the opinion of a permanent resident, Sutherland (1861), and the visiting Rowan (1876) indicated an absence of beavers (Sobey 2007). A Summerside Journal article by Marks (1900) related the words of an old gentleman that the last beaver he saw had been killed 40 years earlier, ca. 1860, and the 31 October 1916 Charlottetown Guardian reported that the late Professor Caven of Prince of Wales College, Charlottetown, had found traces of beaver dams on the Dunk River (Dibblee 1994). Naturalist Francis Bain (1890) reiterated that remains of beaver dams could still be seen.

Glacial and post-glacial history, geography, and dispersal

The current PEI mammalian fauna arrived after glaciers retreated about 11 000 BP (before present, with present defined as 1950; Shaw *et al.* 2006). Although overland access to PEI was necessary for some species and facilitated by a land connection that was in place from 9500 to 5000 years BP across what is now Northumberland Strait (Kranck 1972; Shaw *et al.* 2002), it is unlikely that the now-flooded strait is a barrier to beaver dispersal (Table 1). On PEI, several specimens of River Otter (*Lontra canadensis*), previously regarded as extirpated, have been collected since 2016 (G. Gregory pers. comm. 20 June 2019) including a juvenile that was whelped on PEI, although at least some have swum or travelled on ice across 13+ km of marine waters, identical to distan-

TABLE 1. Unassisted occupation of islands by American Beaver (*Castor canadensis*) and the shortest straight-line distances by water, measured using Google Earth.

Island and jurisdiction	Water body	Distance to mainland or island (km)	Salinity	Reference
Nueva Island, Chile	South of Beagle Channel	6.5–11.5*	Marine	Anderson *et al.* 2009
Lennox Island, Chile	South of Beagle Channel	6	Marine	Anderson *et al.* 2009
Admiralty Island, Alaska	Stephens Channel	3.5	Marine	MacDonald and Cook 1996
Isle Royale, Michigan	Lake Superior	23	Fresh	Mech 1966
Grand Manan Island, NB	Bay of Fundy	11	Marine	Ingersoll and Gorham 1978
Newfoundland, NL	Strait of Belle Isle or other route	17+	Marine	Cameron 1958
Cape Breton Island, NS	Strait of Canso	1	Marine	Cameron 1958
Prince Edward Island	Northumberland Strait	13	Marine	Cameron 1958; this study
George Island, PEI	Malpeque Bay	1	Marine	This study

Note: NL = Newfoundland and Labrador, NB = New Brunswick, NS = Nova Scotia, PEI = Prince Edward Island.
*With possible island hopping, the longest open-water swim using islands is shown as well as the shortest possible distance by water.

ces regularly swum by River Otters in marine waters of Alaska (Blundell *et al.* 2002). The beaver and the otter were regarded as equally effective dispersers in colonizing insular Newfoundland and Labrador (Dodds 1983), and possibly not via the narrow but turbulent Strait of Belle Isle (Cameron 1958).

Beavers from Minnesota, USA, have dispersed to Isle Royale, Michigan, USA, at least twice across 23 km of freshwater in recent times (Mech 1966), far exceeding the 13 km that a beaver would need to swim to PEI. American Beavers commonly occupy inshore islands in Canada (Naughton 2012), and a rejuvenated beaver population in Newfoundland arrived at several smaller offshore islands in the mid-1900s (Dodds 1983). R.C. has twice seen a beaver swimming along the shore in coastal areas of PEI, as well as a beaver dam constructed across a coastal salt marsh. Beavers are well adapted to an aquatic environment, and they have several features that also protect them in marine waters. They breathe only through the nose and can prevent accidental swallowing of water. When they are underwater, flaps close off their nose and ears and a membrane protects the eyes (Naughton 2012). They are also buoyant and predisposed to enter the water, characteristics that enable colonization of islands (Mazza *et al.* 2013).

On Cape Breton Island, Nova Scotia (NS), beaver presence was recorded by 9500 years BP (Gorham *et al.* 2007); thus, they were present in the Maritimes during the 4000-year period when the extensive land connection between PEI and NB and NS was in place (Kranck 1972; Shaw *et al.* 2002).

Archaeological record of beavers on Prince Edward Island

Sobey (2007) acknowledged the beaver incisor excavated at South Lake by Keenlyside (1982, 1983) but did not look for other records. The archaeological record for the Maritimes has been evaluated (Murphy and Black 1996). Because of the great influence of coastal erosion and relative rise in sea level, many possible sites of older coastal encampments of Indigenous peoples have long since disappeared under water. As well, pre-contact shell middens were systematically spread on the land by PEI farmers to counteract soil acidity and, thus, their contents were plundered and/or dispersed (Gesner 1846).

There are 14 archaeological collections of beaver material from six sites, all with deposition dates after the postglacial flooding of Northumberland Strait (Table 2). Incisors are the most easily identified beaver remains and, thus, are often noted immediately when found, as at the Sutherland site, Greenwich (CcCp-7; Keenlyside 2002).

Faunal remains of beaver are currently known from four prominent archaeological sites on PEI (Figure 1). The MacDonald site (CcCm-12), located in South Lake, Kings County (Keenlyside 1982, 1983), consisted of two cultural components: a probable Acadian early-mid 18th century historical occupation, and a second underlying late Maritime Woodland occupation dating to about 600–900 AD. Associated with the earlier indigenous occupation was a cut beaver incisor section that appears to have been used as a bit for a cutting or incising implement. No post-cranial elements were identified in the site faunal sample.

The finds from the Sutherland site at Greenwich (CcCp-7) located on the north shore of St. Peters Bay, Kings County, now part of Prince Edward Island National Park (PEINP; Keenlyside 2002), included a modified incisor recovered from a test pit in a shell midden deposit, one of several found. The site revealed extensive habitation covering 2–3 ha and dates from 800 to 900 AD, a similar period as at the MacDonald site.

The split incisors found at Rustico (Robinson) Island in PEINP were used as a knife by Indigenous

TABLE 2. Known remains of American Beaver (*Castor canadensis*) incisors deposited 500–1650 AD and obtained from archaeological excavations and opportunistic collecting on Prince Edward Island during 1980–2017.

Sample	Location collected	Collection date	Collector*	Approximate years deposited, AD ± SD (range)	Normalized age,† years BP/1950 ± SD	Voucher	Reference documents	Comments
Piece of incisor	MacDonald site, South Lake (CcCm-12)	Several seasons 1980s	DLK	900 ± 100 (800–1000)	1480 ±160	CMC CcCm-12: 506	Keenlyside 1982, 1983; Morlan n.d.	From shell midden
Piece of incisor	MacDonald site, South Lake (CcCm-12)	1980	DLK	900 ± 100 (800–1000)	1480 ±160	CMC CcCm-12: 343	Keenlyside 1982	23–28 cm deep
Incisor	Sutherland site, Greenwich, PEI National Park (CcCp-7)	1994–1995	DLK	750 ± 250 (500–1000)	1200 ± 250	CMC CcCp-7: 1481	Keenlyside 2002	In bank
Two incisor fragments	Sutherland site, Greenwich, PEI National Park (CcCp-7)	1985	DLK	1100 ± 300 (800–1400)	1280 ±100	CMC CcCp-7: 481, 482	Keenlyside 2002; Morlan n.d.	Eroding bank with shell midden; dated by ceramic inclusions; 1.8 cm cut; 1.9 cm fractured and cut (one side only)
Lower incisor	Sutherland site, Greenwich, PEI National Park (CcCp-7)	2000–2001	DLK	1100 ± 300 (800–1400)	1280 ± 100	CMC CcCp-7: 1928	Keenlyside 2002; Morlan n.d.; Stewart 2002	Split, end cut and smoothed; in plough zone
Enamel fragment of incisor and fragment of incisor	Sutherland site, Greenwich, PEI National Park (CcCp-7)	2000–2001	DLK	1100 ± 300 (800–1400)	1280 ± 100	CMC CcCp-7: 2209, 2245	Keenlyside 2002; Morlan n.d.; Stewart 2002	34–43 cm deep
One upper and one lower incisor	Robinsons Island, PEI National Park (CcCt-1)	1987–1988	BWF	1480 ± 50 (1430–1530)	470 ± 50	7F2J1-800: 7F11D5-801‡	Leonard 1989; Wallace Ferguson 1989	Split, ground, and polished for use as a knife
Lower incisor	MacMillan's Point, Covehead Bay	1991	WJ	1560 ± 90 (1470–1650)	320 ± 30	Private collection	Kristmanson pers. comm.	Calcined tooth in a fire pit, plowed field; buried about 30 cm in soil

Table 2. *Continued.*

Sample	Location collected	Collection date	Collector*	Approximate years deposited, AD ± SD (range)	Normalized age,† years BP/1950 ± SD	Voucher	Reference documents	Comments
Lower incisor	George Island, Malpeque Bay (CdDw-5)	2006	HEK	Undated (N/A)	Unknown	To be deposited PEIMHF	Kristmanson 2007, 2009	In woodland opening; no evidence of modification or use-wear
Incisor fragment	George Island, Malpeque Bay (CdDw-5)	2017	HEK	Undated (N/A)	Unknown	To be deposited PEIMHF	Kristmanson 2018	From *in situ* deposits, pre-contact to historic shell midden site, Pitawelkek
Upper incisor	Darnley Basin, Malpeque (CdCw-9)	2017	HEK	Undated (N/A)	N/A	To be deposited PEIMHF	Kristmanson unpubl. data	Surface collected from pre-contact to 18th century site

Note: CMC = Canadian Museum of History, PEIMHF = Prince Edward Island Museum and Heritage Foundation (2 Kent Street, Charlottetown, Prince Edward Island C1A 1M6), SD = standard deviation.

*Collectors: BWF = Birgitta Wallace Ferguson, DLK = David Keenlyside, HEK = Helen Kristmanson, WJ = Wayne Jordan.

†Age of the site based on radiocarbon dating.

‡Parks Canada Collections and Conservation Facility, 50 Neptune Crescent, Dartmouth, Nova Scotia.

people (Leonard 1989; Wallace Ferguson 1989), but not all teeth were modified. For instance, the complete incisor at a George Island (Pitawelkek) site, where exploration continues, showed no modifications of any kind (Kristmanson 2007, 2009), nor did the MacMillan Point specimen. The latter had been found in an old fire pit in a plowed field about 6 km from the Rustico Island site (H.E.K. unpubl. data).

A rib fragment from an immature beaver, an undated phalanx, and incisor fragments were recovered from excavations at the Pitawelkek site on George Island. These are in general association with radiocarbon dates of ca. 700–800 AD through to the recent historical period. For now, the age of the occupation has been cautiously extended back to at least 0 AD based on the collection of diagnostic artifacts at the Pitawelkek site and other locations on George Island (Kristmanson 2019). The Malpeque site is a cultivated field where it is believed that shell middens were spread on the land (Gesner 1846).

Current status of beaver

The history of beaver reintroductions was investigated by Dibblee (1994). Following the earliest importations from Ontario in 1908 and from an unconfirmed source in 1912, the population rose to an estimated 500 beavers over several river systems. However, high fur prices in the 1920s and unregulated trapping resulted in the animals' disappearance. No beaver dams were detected on 1935 aerial photos. In the late 1940s, a migratory birds protection officer, Spurgeon Jenkins, obtained beavers from NB biologist Bruce Wright, and introduced them into PEI. Thus, Dibblee concluded that all beavers now present in PEI originated from NB.

Beavers were initially introduced east of Charlottetown, but by 1973 the population had expanded. Between 1973 and 1979, government personnel removed 32 beavers from eastern PEI where they were considered to be a nuisance and released them into watercourses of Prince County, where no beavers were present. In January 1981, the first short open season for trapping beavers took place in Prince County, when 20 beaver "problems", such as blocked culverts and flooded driveways indicated an expanded population (Dibblee and Curley 1980). By 2000, the island was well populated with beavers, although few were recorded in the hilly central portion of the island with its flashy streams (a flashy stream is one that rapidly collects flows from the steep slopes of its watershed basin and produces flood peaks soon after the rain but the flow quickly subsides after the rainfall ends). This habitat is less suitable for beavers (Novak 1987), and most are situated to the east and west on rivers with low gradients (Figure 1).

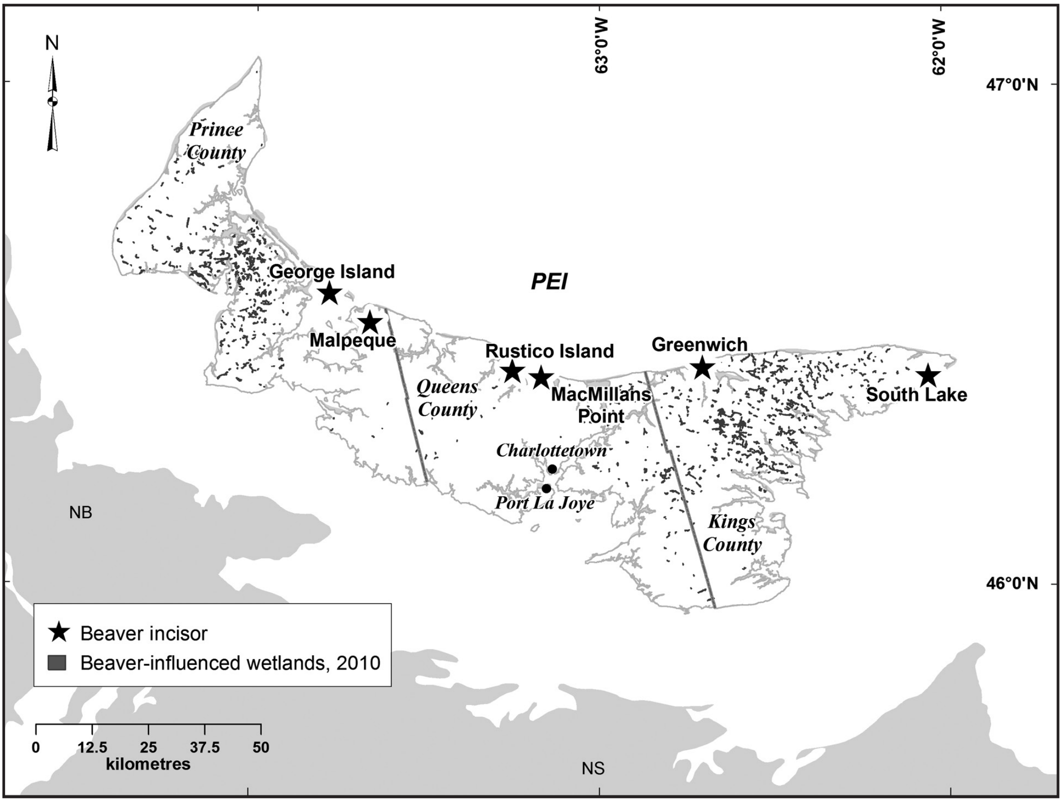

FIGURE 1. Locations of intact or partial American Beaver (*Castor canadensis*) incisors and other geographic points of interest, Prince Edward Island, Canada, plus active and inactive beaver-influenced wetlands delineated in the Prince Edward Island Corporate Land Use Inventory (PEICLUI 2010).

According to data maintained by the provincial fish and wildlife agency, from 1975 to 2015, an average of 465 beavers (one per 11 km^2) were trapped each year, varying from 91 in 1975 to 917 in 2011. Between 1972 and 2002, aerial surveys of index watersheds totalling 1363 km^2 of predominantly forested habitats were conducted by the province. Results indicate a peak of 276 active colonies in 1993 and 160 in 2002. The total wetland area of both active and inactive beaver flowages in PEI was calculated from aerial photography as 2233 ha in 1990, 3395 ha in 2000, and 5304 ha in 2010.

Beavers dams are often perceived as detrimental to salmonid populations (Kemp *et al.* 2012), and watershed enhancement groups express concerns regarding Brook Trout (*Salvelinus fontinalis*) and Atlantic Salmon migration. Beaver numbers fluctuate inversely with fur prices and are a continuing issue for wildlife managers dealing with complaints. Many of the 24 community-based watershed groups have considered beavers in their long-term management plans, as encouraged by the PEI Beaver Management Policy (Anonymous 2011). In practice, plans often direct removal of beavers from the main stem of a river. A local watershed group continues to remove all beavers from northeastern rivers on PEI to support spawning of a unique population of Atlantic Salmon (Moore *et al.* 2014).

Discussion

Previous records of beavers

In evaluating the historical evidence of PEI mammals, Sobey (2007) gave credence to first-hand accounts or records as verifying or disputing the presence of various species. The acceptance of claims that beavers were not present in the province led him to explain away a considerable body of evidence that beavers may have been present. Two (Sutherland 1861 and Rowan 1876) of three mammal recorders who stated that beavers were not present produced their reports in the last half of the 19th century when the few beaver records may have been of new arrivals from the mainland after a long period of absence. Rowan (1876), a travel writer who merely visited the province, also later stated in the same publication that beavers were extirpated from PEI.

These writings likely do not meet the standard of a first-hand account, nor, we assert, would the observations by Denys de La Ronde, a naval officer, who spent only 13 months in PEI beginning in 1721, including time to travel to Louisbourg, Cape Breton Island (Sobey 2002). Although Denys de La Ronde visited all active PEI harbours, the French population in 1721 was perhaps 200 (Harvey 1926). Local knowledge of wildlife would be cursory and cleared land scarce. Denys de La Ronde could not have spoken from personal knowledge of PEI beaver habitats, which would consist mainly of forested river systems extending to the coast in a land mass exceeding 5000 km^2. He may have obtained information from Mi'kmaq traders at Port la Joye, the seat of French government in Ile Saint-Jean, or from fishermen, but he did not acknowledge the source of his information. Harvey (1926) also calls into question his veracity as a reliable reporter.

Novak (1987) reasoned, based on food availability, that beavers likely existed at lower densities in mature forests of the 1500s and the 1600s compared with the high beaver populations in the food-rich early successional riparian forests of today. Beavers prefer young saplings as food and only cut large trees further away from water when saplings are depleted (Gallant *et al.* 2004). PEI has short river systems and human travel in the pre-settlement mature forests dominated by American Beech (*Fagus grandifolia* Ehrhart) was relatively easy, with some exceptions (Sobey 2002). Thus, we speculate that beavers, present according to the archaeological record, were relatively accessible. They live in families of two adults and potentially three or four kits and two or three yearlings (mean group size in central Ontario is 7.5; Novak 1987), and their lodges are easily identified and exploited.

Fur trading began in the Maritimes in the mid-1500s when Basque and French vessels began fishing for cod in the Gulf of St. Lawrence and exchanging goods with the Mi'kmaq (Ray 1987; Cook 1993; Whitehead 1993). Nicolas Denys had an exclusive license to enter into trade for fur and fish in the gulf dating from 1654, and PEI was included in his grant. A cod fisherman and now respected author, Denys (1672) recorded the presence of Basque ships in PEI waters and discussed how beaver pelts were obtained. The Mi'kmaq scared beavers from their lodges in winter, clubbed or harpooned them, taking all within the colony, and also took beavers during ice-free seasons by draining their dams and attacking them with spears and arrows. They met a strong economic demand for beaver pelts from Europeans, and extirpation in PEI in the 1600s or earlier is a possibility, as noted by Sobey (2007). A reinterpretation of Sobey's information discarding Denys de La Ronde's opinion might also indicate that the beaver persisted into the 1800s. The decades of greatest beaver harvest in North America as a whole were 1700–1709 and 1790–1799 (Novak 1987; Obbard *et al.* 1987).

Archaeological record, glacial, and post-glacial history

Sobey's research (2007) does not take into account the archaeological record for PEI. In 1995, archaeological research on PEI constituted only 2% of published and unpublished primary studies in the region (Murphy and Black 1996). Studies are needed from inland freshwater sites where beavers might naturally be found.

Additional factors may also explain the lack of bones. According to religious custom assuring continuation of the beaver, bones from beavers that were consumed by Mi'kmaq were not thrown into the fire or river, nor fed to dogs, although practices vary in detail and by location (Denys 1672; Wallis and Wallis 1955; Robinson and Heller 2017). Bone material and metal goods are generally not preserved in the acidic soils of PEI except in acid-neutralizing shell middens (Murphy and Black 1996). Indigenous peoples consumed beavers, and because beaver incisors were often used as cutting tools, their remains are found in the common areas of preservation, kitchen middens.

Of the 14 records of beaver teeth presented here, not all have been dated, but dated specimens were deposited from about 500 AD to as late as 1650 AD. The teeth could have been imported to PEI as tools (Sobey 2007; M. Betts pers. comm. 12 June 2013) but we have also shown that beavers swim or raft to islands, sometimes far offshore. The simplest explanation for the presence of beaver teeth at PEI archaeological sites is that they are the remains of PEI beavers. As well, the rib bone of an immature beaver at a site that may be 2000 years old, suggests that beavers were breeding on PEI. Discounting this, one must find an explanation as to why beavers did not swim or raft to PEI, as they did to Newfoundland, or disperse to PEI when a land bridge was in place for 4000 years.

With postglacial warming temperatures, vegetation on the island changed rapidly from tundra (suitable for beavers; Aleksiuk 1970; Jung *et al.* 2016; Tape *et al.* 2018) to forest, a spruce (*Picea* sp.)–nonarboreal birch (*Betula* sp.) association between 10 000 and 8000 years BP, followed by pines (*Pinus* sp.; Anderson 1980). The presence of beaver on Cape Breton Island 9500 years BP (Gorham *et al.* 2007) aligns well with the maximum connection of the PEI land mass to the mainland 9000 years BP, a continuous land mass lasting until 5000 years BP (Shaw *et al.* 2002). Beavers are also efficient dispersers (Leege 1968; Hodgdon 1978; Sun *et al.* 2000) and can swim long distances. We cannot identify any impediments to beavers populating the non-island in early post-glacial times or any dramatic ecosystem changes that would preclude beavers colonizing PEI. A land bridge and the presence of beavers in the region might suggest that they inhabited PEI soon after deglaciation. The ability of beavers to swim or raft to islands is convincing evidence that they inhabited PEI prior to 1534. Archaeological evidence indicates the presence of beavers until at least 1650 AD.

Current status of beaver

The second-growth riparian forests of PEI provide suitable beaver habitat and the beaver has populated most of it. It is likely that human conflicts with beavers and their dams will persist as long as beavers flood transportation corridors and are viewed as negatively influencing the spawning success of salmonids.

Conclusion

It is quite credible that the beaver could have been extirpated from PEI in the roughly 200 years before French settlement in 1721. Extinction rates of mammals are orders of magnitude higher on islands than elsewhere and are often related to human predation in historical times (Loehle and Eschenbach 2012). Caribou (*Rangifer tarandus*), Canada Lynx (*Lynx canadensis*), North American Black Bear (*Ursus americanus*), River Otter, and American Marten (*Martes americana*) were all extirpated from PEI following European settlement (Sobey 2007). Although Caribou in Nova Scotia were extirpated by 1921 (Benson and Dodds 1977), none were reported after 1765 in PEI. Human exploitation was also responsible for the loss of Walrus (*Odobenus rosmarus*) from the Gulf of St. Lawrence beginning in the 1500s (McLeod *et al.* 2014), and Great Auk (*Pinguinus impennis*) became extinct in 1844, aided in part by their exploitation at Bird Rock in the Magdalen Islands, Quebec (Montevecchi and Kirk 1996).

Cameron (1958) contended the beaver was "exterminated" from PEI, and the data presented here support its status as native, at least since 500 AD and possibly as early as 9500 years BP. Evidence that might allow determining the point of extirpation is less clear, but it is almost certain that a beaver population was no longer present in PEI after 1860. It may well have been the first mammal extirpated from PEI, before 1700. Although the current beaver population is known to be derived from animals introduced from NB, it is also possible that some individual beavers have reached PEI via natural dispersal from NS or NB and could account for the late 19th century records from PEI. Future genetic studies may shed light on whether NS beavers have contributed to the current gene pool. In addition, and considering there are no known endemic species in PEI because of its geologically recent land connection with the mainland, beavers sourced from NB are predicted to be similar genetically to the original PEI population. It may be possible to test this using more archaeological remains of beavers as they become available. Additional radiocarbon dating of beaver incisors from middens may also reveal new information. Finally, because beaver-chewed sticks were seen as an indication that beavers were native mammals (Cameron 1958), monitoring bogs that are being mined for peat might yield older beaver records.

Although the founders of the current population were introduced to support fur harvesting (Dibblee 1994), the population meets International Union for the Conservation of Nature guidelines as a reintroduction, being "the intentional movement and release of an organism inside its indigenous range from which it has disappeared" (IUCN/SSC 2013: 2). We suggest that the American Beavers now extant on PEI be regarded as a native population and that the provincial government apply the precautionary principle in the unlikely event that population decline threatens the species. The second-growth riparian forests of PEI provide suitable beaver habitat and the beaver has populated most of the island. It is likely that human conflicts with beavers and their dams will occur as long as beavers flood transportation corridors and are viewed as negatively influencing spawning success of salmonids.

Author Contributions

Original Draft: R.C.; Writing – Review & Editing: R.C., D.L.K., H.E.K., and R.L.D.; Conceptualization: R.C.; Investigation: D.L.K., H.E.K., R.C., and R.L.D.; Methodology: R.L.D.; Formal Analysis: D.K. and R.L.D.; Funding Acquisition: H.E.K. and R.L.D.

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Sixty years of White-tailed Deer (*Odocoileus virginianus*) yarding in a Gray Wolf (*Canis lupus*)–deer system

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Abstract

This article synthesizes information from over a six-decade period of studies of White-tailed Deer (*Odocoileus virginianus*) use of a winter yard and subject to Gray Wolf (*Canis lupus*) predation in northeastern Minnesota. It also adds spring migration data from 35 adult female deer and fawns studied there during 1998, 1999, 2001, 2014, and 2017. Twenty-nine of these deer migrated in spring a mean distance of 29 km (SE = 4), a maximum distance of 78 km, and at a mean bearing of 83° (SE = 12; range 21–348). These findings are similar to those from 49 deer (both sexes) from the same yard studied during 1974–1984, that migrated a mean distance of 25 km (SE = 1.8) and a mean bearing of 77° ± 4 SE. Between the two periods, the wolf population fluctuated considerably, the winter range of deer in the area where these deer spent summer greatly diminished, and both derechos and fires disturbed the habitat. This study attests to the selective advantage of the migratory tradition of deer in this yard.

Key words: *Canis lupus*; deer yard; migration; *Odocoileus virginianus*; predation; predator-prey relations; White-tailed Deer; wolf; yarding

Introduction

White-tailed Deer (*Odocoileus virginianus*) migrate between summer and winter ranges in many northern areas (summarized by Nelson 1998). Two main drivers of these migrations have been proposed: (1) the need for optimal protection from adverse winter weather (Townsend and Smith 1933; Severinghaus and Cheatum 1956; Ozoga 1968) and (2) grouping to minimize predation risk (Nelson and Mech 1981, 1991; Messier and Barrette 1985).

Most studies of migratory deer populations have been short term, describing migration distances, timing, and triggers for seasonal movements. One exception is an investigation of deer movements in southeastern Quebec that also depicted the extent of two deer yards over three decades (Lesage *et al.* 2000). Studies of deer migratory behaviour in areas where Gray Wolves (*Canis lupus*) are the primary predator of deer have been conducted for as long as 10 years (Forbes and Theberge 1995; Theberge and Theberge 2004), 15 years (Fieberg *et al.* 2008), and 28 years (Hoskinson and Mech 1976; Nelson and Mech 1981, 1987; Nelson 1995, 1998; Nelson *et al.* 2004). However, we know of no migratory White-tailed Deer herd subject to wolf predation that has been investigated for more than three decades.

As part of a long-term study of wolf ecology and population trend in northeastern Minnesota (Mech 2009), we have also researched White-tailed Deer there since 1964 (Mech and Frenzel 1971; Hoskinson and Mech 1976; Nelson and Mech 1981, 1987; Nelson 1998; Nelson *et al.* 2004). During that time, the amount of winter range of the deer herd we studied diminished greatly (Mech and Karns 1977). Forty-five years later, some 3000 km^2 that deer previously used for decades during winter remained devoid of wintering deer (Nelson and Mech 2006), and most, and probably all, of it still remains devoid of wintering deer (Mech *et al.* 2018). In addition, various habitat disturbances and other important changes detailed below have occurred in the wolf study area.

The wolf study area (Figure 1) lies in northeastern Minnesota, USA at about 47.60°N to 48.7333°N and 90.8167°W to 91.8333°W excluding the northwest quarter of that region and includes much of the Garden Lake deer yard (GLY) along its western edge

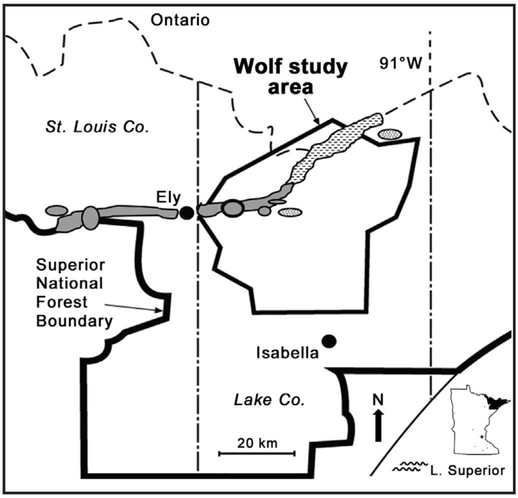

FIGURE 1. The wolf study area with the Garden Lake Yard (GLY). Irregular grey and stippled areas represent the GLY as described by Mech and Karns (1977). Grey and stippled ovals represent areas listed as deer yards by Arnold *et al.* (1961). Stippled areas (both irregular and oval) are where deer have not overwintered since the early 1970s (Mech and Karns 1977; Nelson and Mech 2006; Mech *et al.* 2018). The darker bold oval just east of Ely is the GLY proper, where White-tailed Deer (*Odocolieus virginianus*) from previous studies mentioned in the Introduction and the present study were radio-collared. Inset map shows location of Superior National Forest (black) in Minnesota.

near Ely, Minnesota, USA. The GLY is named for the area around Garden Lake and the adjacent area near the Winton Hydroelectric Power Plant where wintering deer concentrate the most under the most severe conditions and where deer were fed artificially in the early 1970s and probably for some time before that. Deer have continued to concentrate in the GLY during winter and to migrate to summer ranges in and through the wolf study area for over 60 years. We studied the migratory behaviour of deer in this yard from 1974 through 1984 (Hoskinson and Mech 1976; Nelson and Mech 1981, 1987, 1991; Nelson 1998) and again during 1998 through 2017. We document here the continued winter concentration of deer in that yard and their annual migrations despite those changes and despite a wolf population that depends on them for most of their diet (Barber-Meyer and Mech 2016). We also compare 1998–2017 demography and migratory status of the deer in that yard with results from 1974–1984 (Nelson and Mech 1981, 1987). The objective of this study is to demonstrate the extreme degree to which a migratory tradition in a given deer yard under natural conditions of wolf predation can persist, a record duration to our knowledge, and to compare the migratory behaviour over the period of this study.

Study Area

The extent of the GLY over the years has been described variously, no doubt because (1) deer populations fluctuate greatly over the decades, and (2) deer use of winter range, and thus their migration movements, vary considerably by season, temperature, and snow conditions (Nelson 1995). As these conditions change, deer may move toward or away from winter yards, sometimes wintering for long periods only partly along their route to areas where they would concentrate more during the most extreme conditions (Nelson and Mech 1981). The Pohenegmook and Lac Temiscouata deer yards in southeastern Quebec, Canada provide a good example of such changes (see Figure 3 in Lesage *et al.* 2000).

In 1953, the GLY was thought to encompass 128 ha, not including other yards west and east-northeast of the GLY (Erickson *et al.* 1961). Mech and Karns (1977) considered the GLY more inclusively, stretching from about 35 km west-southwest of Ely to Ely, about 25 km east of Ely, and then northeast about 12 km, totalling about 72 km long, and centring on the Garden Lake area (Figure 1). In the mid-1970s the GLY was thought to extend about 16 km east-northeast (Hoskinson and Mech 1976) and later as holding ≤800 deer (Nelson and Mech 1987). East of Garden Lake, deer currently continue to winter along the area that Hoskinson and Mech (1976) described at times as far as some 18 km east of Garden Lake.

Whether deer wintering elsewhere in the more expansive GLY other than those from the capture area (Nelson and Mech 1981, 1987, this study) migrate in the same direction to summer ranges as those deer radio tracked is unknown.

The GLY lies along the western edge of our long-term wolf study area (Mech 2009) which covers about 2060 km^2 including the migration routes along which the wintering GLY deer travel to their summer ranges (Figure 1). The wolf study area is situated well within the Minnesota wolf range (Fuller *et al.* 1992), and wolves have never been extirpated from the wolf study area. The area is replete with lakes and waterways, and American Beaver (*Castor canadensis*) and Moose (*Alces americanus*) are also available to wolves there (Mech and Karns 1977; Barber-Meyer and Mech 2016; Mech *et al.* 2018). Black Bear (*Ursus americanus*) is the only other major predator of deer in the region (Kunkel and Mech 1994), although Coyote (*Canis latrans*), Fisher (*Martes pennant*), Bobcat (*Lynx rufus*), and Canada Lynx (*Lynx canadensis*) inhabit the area and could prey on fawns. General habitat, topography, and weather in the study area were described by Nelson and Mech (1981, 2006) and Heinselman (1996).

In July 1999, a derecho windstorm leveled about 1600 km^2 of the forest through which some of the GLY deer migrate (National Oceanic and Atmospheric Administration 1999; Nelson and Mech 2006). Another derecho struck in 2016 that also affected the migration routes of these deer (Minnesota Department of Natural Resources 2016).

In 2000 and 2007, fires burned 431 km^2, just northeast beyond where radio-collared GLY deer migrate to but which could include summer ranges of other GLY deer (Fites *et al.* 2007). In 2011, the Pagami Creek fire burned 376 km^2 in which some GLY deer summered, or through which they migrated (Nelson and Mech 1987). Other habitat changes during the study included forest maturation, and alterations and variation in logging practices from clear cutting to total protection.

Weather conditions also changed considerably throughout the study. Snow depth, density, and persistence, especially during the past decade, differed from earlier in the study, including winter 2010–2011 when snow depth was extremely low and winter 2013–2014 when snow was very deep and fluffy.

White-tailed Deer have inhabited the region for many decades. Johnson (1922) considered deer common from 1912 to 1915. In 1938, Olson (1938: 330) published a map showing deer present in every township in the wolf study area. From 1948 to 1952, Stenlund (1955) documented wolf-killed deer in winter on most of the major lakes there. Erickson *et al.* (1961) stated that deer were abundant in the Northern Forest Zone, which included our wolf study area, for more than 40 years, and those authors listed 16 winter yarding areas they checked in or near our wolf study area between 1949 and 1958. Estimated deer densities in the Northern Forest Zone (although not necessarily in our wolf study area) ranged from 5.9 to more than 7.8/km^2 in the late 1930s (Erickson *et al.* 1961).

By the mid-1970s, almost no deer spent winter in the northeastern third of the wolf study area, and wolves there lived primarily on Moose and probably beavers (Mech and Karns 1977). Deer that had wintered there had succumbed to a combination of deteriorating habitat (maturing forests), a long series of severe winters, and heavy wolf predation (Mech and Karns 1977). Deer have not been observed overwintering there since, despite regular winter flights (Nelson and Mech 2006; Mech *et al.* 2018). Deer numbers along the southern and western edges of this area dropped to about 0.8 deer/km^2 (Floyd *et al.* 1979) and in 2011 pre-fawn densities averaged <2/km^2 (Lenarz and Grund 2011). To the east of the wolf study area, deer migrated during autumn to winter yards along the shore of Lake Superior (Nelson and Mech 1981) and reached yarding densities during 1968–1976 of 39 to 55/km^2 (Mech and Karns 1977). Deer from those yards moved at least 22 km northwest inland (Morse and Zorichak 1941; Nelson and Mech 1981).

Deer that wintered in yards along the west side of the wolf study area, primarily in and around Garden Lake, 8.8 km east-northeast of Ely, migrated in spring southeastward to northeastward for up to 54 km at a mean bearing of 77° (Nelson and Mech 1987).

Moose have also occupied the region for many decades. Johnson (1922) found Moose very common in 1912–1915 but scarce in 1920. Olson (1938) estimated a Moose density of 1/6.4 km^2 based on his observations during 1920–1936 and his discussions with various wardens, trappers and other woodsmen, but Stenlund (1955: 22) considered their numbers "not high" during 1948–1952. An historical estimate of Moose density from 1915 to 1970 over the entire northeastern Minnesota Moose range, which included our wolf study area, was 1/3.8 km^2 to 1/21.9 km^2 (Peek *et al.* 1976). From 1984 to 2016 in this Moose range, densities based on annual aerial counts were 1/1.7 km^2 to 1/5.5 km^2 (calculated from Moose-count data; Mech *et al.* 2018). Moose numbers in the overall northeastern Minnesota Moose range peaked in 1989, 1996, and 2006, declined to less than half their 2006 level by about 2012, and then leveled off for several years (DelGiudice 2017; Mech *et al.* 2018).

Wolves have inhabited the region throughout recorded history (Olson 1938; Stenlund 1955; Mech and Frenzel 1971). Wolf numbers in the wolf study area varied from 23–32 in winter 2016–2017 (L.D.M. and S.M.B.-M. unpubl. data) to 97 in 2008–2009, a density ranging from 11–16/1000 km^2 to 47/1000 km^2 during 1968–2017 (Mech 1973, 1986, 2009; Mech *et al.* 2018). During and after the major deer decline in the 1970s, wolf numbers there also declined considerably and did not reach former levels until about 2000 after recovering from a prolonged infection by canine parvovirus (Mech *et al.* 2008). A few years after Moose numbers began declining in 2006 and deer numbers declined due to severe winters, the wolf population began dropping to its lowest level during the study, 23–32 animals (Barber-Meyer and Mech 2016; Mech *et al.* 2018).

The primary migration routes and many of the summer ranges of the GLY deer we studied usually fell within the territories of two wolf packs, known as the Wood Lake and Ensign Lake Packs in earlier publications (Mech 1973, 1986). Over the decades, the actual locations of these pack territories varied considerably, and other packs that used parts of the GLY, the deer migration routes, or the summer ranges of the GLY deer formed and disintegrated as well. At times, as many as four radioed packs, totalling up to 29 members during winter used the GLY (L.D.M., S.M.B.-M., and M.E. Nelson unpubl. data). In addition, wolf packs sometimes inhabited the GLY year around. One such pack that inhabited 39 km^2 including Garden Lake itself hosted the highest wolf density ever recorded anywhere, 182 wolves/1000 km^2 during winter, from 1 April 1998 through 30 March 1999 (Mech and Tracy 2004).

Based on 39 years during which the Wood Lake Pack was radio-collared and 24 years in which the Ensign Lake Pack was radio-collared between 1973 and 2017, their winter pack sizes averaged 5.3 ± 0.41 SE and 5.6 ± 0.55 SE and ranged up to 11 and 12 members, respectively (L.D.M., S,.M.B.-M., and M.E. Nelson unpubl. data). The numbers of wolves in these packs did not follow the trajectory of the overall wolf numbers in the wolf study area, but rather remained relatively constant from winter 1973–1974 through about 2006, although they declined after that (Mech 1973, 1986, 2009; L.D.M.,S.M.B.-M., and M.E. Nelson unpubl. data). In any given year, the packs that used the area including the GLY deer summer ranges and migration routes usually migrated to the Garden Lake area itself during autumn and back to the deer summer ranges in spring (Mech and Boitani 2003; L.D.M. and S.M.B.-M. unpubl. data) except when resident packs resided year around there.

Methods

Using Clover traps from 1998 to 2017, we live trapped, anesthetized, ear tagged, and radio collared deer within 1.4 km of the GLY (Mech and Barber-Meyer 2020). Three others were captured near Snowbank Lake, some 23 km east northeast of Garden Lake but still in the more expansive definition of the GLY discussed above. In the current study we excluded the three Snowbank Lake deer (included in a study by Nelson *et al.* [2004]) because that area was not included in the Nelson and Mech (1987) area with which we compare our data. Our GLY captures were basically in the same area where deer (both sexes) from this yard were studied earlier (Hoskinson and Mech 1976; Nelson and Mech 1981, 1987). We extracted an incisor from adults for aging by Matson's Laboratory (Missoula, Montana, USA). We located the deer by aerial radio tracking or by global positioning system (GPS) collar locations during June, July, and August until at least two consecutive locations were in the same general area to determine their summer ranges (because generally once on summer range they remain in a relatively small area [Nelson and Mech 1999]) and again each winter when they returned to the winter yard (Nelson *et al.* 2004). We examined the approximate spring migration routes of deer collared with prototype Advanced Telemetry Systems (Isanti, Minnesota, USA) drop-off GPS radio collars (details in Merrill *et al.* 1998), including some studied by Nelson *et al.* (2004).

We plotted individual deer summer locations and a summary location representing the centre of the winter deer capture locations on Google Earth Pro 7.1.7.2606 and measured the migration distances and directions via the Google Earth Tool function after converting UTMs of these locations to latitudes and longitudes via "Convert Geographic Units online" (http://www.rcn.montana.edu/resources/converter.aspx). Although fawns captured during the same year and at the same location as an adult female and migrating to the same summer range as the adult (or not migrating but remaining at the same summer range as the adult) might have been fawns of the adult, we still included the fawns as independent data. We used Statistix 9.0 (2008) to compare migratory status (including fawns) between our 1998–2001 and our 2014/2017 results using Fisher's Exact Test, respectively, and also to those from a previous study in the same area (Nelson and Mech 1981, 1987). We compared age structures (excluding fawns) between 1998–2017 and those from the previous study (Nelson and Mech 1981, 1987) via the Mann-Whitney *U*-test in R version 3.5.1 (R Core Team 2018). We considered all differences significant at alpha = 0.05.

Results

We live-trapped and radio-collared 27 adult does and eight fawns during winters 1998–2001, 2014, and 2017 in or near the GLY and aerially radio-tracked them to their summer ranges (Table 1), including eight whose spring migrations were studied in detail by Nelson *et al.* (2004). Apart from fawns, their mean age was 6.3 (SE = 0.8) years (Figure 2). All of the 19 deer we radio-collared in 1998–2001, including fawns, migrated to summer ranges, but six (including two fawns) of the 16 that we followed in 2014 and 2017 remained during summer within 3 km of their winter capture point, a significant difference between these two periods (Fisher's Exact = proportion

TABLE 1. Female White-tailed Deer (*Odocoileus virginianus*) or fawns of either sex radio-collared (first capture only) in Garden Lake Yard, Ely, Minnesota, USA, 1998–2017 and radio-tracked to their summer ranges. Six deer did not migrate.

Year	*n* (# fawns)	Age (year)*	
		Mean	Range
1998	8 (2)	5.6	3–11
1999	5 (0)	7.2	1–13
2001	6 (1)	3.7	1–13
2014	4 (1)	6.3	5–8
2017	12 (4)	7.1	2–13
1998–2017	35(8)	6.3	1–13

*27 adults and yearlings; excludes two adults of unknown age.

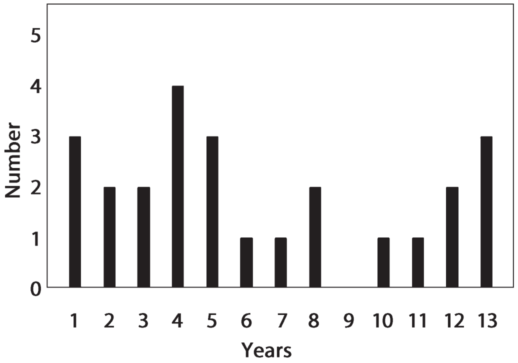

FIGURE 2. Age structure of adult and yearling female White-tailed Deer (*Odocolieus virginianus*) live-trapped (first capture only), in or near the Garden Lake Yard, Minnesota, 1998–2017, radio-collared, and followed to summer range.

difference 0.375, $P = 0.005$). The mean age of the four adult non-migrating deer was 7.3 and that of the 21 non-fawn migrators was 6.1. The age structures of the groups did not differ (W = 33, $P = 0.53$).

The 35 adults and fawns migrated in spring a mean distance of 29 km (SE = 4), a maximum distance of 78 km, and at a mean bearing of 83° (SE = 12; range = 21–348) excluding the six non-migrators (Table 2; Figure 3). Although the deer during different years of the study varied in the distances and directions to which they migrated, most of the annual mean migration distances were 21–36 km, and most of the annual mean migration bearings were 58–90° (Table 2). The 114° mean bearing for five deer in 1999 was heavily influenced by one deer whose migration bearing was 348°. Excluding that deer, the mean bearing was 55° (SE = 14). Notably, two other deer captured in the same general location as deer that migrated east-northeastward migrated in markedly different directions southwest, and south. Excluding all three deviant deer, and the non-migrators, the mean summer migration bearing was 65° (SE = 4; $n = 26$), the basic direction that the GLY extended. The mean migration distance of this sample was 29 km (SE = 4; 4–78 km).

Discussion

The sample of 35 does and fawns we studied from 1998 through 2017 generally was similar to that of the does and fawns studied from 1974–1984 in the same area (Nelson and Mech 1981, 1987). We compared these two periods (19 and 10 years long) because those were the periods for which we had comparable data. There was no significant difference in the radio-collared doe:fawn ratios (37:19 versus 39:28) between the early and later capture samples (Fisher's Exact = proportion difference 0.079, $P = 0.46$). The mean age of adult does of the earlier sample was 5.0 years and that of the later sample was 6.3 years. The age structures of the groups did not differ (W = 359, $P = 0.24$). The 1998–2017 sample of does and fawns that we followed through spring migration migrated similarly in mean distance (25 km ± 1.8 SE) to those from 1974–1984, but not maximum (78 km this study versus 54 km, measured from Nelson and Mech [1987: Figure 2.2]). They were also similar in the general directions they migrated (77° ± 4 SE; Nelson and Mech 1987). Of the 49 GLY deer (18 males: 31 females) whose spring migrations were studied from 1974 to 1984, 42 migrated (Nelson and Mech 1987), and with our 1998–2017 sample of 35 does and fawns, all except six migrated, a non-significant difference between proportions of migrators during the two periods (Fisher's Exact = proportion difference 0.029, $P = 0.77$).

The demography and migration we studied in the sample of deer wintering in the GLY differed little

TABLE 2. Migration distance and direction of White-tailed Deer (*Odocoileus virginianus*) that were radio-collared during 1998 through 2017 and followed to their summer ranges. Fawns possibly of collared does were included separately.

Year	No. of deer	No. migrating	Summer migration				Remarks
			Distance (km)		Direction (°)		
			$\bar{x}$ ± SE	Maximum	$\bar{x}$ ± SE	Range	
1998	8	8	36 ± 6	62	64 ± 8	26–97	
1999	5	5	31 ± 4	45	114 ± 60	21–348	
2001	6	6	26 ± 10	58	78 ± 17	39–153	
2014	4	1	2 ± 2	8			Includes three non-migrators
2014	4	1	8	8	58	—	Excludes three non-migrators
2017	12	9	21 ± 7	78			Includes three non-migrators
2017	12	9	28 ± 7	78	90 ± 18	36–226	Excludes three non-migrators
1998–2001	19	19	31 ± 4	62	81 ± 16	21–348	
2014–2017	16	10	16 ± 5	78			Includes six non-migrators
2014–2017	16	10	26 ± 7	78	87 ± 16	36–226	Excludes six non-migrators
1998–2017	35	29	24 ± 3	78			Includes six non-migrators
1998–2017	35	29	29 ± 4	78	83 ± 12	21–348	Excludes six non-migrators

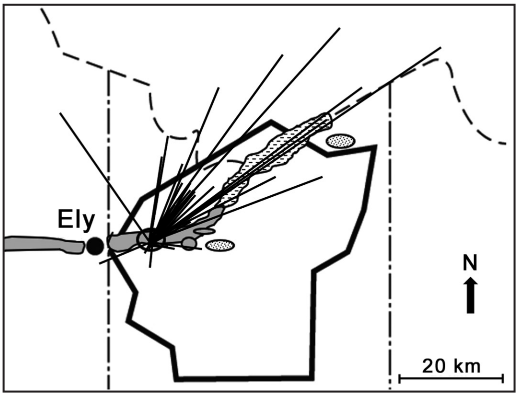

FIGURE 3. Distances and directions of spring migrations of 29 adult female and fawn White-tailed Deer (*Odocolieus virginianus*) radio-collared in the Garden Lake Yard during five winters between 1998 and 2017 (Table 1). Six of the original sample of 35 did not migrate.

from those studied there during 1974–1984. During the interim, several important environmental changes took place, as discussed in the Introduction.

Throughout this period and despite the changing deer, Moose, and wolf populations, as well as the widespread habitat upsets (e.g., derechos, forest fires, snowpack differences, changes in forestry practices), the majority of GLY deer continued to migrate each winter to the GLY the way they have for decades. Furthermore, we cannot extrapolate our findings to other migrating ungulate-wolf systems and would expect each deer yarding situation to be different because each local yarding ecology will be different.

Nelson (1995, 1998) and Nelson *et al.* (2004) provided details of the earlier migrations. The wolves that inhabited the major portions of the GLY deer summer and winter ranges maintained their numbers through about 2006. After Moose began to decline in 2006, the number of these wolves decreased, but packs continued to migrate each year for which we had data, presumably in response to the deer migration (L.D.M. and S.M.B.-M. unpubl. data), similar to wolf packs in Algonquin Park, Ontario, Canada (Forbes and Theberge 1995; Theberge and Theberge 2004).

During summer, the major age class of deer that local wolves kill are fawns (Nelson and Mech 1986; Barber-Meyer and Mech 2016), although the availability of beavers and Moose might buffer that predation (Mech and Karns 1977; Barber-Meyer and Mech 2016). Evidence from other parts of the wolf study area suggests that individual fawns are visited by wolves on average in summer about 5.5 times/100 days (Demma and Mech 2009) to daily (Mech *et al.* 2015), although the rate of fawn predation is unknown. Regardless, even though fawns comprise a high percentage of the diet of wolves in summer (Barber-Meyer and Mech 2016), enough fawns have survived in the summer ranges of the GLY deer each year to sustain the migrating deer population over the decades.

GLY migrating deer spend 31–356 hours during migration and adhere closely to a straight line during the trip (Nelson *et al.* 2004). While migrating, deer are much more vulnerable to wolf predation than at any other time as adults (Nelson and Mech 1991), so the persistence of GLY deer either abandoning summer range or favouring winter range or both during winter must have some strong adaptive value. Reducing vulnerability to wolf predation during winter when deer are in poor nutritional condition (DelGiudice *et al.* 1992) and hindered by snow conditions (Mech *et al.* 1971) was the explanation Nelson and Mech (1981) gave for deer in this area migrating to areas of high deer density, i.e., the GLY, listing several advantages to yarding. This benefit was one of the points Nelson and Mech (1981) proposed as an anti-predator effect of yarding. We further note that Poszig and Theberge (2000) did find that non-yarding deer in their study were “highly vulnerable” when migrating wolves returned to their territory.

Kolenosky (1972) had already shown that wolves tended to kill deer along the edges, rather than the centre of the deer yards he studied, and further support for the antipredator explanation for deer migration and yarding has since been found in other studies. In northwestern Minnesota, wolves also tended to kill deer along the edges of yarding areas rather than in the densest areas (Fritts and Mech 1981) as did Coyotes in Quebec (Messier and Barrette 1985).

On the other hand, Poszig and Theberge (2000) found evidence in Ontario that tended to dispute the hypothesized antipredator advantages of deer yarding. The only benefit of yarding they proposed would be an enhanced trail network through the snow that might give deer in high densities more of an advantage in escaping wolves.

Henderson *et al.* (2018) emphasized the role of density-dependent competition for home ranges in winter that forced deer to space out during summer to obtain adequate nutrition. The spacing out of migrating deer to their summer ranges, where their fawns are born, provides far more habitat per deer to obtain nourishment, with summer being the season of annual replenishment (Silver *et al.* 1969; Moen 1978; DelGiudice *et al.* 1992). However, it also brings several other survival benefits related to wolf predation: (1) familiar escape terrain and habitat; (2) an area with a proven history of survival characteristics; and (3) separation from other fawns that would attract predators. Fawns are most vulnerable during late spring and early summer (Kunkel and Mech 1994; Carstensen *et al*. 2009), so widely spaced fawns reduce the chance that any individual fawn would be detected by predators, thus increasing survivability (although reducing potential benefits of group vigilance and defense).

None of these benefits of return to summer range or migration to winter range (Nelson and Mech 1981) conflict with the Henderson *et al*. (2018) findings, for in complex ecosystems both foraging and predation risk are factors between which animals must find trade-offs that enhance their survival (Lima and Dill 1990). Within the context of these trade-offs, our study demonstrates that, in an area where wolf predation is the major natural mortality for adult deer, long deer migrations between winter and summer ranges and yarding in winter produces strong enough survival value for the behaviour to have persisted for over six decades and many generations.

Author Contributions

Writing – Original Draft: L.D.M.; Writing – Review & Editing: L.D.M. and S.B.-M.; Conceptualization: L.D.M.; Investigation: S.B.-M.; Methodology: L.D.M.; Formal Analysis: L.D.M. and S.B.-M.; Funding Acquisition: L.D.M.

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Nest site characteristics of cavity-nesting birds on a small island, in Haida Gwaii, British Columbia, Canada

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Abstract

Many studies of cavity-nesting birds in North America are conducted in large continental forests and much less is known about them in island ecosystems. We describe a 29-year study of tree species, nest site characteristics, and fledge dates of cavity-nesting birds on a small island in Haida Gwaii, British Columbia (BC). Seven cavity-nesting bird species were documented on East Limestone Island and 463 nests were found in 173 different trees. Nest trees were significantly taller and had a greater diameter than a random sample of snags. Tree height did not differ among bird species but diameter at breast height was larger for trees used by Brown Creeper (*Certhia americana*) than for other species. Cavity-nesters selected tree decay classes 2–7 (all dead/near dead [snags]), with 85% in decay class 4 (35%) or 5 (50%), similar to the random snag sample (class 4, 32%; class 5, 42%). Cavity height ranged from 2.6 to 44.9 m and for all species, except Brown Creeper, the mean nest height was >60% of the mean tree height. Nest heights were generally greater than observed elsewhere in BC. Nest cavity orientation was random except for Red-breasted Sapsuckers (*Sphyrapicus ruber*), for which only 13% of the cavity entrances faced southeast. Median fledging dates ranged from 7 June (Chestnut-backed Chickadee [*Poecile rufescens*]) to 28 June (Northern Flicker [*Colaptes auratus*]). Estimated median dates of clutch completion were similar for all species. Our results show that large snags provide habitat for a high diversity of cavity-nesting birds on Haida Gwaii.

Key words: Wildlife trees; cavity-nesters; excavators; nest site; timing of breeding

Introduction

Dead and dying trees are essential for creating high quality nest sites for cavity-nesting birds (Li and Martin 1991) and primary excavators (those species that normally excavate new nest sites each year) are essential to many secondary species in providing the necessary conditions for them to nest or find shelter (Aitken and Martin 2007). Many factors can contribute to nest-site quality including tree height, nest height, nest-hole orientation, and the state of tree decay (McClelland and Frissell 1975; Inouye 1976). The selection of a nest tree and characteristics of nest sites are known to contribute to the reproductive success of cavity-nesters by affording protection for the breeder and their offspring from predators and improved microclimate in the nest cavity (Von Haartman 1957; Wesołowski 2002; Maziarz and Wesołowski 2013).

Cavity-nesting birds can be divided into three groups related to how they acquire their cavity: (1) primary cavity-nesters excavate their own holes in live or dead trees and typically excavate a new hole each year, (2) secondary cavity-nesters use holes excavated by other species (usually primary cavity nesters), use a naturally occurring hole and may re-use nests, and (3) weak cavity-nesters either make their own hole in a heavily decaying tree, nest in a cavity excavated by another species, or expand a naturally occurring hole. A bark nester, Brown Creeper (*Certhia americana*), has also been included in this paper, though it mainly nests under loose bark (Davis 1978).

Nest site characteristics vary among and within bird species by geographic location and forest type (Scott *et al.* 1977; Newton 1994). Characteristics of cavity-nests most often reported include nest tree species, height, diameter, state of decay (or decay class), height of the nest site above the ground, and the cardinal direction of the cavity entrance. Most studies examined these characteristics for continental forests (e.g., Carlson *et al.* 1998; Martin *et al.* 2004; Vaillancourt *et al.* 2008), usually in relation to forest management guidelines in order to maintain stand structure to support cavity-nesters (e.g., Steeger and Dulisse 2002). Few studies have examined these

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characteristics in small island ecosystems. These may differ from continental ecosystems in having fewer suitable nest sites due to the limited forest area available and/or having more pronounced edge to interior effects, thus increasing risks from predation.

The purpose of our study was to identify nest site characteristics of cavities as well as timing of breeding for all regularly-occurring cavity-nesting species on a small island in Haida Gwaii. Nest site characteristics were measured within the island's mature forest ecosystem by researchers and citizen scientists of the Laskeek Bay Conservation Society (http://www.laskeekbay.org), a local non-profit organization founded in 1990, with a well-established annual field program. We examined characteristics of nest trees selected by cavity-nesters and compared them with a random selection of available trees. We also compare the results from our island study to other ecosystems and discuss the likely selection pressures governing nest site choice in this ecosystem.

Study Area

Data were collected on East Limestone Island, Haida Gwaii, British Columbia (BC), Canada (52.90747°N, 131.613°W), a 48 ha island located in Laskeek Bay in the K'unna Gwaay heritage site/conservancy. It is adjacent to the southeast tip of Louise Island (27 200 ha) and is separated from it by only 400 m at the closest point. The island is mostly flat, or gently sloping, with the highest point of elevation being 65 m on the south ridge. Elevation gradients are most prominent along the east and west coasts where multiple coves lead to the sea via steep slopes. The northern coast of the island is the site of a large cove that encompasses most of that coast.

East Limestone Island is in the Coastal Western Hemlock Zone, wet Hypermaritime subzone, a BC biogeoclimatic category characterized by cool winters and mild, cool, wet summers with periodic dry warm spells (Banner *et al.* 2014). Strong winds are common and form an important climatic feature. Rainfall can exceed 1000 mm annually. The forest is primarily dominated by mature Sitka Spruce (*Picea sitchensis* (Bongard) Carrière), Western Hemlock (*Tsuga heterophylla* (Rafinesque) Sargent), and Western Red Cedar (*Thuja plicata* Donn ex D. Don). Red Alder (*Alnus rubra* Bongard), Pacific Crabapple (*Malus fusca* (Rafinesque) C.K. Schneider), Sitka Alder (*Alnus alnobetula* ssp. *sinuata* (Regal) Raus), and Scouler's Willow (*Salix scouleriana* Barratt ex Hooker) are present along the shoreline and in a few places within the interior forest. The understorey is sparse due to shade from the mature trees and intense browsing by the invasive Black-tailed Deer (*Odocoileus hemionus*; Stockton *et al.* 2005). Although shrubs are sparse, they occur throughout the island and include *Vaccinium* species (Red Huckleberry [*Vaccinium parvifolium* Smith], Oval-leaved Blueberry [*Vaccinium ovalifolium* Smith]), Salal (*Gaultheria shallon* Pursh), and Red Elderberry (*Sambucus racemosa* L.).

The forest has not been commercially logged and most trees have been estimated to be more than 100 years old (K.M. pers. obs.). Like most temperate coastal old-growth systems, wind is a major factor for disturbance on the island, with windthrow the most common reason for gap creation and tree mortality (Pojar and MacKinnon 1994), in part due to shallow soils and high edge-interior effects. In 2010, a major windstorm hit Laskeek Bay and ~50% of the forest on East Limestone Island was blown down, resulting in high mortality for mature Western Hemlock and Sitka Spruce.

Methods

Nest location and monitoring

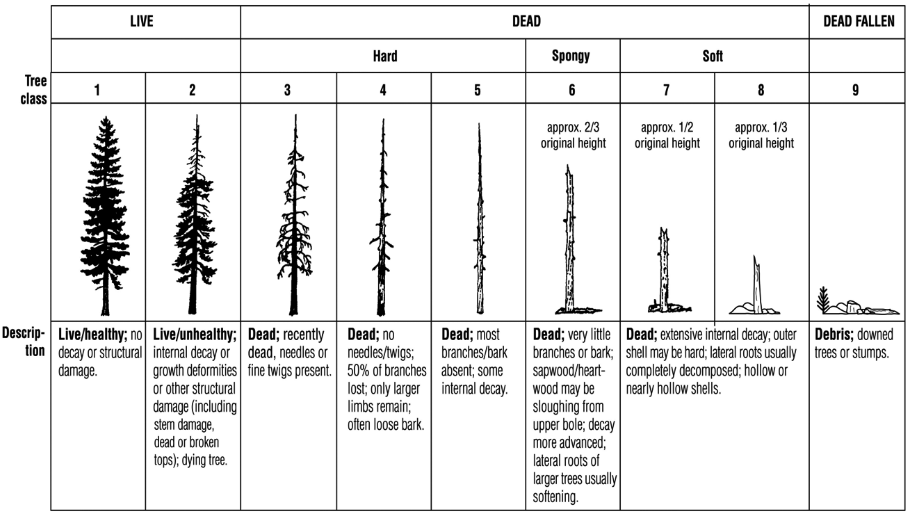
Between 1991 and 2018, staff and volunteers of the Laskeek Bay Conservation Society searched for and recorded cavity-nests on East Limestone Island. Observations were made of the tree characteristics, the nest cavities, and the species that occupied them. This comprised the "wildlife tree monitoring program", a citizen science effort involving numerous staff and volunteers each year from 1990 to 2018. Observations were made throughout May and June in all years and up to 9 July in all but five years (1990–1992, 2002, 2003, and 2011). From the beginning of the monitoring program, trees containing active nests were tagged with unique numbers and mapped. In 1990, observations were incidental to other work. The next year a systematic methodology to detect occupied breeding sites was designed and occurred annually using a written protocol. From 1991 to 1995, nests were located by listening for begging chicks during the nestling period. From 1996 onwards, all trees used at least once during the previous five years were included in that year's sample of nest trees and observed three times for 30 min in late April or May during the nest building, egg laying, and incubation phases of breeding. The observations were made, generally, within a few days of each other by one or two observers with binoculars situated at least 15 m from the nest tree. If no activity was observed after these three visits the tree was considered inactive for that season. If activity was observed, the tree was considered active and checked for 30 min every three days during June for evidence of breeding activity (e.g., adults feeding nestlings or chicks calling). Once chicks were heard calling, nests were checked every two days for 30 min (weather permitting) to determine when chick calling ceased, assumed to be a sign that the nestlings had fledged. Up to three times per season (late-May to mid-July) a survey of the entire 45 ha island was conducted to locate any new nest sites; the island was divided into four quadrants and four to six observers would spend several hours moving slowly throughout them, watching and listening for cavity nesting birds. Once active nests were confirmed and chicks were being fed, all the remaining wildlife trees that had been surveyed earlier in the season were visited again and monitored for 10 min to confirm vacancy—ensuring that no active nests had been missed. This protocol was thought to have a very high chance of success for the primary cavity nesters, as all have young that call loudly from the nest site and in every year, four to six observers were present on the island throughout the nesting season. However, our inventory was not likely to be complete for the other species, especially Brown Creeper, which has rather quiet young. All new nest trees were numbered, added to the monitored nest inventory, nest site characteristics measured and recorded, and location mapped. At the end of each season, any nest tree that had been inactive for five seasons was removed from the "active" inventory.

Fledging date was assigned to the average of the last date when chicks were seen or heard and the first date with no sound or visuals. Sightings of fledglings out of the nest were also used as an indication of fledging date. For species with 10 or more records of active nest sites on the island, the dates of the onset of incubation were estimated by taking the estimated date of fledging from the field surveys and subtracting incubation and fledging periods provided by the relevant species accounts in the Birds of North America (https://birdsna.org/Species-Account/bna/). Durations of incubation and fledging periods applied are given in Appendix 1.

Multiple characteristics were noted for each active nest tree: bird species, tree species, total tree height (m), percent cover bark (main stem), tree classification (including number of bracket fungi; see Guy and Manning 1995), nest cavity entrance height, tree diameter at breast height (dbh), and nest cavity orientation. These characteristics were recorded when a hole was first discovered and subsequently if any changes occurred (e.g., tree height). In this paper, we use the BC Tree Classification System (Guy and Manning 1995) to determine the current level of decay of each tree when first used. The BC Tree Classification System has nine categories, ranging from 1—live/healthy to 9—debris (Figure 1). The term snag refers to a standing dead or dying tree. British Columbia's Tree Classification class 2 is live/unhealthy and, in this paper, will be referred to as a snag. All the characteristics listed in BC Tree Classification System (Figure 1) were used to determine what decay class a snag was considered to be. If characteristics of different decay classes were found in one snag, the snag was classified according to the maximum number of characteristics.

Random sample of available nest trees

In July 2004, an island-wide survey was carried out to obtain a random sample of all possible trees available for cavity-nesters in decay class 2 or higher. We selected random trees at 50 m intervals along the two main trails on the island. At each interval, we took a 90° bearing, perpendicular to the trail, and



	LIVE		DEAD						DEAD FALLEN
			Hard			Spongy	Soft		
Tree class	1	2	3	4	5	6	7	8	9
						approx. 2/3 original height	approx. 1/2 original height	approx. 1/3 original height	
Description	**Live/healthy;** no decay or structural damage.	**Live/unhealthy;** internal decay or growth deformities or other structural damage (including stem damage, dead or broken tops); dying tree.	**Dead;** recently dead, needles or fine twigs present.	**Dead;** no needles/twigs; 50% of branches lost; only larger limbs remain; often loose bark.	**Dead;** most branches/bark absent; some internal decay.	**Dead;** very little branches or bark; sapwood/heartwood may be sloughing from upper bole; decay more advanced; lateral roots of larger trees usually softening.	**Dead;** extensive internal decay; outer shell may be hard; lateral roots usually completely decomposed; hollow or nearly hollow shells.		**Debris;** downed trees or stumps.

Figure 1. British Columbia's Tree Classification System (Guy and Manning 1995).

laid out a 20 m transect, measuring all dead/near dead (decay class 2–8) trees that fell within ~5 m of either side of the transect. The same characteristics were recorded for these trees that were recorded for the occupied nest trees.

Statistical analysis

Five cavity-nesting species for which sample sizes were more than five were used in statistical comparisons: Red-breasted Sapsucker *(Sphyrapicus ruber)*, Hairy Woodpecker (*Dryobates villosus*), Northern Flicker (*Colaptes auratus*), Chestnut-backed Chickadee (*Poecile rufescens*), and Brown Creeper. The first three species are primary cavity-nesters and the fourth and fifth are, respectively, a weak excavator and a bark nester. For the analysis of tree characteristics used by cavity-nesters—tree height, tree species, dbh, and state of decay—we used the characteristics as described the first time that a tree was found in use by each bird species, regardless of how many years a nest tree was active. When analyzing individual nest height and orientation, all nests across all years were analyzed.

Most statistical analysis were conducted using PAST3 (Hammer *et al.* 2001) for Mac OSX: analysis of variance (ANOVA) with Tukey's pairwise tests were used to compare tree height, nest height, and dbh among the cavity-nesting species. A two-sample *t*-test was used to compare the trees used by cavity-nesting species to a random sample of trees of similar decay class for tree height and nest height. Statistical program R version 3.4.3 (R Core Team 2017) was used to conduct a Rayleigh test of uniformity to compare nest hole orientations among species. Means are given ± 1 SD. Some data were not recorded for some nests, so that sample sizes are not the same for all analyses.

Results

During our study, the island supported seven cavity nesting birds: three primary cavity nesters: Red-breasted Sapsucker, Hairy Woodpecker, and Northern Flicker; two weak excavators: Chestnut-backed Chickadee and Red-breasted Nuthatch (*Sitta canadensis*); a bark nester: Brown Creeper; and a secondary cavity nester: Northern Saw-whet Owl (*Aegolius acadicus*). A total of 463 nests were found in 173 different trees: Red-breasted Sapsucker (*n* = 344), Hairy Woodpecker (33), Northern Flicker (9), Chestnut-backed Chickadee (47), Red-breasted Nuthatch (9), Brown Creeper (19); and Northern Saw-whet Owl (2). The main excavator on the island was overwhelmingly Red-breasted Sapsucker, which occupied 74% of the cavity nests found.

Tree characteristics

We located and tagged 173 trees used by cavity-nesting birds between 1990 and 2018 (Table 1). Most of the cavity-bearing trees were Sitka Spruce (60%) or Western Hemlock (32%) with a small percentage of Red Alder (3%) and Western Red Cedar (1%), and a few of unknown identity, either because the species were missing in data records or the decay class did not allow species determination (4%; Table 2).

Table 1. Mean, SD, minimum and maximum tree heights, and tree diameters of bark nesting (Brown Creeper [*Certhia americana*]) and cavity-nesting birds and random sample of snags on East Limestone Island, Haida Gwaii, from 1990 to 2018.

	n	Tree height (m)			Tree diameter (dbh; cm)		
		Mean	SD	Range	Mean	SD	Range
Red-breasted Sapsucker (*Sphyrapicus ruber*)	130	22.7	10.4	7.2–52.8	104	40	40–260
Hairy Woodpecker (*Dryobates villosus*)	27	20.7	9.7	3.8–40.8	93	32	50–200
Northern Flicker (*Colaptes auratus*)	8	19.7	6.0	14.1–32.8	93	41	46–170
Chestnut-backed Chickadee (*Poecile rufescens*)	29	22.2	12.8	5.1–46.6	119	57	31–240
Red-breasted Nuthatch (*Sitta canadensis*)	5	21.5	7.5	15.4–33.9	104	32	68–154
Northern Saw-whet Owl (*Aegolius acadicus*)	2	12.6	3.6	10.0–15.1	96	49	61–130
Brown Creeper (*Certhia americana*)	16	22.4	13.7	7.2–58.5	133	54	54–260
All cavity-bearing trees*	173	21.7	11.1	3.8–58.5	104	43	31–260
Random selection of snags	100	12.6	11.1	1.3–63.3	62	46	11–229

*Total number of nest trees used throughout the study. These trees were used more than once by various bird species.

TABLE 2. Percentages of tree species used by various cavity-nesting birds on East Limestone Island, Haida Gwaii.

Species	Sitka Spruce (*Picea sitchensis*)	Western Hemlock (*Tsuga heterophylla*)	Red Alder (*Alnus rubra*)	Western Red Cedar (*Thuja plicata*)	Unknown
Red-breasted Sapsucker (*n* = 130) (*Sphyrapicus ruber*)	56.9	36.9	1.5	0.0	4.6
Hairy Woodpecker (*n* = 26) (*Dryobates villosus*)	65.4	34.6	0.0	0.0	3.9
Northern Flicker (*n* = 8) (*Colaptes auratus*)	75.0	12.5	12.5	0.0	0.0
Chestnut-backed Chickadee (*n* = 29) (*Poecile rufescens*)	79.3	17.2	3.5	0.0	0.0
Red-breasted Nuthatch (*n* = 5) (*Sitta canadensis*)	60.0	40.0	0.0	0.0	0.0
Brown Creeper (*n* = 16) (*Certhia americana*)	75.0	18.8	0.0	6.3	
Northern Saw-whet Owl (*n* = 2) (*Aegolius acadicus*)	100.0	0.0	0.0	0.0	0.0
All cavity-bearing trees (*n* = 173)	59.5	31.8	2.9	1.2	4.6
Random selection of snags (*n* = 100)	64.0	31.0	4.0	1.0	0.0

The percentage distribution of cavity trees was similar to the distribution of a random selection of snags throughout the island (Sitka Spruce = 64%, Western Hemlock = 31%, Red Alder = 4%, Western Red Cedar = 1%). Among cavity-nesting species with five or more active nest trees, use of Sitka Spruce ranged from 57 to 79%, Western Hemlock from 13 to 40%, Red Alder from 2 to 13%, and Western Red Cedar from 1 to 6%. There was no evidence of inter-species differences in nesting tree preference (Table 2).

The nest trees of Red-breasted Sapsucker, Hairy Woodpecker, Chestnut-backed Chickadee, and Brown Creeper were significantly taller and larger in diameter than a random sample of snags on the island (Table 3); Northern Flicker nest trees were taller but not significantly larger in diameter. Nest tree height did not differ significantly among the bird species (ANOVA $F_{4,206} = 0.27$, $P = 0.93$), but diameter was significantly different among species ($F_{4,204} = 2.44$, $P = 0.04$), with Brown Creeper using trees with significantly larger diameter than Hairy Woodpecker (Tukey's pairwise: $P < 0.05$). Height and diameter were positively correlated for both the active and the randomly selected snags (active: $r^2_{166} = 0.37$, $P < 0.001$; random $r^2_{98} = 0.31$, $P < 0.01$).

Cavity-nesters used trees in decay classes 2 through 7 and showed a strong preference for decay classes 4 and 5 (Table 4, Figure 2); 50% of all active nest trees were in snags of decay class 5 and 35% were class 4. Trees in classes 4 (32%) and 5 (42%) were also the most common in the randomly selected snag sample, but the proportion of snags in decay class 2 and 3

TABLE 3. Analyses comparing mean tree heights and diameters of nest trees to a random sample of snags (*n* = 100), East Limestone Island, Haida Gwaii.

	n	Tree height (m)		Tree diameter (dbh; cm)		Effect size
		t	*P*	*t*	*P*	*d**
Red-breasted Sapsucker (*Sphyrapicus ruber*)	126	7.0	< 0.01	7.1	< 0.01	2.94
Hairy Woodpecker (*Dryobates villosus*)	27	3.4	< 0.01	3.2	< 0.01	2.88
Northern Flicker (*Colaptes auratus*)	8	2.9	0.01	1.8	0.07	4.41
Chestnut-backed Chickadee (*Poecile rufescens*)	29	3.9	< 0.01	5.4	< 0.01	2.32
Brown Creeper (*Certhia americana*)	16	3.1	< 0.01	5.5	< 0.01	2.17

*Cohen's *d*.

TABLE 4. Decay classes of nest trees used by cavity-nesting birds and a random sample of snags on East Limestone Island, Haida Gwaii.

Species	*n*	Decay class		
		Mean	SD	Range
Red-breasted Sapsucker (*Sphyrapicus ruber*)	124	4.6	0.7	2–6
Hairy Woodpecker (*Dryobates villosus*)	26	4.8	0.9	2–6
Northern Flicker (*Colaptes auratus*)	8	5.0	0.5	4–6
Chestnut-backed Chickadee (*Poecile rufescens*)	27	4.7	0.7	3–6
Red-breasted Nuthatch (*Sitta canadensis*)	5	5.0	0.7	4–6
Brown Creeper (*Certhia americana*)	14	4.9	1.2	2–7
Northern Saw-whet Owl (*Aegolius acadicus*)	2	4.5	0.7	4–5
All cavity-bearing trees	163	4.7	0.8	2–7
Random selection of snags	100	4.5	0.9	3–7

in the random sample significantly exceeded the proportion among used trees (14% versus 3%, respectively; contingency test, $\chi^2_2 = 14.8$, $P < 0.001$). Hence, it appears that primary cavity excavators preferred trees in a more advanced state of decay than those in the random sample.

Cavity characteristics

Nest cavity heights ranged from 2.6 to 44.9 m from the base of the tree (Table 5). The Northern Flicker and Chestnut-backed Chickadee nests were, on average, the highest of the cavity-nesting species at 19.0 and 18.0 m, respectively. The lowest nests were the Northern Saw-whet Owl, but only two nests were found during the study period. For all but Brown Creeper, the mean nest height was more than 60% of the mean tree height (Table 5); Brown Creeper mean nest height of 9.0 ± 4.2 m was significantly lower than those of Red-breasted Sapsuckers, Hairy Woodpeckers, Northern Flickers, and Chestnut-backed Chickadees (Table 5).

Entrance orientation was not statistically significant for most species ($P > 0.05$; Table 6) with the exception of Red-breasted Sapsucker, for which fewer cavity openings than expected faced southeast (91°–180°; 13% of nests, $P = 0.01$); however, sample sizes for other species were much smaller.

Timing of breeding

Breeding of cavity-nesting species ranged from 21 May to 9 July (Figure 3). For Red-breasted Sapsuckers, the most common cavity-nesting species on East Limestone Island, the annual median fledging dates spanned a 16-day period from 10 June. Chestnut-backed Chickadees were usually the first to fledge, with a median date of 7 June (Table 7). Northern Flicker had the latest median fledging

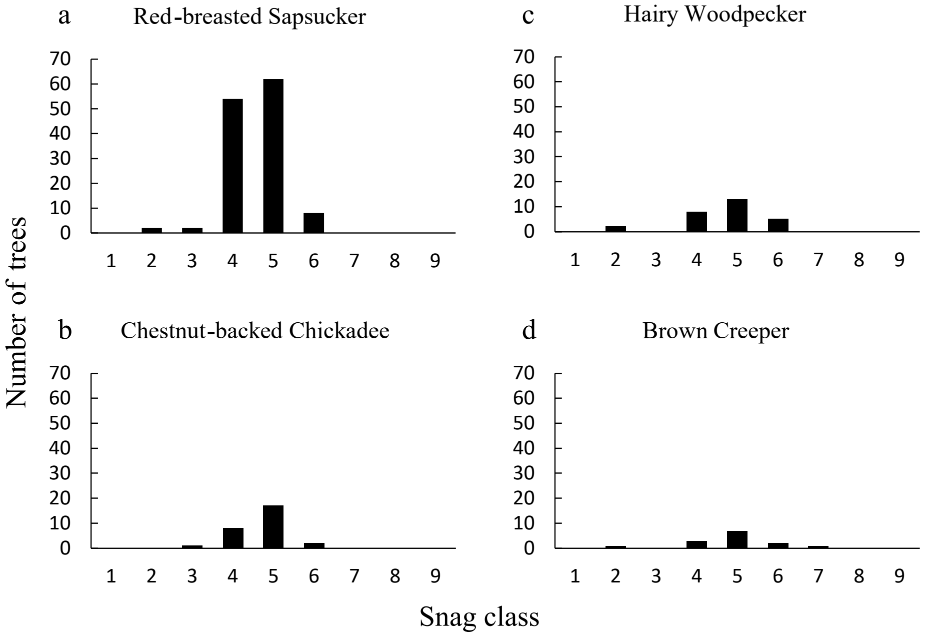


FIGURE 2. Distribution of snag classes used by different species of cavity-nesters on East Limestone Island, British Columbia, Canada (only species with $n > 10$).

TABLE 5. Nest heights of cavity-nesting species on East Limestone Islands, Haida Gwaii compared to provincial data (Campbell *et al.* 1990, 1997).

Species	*n*	Nest height (m)			% Tree height	Birds of BC
		Mean	SD	Range		Min–max (>50% range)[‡]
Red-breasted Sapsucker (*Sphyrapicus ruber*)	191	17.3[*]	7.7	3.8–44.9	76.2	1.8–24 (3–9)
Hairy Woodpecker (*Dryobates villosus*)	26	16.8[*]	8.2	5.4–32.8	81.2	0.9–38 (2–6)
Northern Flicker (*Colaptes auratus*)	7	19.0[*]	6.2	13.0–31.8	96.4	0–27 (<3)
Chestnut-backed Chickadee (*Poecile rufescens*)	26	18.0[*]	11.3	2.6–41.3	81.1	0–26 (2–6)
Red-breasted Nuthatch (*Sitta canadensis*)	5	13.4	0.8	12.7–14.5	62.3	0.5–20 (3–6)
Northern Saw-whet Owl (*Aegolius acadicus*)	2	9.3	0.4	9.0–9.6	73.8	2.5–13.5
Brown Creeper (*Certhia americana*)	12	9.0[†]	4.2	4.0–16.0	40.2	0.2–15 (2–6)

[*] Differs significantly from † at $P < 0.05$, Duncan Multiple Range Test.
[‡] Range within which greater than 50% of nests occurred.

TABLE 6. Number of cavity entrances facing northeast (NE; 1°–90°), southeast (SE; 91°–180°), southwest (SW; 181°–270°), and northwest (NW; 271°–0°) for four cavity-nesting species and *P*-values from a Rayleigh's test for uniformity for their nest cavity entrance orientation ($P < 0.05$ for a Rayleigh's test indicates clustering).

Species	NE	SE	SW	NW	*P*
Red-breasted Sapsucker (*Sphyrapicus ruber*)	70	30	55	64	0.0077
Hairy Woodpecker (*Dryobates villosus*)	6	3	4	3	0.5854
Chestnut-backed Chickadee (*Poecile rufescens*)	2	1	4	2	0.5721
Brown Creeper (*Certhia americana*)	2	3	4	1	0.7109

date of 28 June. Median dates for the start of incubation were estimated to fall between 6–9 May for the four species with the largest sample sizes (Table 7). No evidence of second broods was found for any species, but four fledging dates for Chestnut-backed Chickadees fell after 21 June, two weeks after the long-term median in early June suggesting that some chickadees either laid very late or replaced earlier failed broods.

Discussion

Tree species

On East Limestone Island, cavity-nesting species primarily used spruce and hemlock trees for nesting and these were used in proportion to the available snags on the island; very few nests were in Red Alder and only Brown Creeper was found in Western Red Cedar. This was not surprising as most alders on the island were young, small diameter trees that were not very tall or in a state of decay. In other parts of BC, deciduous trees are used by cavity-nesters, for example, Martin and Eadie (1999) and Martin *et al.* (2004) found 95% of cavities in the Cariboo-Chilcotin region of central interior BC were in Trembling Aspen (*Populus tremuloides* Michaux). The majority of these were created by Red-naped Sapsucker (*Sphyrapicus nuchalis*), Hairy Woodpecker, and Northern Flicker—a very similar primary excavator community to that on East Limestone Island.

Tree height and cavity height

Of the cavity-nesters with more than five active nest trees during the study period, the mean heights of nest trees were significantly higher than a random selection of snags, strongly suggesting that height is an important factor for the location of nest cavities on this island. In addition, all bird species except Brown Creeper created or used nest cavities in the top half of the tree. Nests were also generally much higher

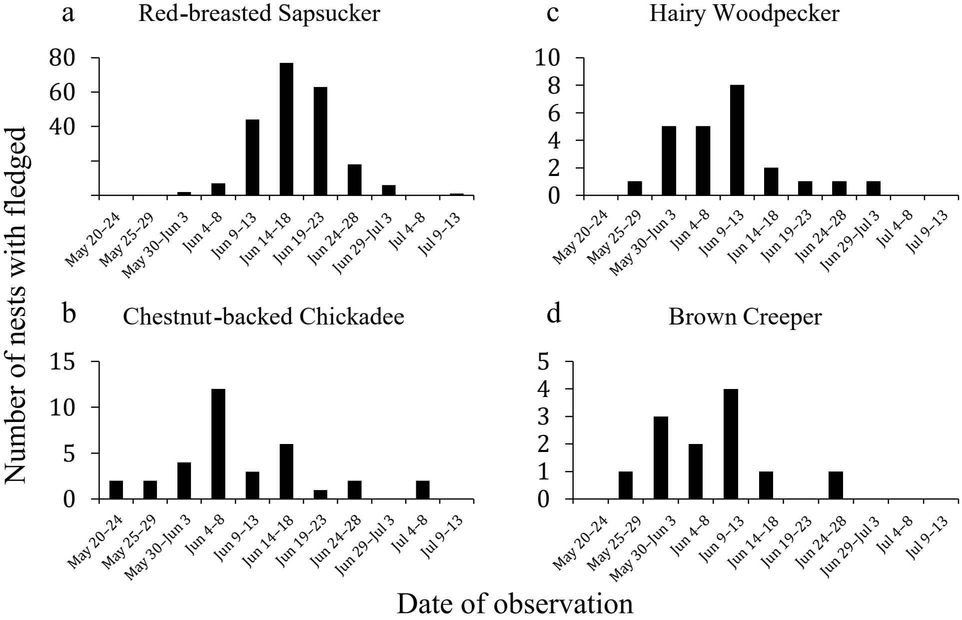


FIGURE 3. Observed fledging dates for cavity-nesting species on East Limestone Island, Haida Gwaii, British Columbia, Canada (1990–2018).

TABLE 7. Estimated median incubation and median and extreme fledging dates for cavity-nesters on East Limestone Island, Haida Gwaii, 1990–2018.

Species	*n*	Estimated median start of incubation	Median date of chick fledging	Earliest fledging date	Latest fledging date
Red-breasted Sapsucker (*Sphyrapicus ruber*)	219	7 May	17 Jun	1 Jun	13 Jul
Hairy Woodpecker (*Dryobates villosus*)	24	6 May	10 Jun	29 May	30 Jun
Northern Flicker (*Colaptes auratus*)	5	—	28 Jun	3 Jun	5 Jul
Chestnut-backed Chickadee (*Poecile rufescens*)	34	6 May	7 Jun	21 May	1 Jul
Red-breasted Nuthatch (*Sitta canadensis*)	3	—	12 Jun	31 May	16 Jun
Brown Creeper (*Certhia americana*)	10	9 May	10 Jun	28 May	28 Jun

than those reported as 'typical' (>50% of nests) by Campbell *et al.* (1990, 1997), with mean nest heights on East Limestone Island more than twice the maximum of the typical range elsewhere for all species except Red-breasted Sapsucker and Brown Creeper.

The high nest sites on East Limestone Island could be a function of predation risk, with higher nests having lower risk (Kilham 1971; Nilsson 1984). The main potential nest predator of cavity-nesting birds was Red Squirrel (*Tamiasciurus hudsonicus*), while adults might have been susceptible to predation by Red-tailed Hawk (*Buteo jamaicensis*) and Sharp-shinned Hawk (*Accipiter striatus*), both of which occur on the island. Red Squirrel was introduced to Haida Gwaii in 1950 (Golumbia *et al.* 2008) and recorded on East Limestone Island by 1983. The species is an active predator on songbird nests in the area (Martin and Joron 2003). It was the only potential predator seen entering nest cavities on East Limestone Island (A.J.G. pers. obs.). The density of squirrels on the island fluctuates significantly among years (Martin *et al.* 2008) and is high in comparison with nearby larger islands that have other mammalian predators (e.g., Pine Marten [*Martes americana*], Black Bear [*Ursus americanus*]). One possible explanation for nest heights is that squirrels avoid tall trees denuded of leaves and branches to avoid avian predators, such as Red-tailed Hawk (visitors to East Limestone Island), or the resident Common Raven (*Corvus corax*). Furthermore, a nest near the top of a snag could result in less rainwater running into the cavity hole, compared with a cavity further down the tree (Conner 1975).

Brown Creeper nests lower than other species and build cryptic nests behind bark or rotten wood. Unlike other cavity-nesters, Brown Creeper nestlings do not call loudly from the nest when the parents are absent. Brown Creeper may depend on these cryptic habits to avoid detection and minimize predation. As a predator of small mammals and birds (Rasmussen *et al.* 2008), Northern Saw-whet Owl may be sufficiently intimidating to deter squirrels from entering their nests, which might explain why both the two owl nests found were much lower (9.0 m and 9.6 m) than the average for other species. Only three nests of the Haida Gwaii subspecies of Saw-whet Owl (*Aegolius acadicus brooksii*) had been found by 2008 (Rasmussen *et al.* 2008), one of which was on East Limestone Island. Data are too limited to know whether low nest sites are characteristic of this subspecies. However, elsewhere in BC the species uses holes at similar heights to those found on East Limestone Island (Campbell *et al.* 1990).

Tree diameter

Red-breasted Sapsucker, Hairy Woodpecker, Chestnut-backed Chickadee, and Brown Creeper all used trees with significantly greater mean dbh than that of randomly selected snags (Table 3), a finding also made by Martin *et al.* (2004) in interior BC and by Raphael and White (1984) in the Sierra Nevada. Brown Creeper selected significantly larger tree diameters than those used by Hairy Woodpecker. Height and dbh are correlated so we cannot distinguish which has the greater influence of nest site choice. While height may confer protection from predation and better drainage, greater girth may allow for deeper nests or better thermal protection (O'Connor 1978; Van Balen 1984). In addition, a larger cavity size could increase space for nestlings, reducing competition among them when being fed (Slagsvold 1989).

As a bark nesting species, Brown Creeper (Davis 1978) has different selection criteria from the other species. It tends to select trees with large sections of loose bark to nest underneath, perhaps more frequently available on larger diameter trees. The species also prefers large diameter trees for foraging (Poulin *et al.* 2008) and choosing their nest site close to their food source could be advantageous.

Decay

Trees used for cavities on East Limestone Island were mostly in an advanced state of decay, with mean decay classes ranging from 4.5–5.0 (Figure 2). These trees would have decayed heartwood with relatively hard sapwood. Such trees may be more suitable as nest trees due to the decayed heartwood being soft enough for easy excavation, with an outer shell of relatively strong sapwood surrounding and protecting the nest cavity (Kilham 1971; Conner *et al.* 1976; Miller and Miller 1980). It is worth noting that the value of differing decay states of different species of trees is not adequately represented by the BC Tree Classification System (*cf.*, Guy and Manning 1995). Trees may have a similar appearance but be harder or softer depending on their location. The location could be subject to different, perhaps stronger winds, or different climatic conditions, all of which would give the tree a different appearance, hence a different decay class.

Cavity orientation

Orientation was measured to understand nest site selection relative to microclimate. The orientation of Red-breasted Sapsucker cavity entrances was not random, perhaps because they attempt to regulate nest microclimate by orienting their nest entrances away from the prevalent southeast winds, which bring the heaviest rainfall to the island. In addition, the topography of the island allows for winds from this direction to be funneled into the interior of the island, strengthening its effect and perhaps strengthening the effect of cavity orientation. The apparent lack of preferred cavity orientation among other species may be a result of small sample size. Additional research is needed for Saw-whet Owl, as well as Northern Flicker and Red-breasted Nuthatch to shed further light on the nest site preferences of these species.

Timing of breeding

All of our nesting dates fell within the ranges indicated by Campbell *et al.* (1990, 1997) for individual species. However, Campbell *et al.* (1990, 1997) indicated a longer season (early May to end of July) for all species found on East Limestone Island. It appears that breeding on East Limestone Island varies little among species, with all initiating incubation in the first half of May, and most nesting completed by the end of June. One exception was the case of Red-breasted Sapsucker in 1999, when median fledging was six days later than in the next latest year. Breeding of open nesting species was later and less successful in 1999 because of low temperatures associated with a strong La Niña event (Gaston *et al.* 2005) and this may also have caused the late breeding of the sapsuckers.

Conclusion

This 29-year study has provided insights into the significant characteristics of nest sites created or used by cavity-nesting birds on a small island in Haida Gwaii. The results of this work suggest that a rich diversity and healthy populations of cavity-nesting species can be supported on small islands with intact mature forests. The predominance of Red-breasted Sapsucker, a primary excavator, over other hole-nesting species, suggests that suitable holes are probably abundant for secondary species, such as chickadees and nuthatches, both of which used old sapsucker holes on occasion. On the mainland, cavity nests are found in a greater variety of trees, often in live deciduous trees at much lower heights. In future, when surveys are conducted on small islands it is important that attention is paid to the upper parts of large snags to ensure that cavity nests are not overlooked. Our results support the proposal that the protection of large old snags within northwest coastal forest ecosystems is essential to providing a healthy community of cavity-nesting birds (Cockle *et al.* 2011).

Author Contributions

Writing – Conceptualization & Field Work Design: A.G., K.M., J.S.; Field Work Oversight: K.M., J.S., N.P.; Data Analysis & Original Draft: N.P. & A.G.; Writing – Review & Editing: all authors.

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APPENDIX 1. Incubation and fledging periods used in estimating dates of clutch completion for species with 10 or more records.

Species	Incubation period (days)	Fledging period (days)	Reference
Hairy Woodpecker (*Dryobates villosus*)	13	29	Jackson *et al.* 2018
Red-breasted Sapsucker *(Sphyrapicus ruber)*	14	27	Walters *et al.* 2014
Chestnut-backed Chickadee (*Poecile rufescens*)	13	20	Dahlsten *et al*. 2002
Brown Creeper (*Certhia americana*)	15	17	Poulin *et al.* 2013

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The Canadian Field-Naturalist

Rooting depth and below ground biomass in a freshwater coastal marsh invaded by European Reed (*Phragmites australis*) compared with remnant uninvaded sites at Long Point, Ontario

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Abstract

Invasive European Reed (*Phragmites australis* subsp. *australis*) outcompetes native vegetation, reducing floristic diversity and habitat value for wildlife. Research in coastal salt marshes has indicated that *P. australis* invasion may be facilitated by its relatively deep rooting depth, but in freshwater marshes the growth pattern of below ground tissues in relation to water depth is uncertain. To determine if *P. australis* is rooting more deeply than resident wetland plant species in a freshwater coastal marsh on Lake Erie, Ontario, we measured the vertical distribution of below ground biomass in *P. australis* invaded marsh sites and compared it to the below ground biomass distribution in nearby sites not yet invaded by *P. australis*. These invaded and uninvaded sites were paired by water depth, which is known to influence resource allocation and rooting depth. Below ground biomass in invaded sites was greater than in uninvaded sites ($t_{28} = 3.528$, $P = 0.001$), but rooting depth (i.e., the depth at which 90% of total below ground biomass is accounted for) was comparable ($t_{28} = 0.992$, $P = 0.330$). Using water depth and site type, general linear models could predict below ground biomass ($F_{2,55} = 9.115$, $P < 0.001$) but not rooting depth ($F_{2,55} = 1.175$, $P = 0.316$). Rooting depth is likely affected by other factors such as substrate type and the depth of the organic soil horizon.

Key words: Below ground biomass; coastal marsh; Common Reed; ecosystem effects; invasive species; Lake Erie; rhizomes; roots; wetland

Introduction

European Reed (*Phragmites australis* (Cavanilles) Trinius *ex* Steudel subsp. *australis*) is considered highly invasive in North America (Saltonstall 2002) and has profound negative effects on both coastal and inland wetlands and shores. Researchers have reported that *P. australis* replaces native vegetation (Able *et al.* 2003; Tulbure and Johnston 2010), lowers plant biodiversity (Keller 2000), and disrupts wetland integrity and ecological function (Windham and Ehrenfeld 2003; Rothman and Bouchard 2007; Tulbure and Johnston 2010; Duke *et al.* 2015). *Phragmites australis* invasion may also lead to sediment accretion, terrain flattening, and a reduction in water-filled depressions due to the accumulation of leaf litter and rhizome biomass (Able *et al.* 2003). These invasion-driven changes in wetland habitat have consequences such as the loss of toad breeding habitat (Greenberg and Green 2013), reduced abundance of at-risk birds (Robichaud and Rooney 2017), and fewer suitable nesting areas and poor microhabitats for turtle eggs (Bolton and Brooks 2010; Cook 2016). Consequently, *P. australis* was named the worst invasive plant species in Canada (Catling and Mitrow 2005, 2011).

In the Great Lakes region, *P. australis* has replaced thousands of hectares of freshwater coastal wetlands. Around Lake Erie alone, invasion estimates range from 2553 ha within the coastal wetlands (Carson *et al.* 2018) to 8233 ha within a 10 km buffer around the American portion of Lake Erie (Bourgeau-Chavez *et al.* 2013). At Long Point on Lake Erie, *P. australis* invasion is predicted to continue expanding rapidly until 2022 (Jung *et al.* 2017), and the wetland communities most commonly replaced are cattail, meadow marsh, sedge and grass hummocks, and other mixed emergent communities (Wilcox *et al.* 2003).

The invasion success of *P. australis* is due to advantageous morphological features and its ability to modify its environment. For example, *P. australis* stems can grow up to five metres tall, intercepting light and shading competitors (Hirtreiter and Potts

2012). With its large seed heads, *P. australis* can produce hundreds of wind-dispersed seeds (Tulbure and Johnston 2010), which is an important strategy for creating new individuals (Albert *et al.* 2015). However, local expansion mainly occurs by vegetative growth (Albert *et al.* 2015), using stolon fragments and rhizomes (Mal and Narine 2004; Tulbure and Johnston 2010). Rhizomes are also important storage organs that enable *P. australis* to send up spring ramets in advance of resident species and to manage nitrogen limitation (Granéli *et al.* 1992).

Below ground, *P. australis* engineers its habitat to optimize its competitive advantage over native species (Minchinton *et al.* 2006). For example, a study on *P. australis* roots reported that hypodermal layers around roots and rhizomes protect against toxic organic compounds and anoxia (Armstrong and Armstrong 1988). Aerenchyma channels, which send atmospheric oxygen from emergent plant tissues to plant parts in anoxic soils, also allow *P. australis* to sustain deep rooting depths (Armstrong and Armstrong 1988). For example, studies from a marine coastal marsh gave estimates of *P. australis* roots growing from <1–4 m deep (Moore *et al.* 2012; Packer *et al.* 2017).

The deep rooting of *P. australis* may be an important strategy for invasion; species with deeper rooting depths are able to access nutrients and minerals lower in the soil profile compared to species with shallow rooting depths (Jobbágy and Jackson 2004). For example, in a New Hampshire study, *P. australis* had deeper rooting depths in more physically stressful environments that allowed it to access deeper, less saline groundwater and more available nutrients (Moore *et al.* 2012). Despite the competitive advantage that deep rooting may provide to *P. australis* in salt marshes (Moore *et al.* 2012), we are not aware of other studies quantifying its rooting depth in freshwater coastal marshes.

Other than the influence of salinity (Moore *et al.* 2012), variation in *P. australis* rooting depth may be due to differences in water depth, the frequency of water depth fluctuation, and substrate type, which may all influence redox conditions and oxygen availability. For example, in a greenhouse experiment, Hanslin *et al.* (2017) reported that increased amplitude of water level fluctuations resulted in increased *P. australis* rooting depths but decreased below ground biomass in the top soil regions. This finding has yet to be corroborated by studies of natural systems.

To the best of our knowledge, there are no studies in the Great Lakes region that quantify the vertical distribution and biomass of *P. australis* below ground tissues compared to resident vegetation, particularly not across a gradient in water depth. Differences in rooting depth between invasive *P. australis* and resident plant communities in these freshwater wetlands may help explain the success of *P. australis* invasion. Importantly, such differences may also have implications for the ecological effects of invasion. For example, deeper rooting could expand the penetration of oxygen into saturated wetland soils (Faußer *et al.* 2016), mobilizing carbon pools and metals that were otherwise inactive (e.g., Jacob and Otte 2003). We sought to determine if freshwater coastal marsh communities dominated by invasive *P. australis* have greater below ground biomass or deeper rooting depths compared with resident uninvaded marsh. We predicted that more below ground biomass would be produced by *P. australis* than resident plant communities because *P. australis* is so productive (Rothman and Bouchard 2007). Also, because *P. australis* has deeper rooting depths than native vegetation in marine coastal marshes (Moore *et al.* 2012), we predicted that the same trend would be true in freshwater. In addition, because water depth may affect rooting depth (Hanslin *et al.* 2017), we also tested the prediction that below ground biomass and rooting depth of *P. australis*-dominated communities would be positively correlated with water depth across a naturally occurring gradient and compared this with resident vegetation communities.

Methods

Site selection

Our study was situated at Long Point, Canada (42.581°N, 80.381°W), a sand spit that sustains over 70% of the remaining intact coastal marsh on the north shore of Lake Erie (Ball *et al.* 2003). The 40 600 ha area is a designated World Biosphere Reserve by the United Nations Educational, Scientific and Cultural Organization (UNESCO), and an internationally important wetland under the Ramsar Convention (Ministry of Natural Resources and Forestry 2017). This ecologically important region is threatened by continuing expansion of high-density *P. australis* (Jung *et al.* 2017).

Sample sites within Long Point were established across a range of water depths at which *P. australis* invasion is common (13.7–55.7 cm), with sites dominated by high density *P. australis* monocultures paired by water depth with sites either dominated by cattails (*Typha* spp.; >30 cm water depth) or by meadow taxa, including graminoids, sedges, and forbs (<40 cm water depth). Sites in the 30–40 cm depth range were either meadow marsh or *Typha* spp. marsh, as the two communities stratify by depth and rarely mix. Sites were dispersed across the Crown

Marsh and Long Point Provincial Park management units, spaced between 100 and 2000 m apart. This area is representative of wet meadow and emergent lacustrine marsh in Lake Erie, with substrate ranging from organic in shallower depths to pure sand in deeper locations.

Core collection

Fieldwork was conducted in May 2017. Using a 2.54 cm diameter soil gouge auger, soil cores (0.3–0.75 m deep) were sampled from sites invaded by *P. australis* and paired uninvaded marsh sites. It was not possible to obtain cores of uniform length due to differences in the thickness of the organic horizon and difficulties penetrating the underlying sand substrate. In total 29 pairs of cores were collected. The cores were then sub-sectioned into 10 cm long segments and frozen until they could be processed. For comparison, Moore *et al.* (2012) who also examined belowground biomass trends in marsh invaded by European *P. australis*, collected 100 cm long cores from 10 tidal marshes along New Hampshire's Atlantic coast using the same diameter gouge auger and sub-sectioned them into 5 cm long segments.

Core processing

Core segments were thawed for about 24 h and then washed over two nested sieves: a coarser (1.7 mm) sieve over a finer (425 µm) sieve. All live rhizomes and all root tissues were retrieved and dried at 80°C to a constant weight (minimum 48 h). Dead roots may have been included in our weights as we did not find it possible to reliably differentiate live and dead roots. The dried below ground tissues were then weighed on a Mettler Toledo analytical balance (MS204S, Columbus, Ohio, USA) with a 0.0001 g accuracy. For comparison, Moore *et al.* (2012) picked live roots and rhizomes from trays partially filled with water and then oven dried to a constant weight at 65°C for a minimum of 48 h.

Data analysis

For the purposes of this study, rooting depth was defined as the depth (cm) at which 90% of the cumulative below ground biomass was accounted for. Below ground biomass was defined as the total root and rhizome mass per unit area (g/m^2), recognizing that the core depths varied with the thickness of the organic horizon. To test whether below ground biomass was greater in *P. australis* invaded sites compared to uninvaded sites, we used a paired-samples, one-tailed *t*-test. To test whether rooting depth was greater in *P. australis* invaded sites than uninvaded sites, we used another paired-samples, one-tailed *t*-test. Lastly, to test whether water depth is a significant predictor of below ground biomass and rooting depth, we used general linear models (GLM) with a least squares estimation framework to model variation in below ground biomass and rooting depth based on water depth, site type (*P. australis* invaded or uninvaded), and their interaction. Models are thus represented by the general form:

$$y = \beta_1 W + \beta_2 T + \beta_3 T \times W + \beta_0 + \varepsilon,$$

where W is water depth, T is site type, and ε is error. If the interaction terms were not significant, the model would be re-run to only include the main factors: water depth and site type. In all cases, we used an alpha value of 0.05 and Type III sums of squares. Analyses were completed using IBM SPSS Statistics 20.

Results

Paired-samples t*-tests for below ground biomass and rooting depth*

Phragmites australis invaded marsh had greater below ground biomass than uninvaded marsh habitat, when meadow and *Typha* spp. marsh are considered jointly (paired-samples *t*-test, $t_{28} = 3.528$, $P = 0.001$; Figure 1a). Although the difference between *Typha* spp. dominated cattail marsh and *P. australis* invaded marsh is negligible, it revealed that the difference is primarily between *P. australis* invaded and meadow marsh sites (Figure 1a).

There is no significant difference in rooting depth between *P. australis* invaded marsh and uninvaded marsh (paired-samples *t*-test, $t_{28} = 0.992$, $P = 0.330$; Figure 1b). This appears evident in both meadow marsh and cattail marsh components of the uninvaded sites (Figure 1b).

The down-core distribution of below ground biomass suggests that core depths were sufficient to capture the bulk of total below ground tissues (Figure 2). This was true for invaded (Figure 2a) and uninvaded (Figure 2b) sites, across a range of water depth intervals between 13.7 and 55.7 cm. Below ground biomass was detected to a maximum of 80 cm soil depth yet peaked within the top 30 cm of the soil profile, regardless of site type (Figure 2).

General linear models for below ground biomass and rooting depth

For below ground biomass, the interaction term was not significant (Table S1a, Figure S1), so we removed it and re-ran the GLM as

$$\textit{below ground biomass} = \beta_1 W + \beta_2 T + \beta_0 + \varepsilon.$$

This model provided a reasonable fit (adjusted $r^2 = 0.222$; GLM, $F_{2,55} = 9.115$, $P < 0.001$; details in Table S1b). Likewise, for rooting depth, the interaction term was not significant (Table S2a), so we removed it and re-ran the GLM as

$$\textit{rooting depth} = \beta_1 W + \beta_2 T + \beta_0 + \varepsilon.$$

However, this model proved to be a poor predictor

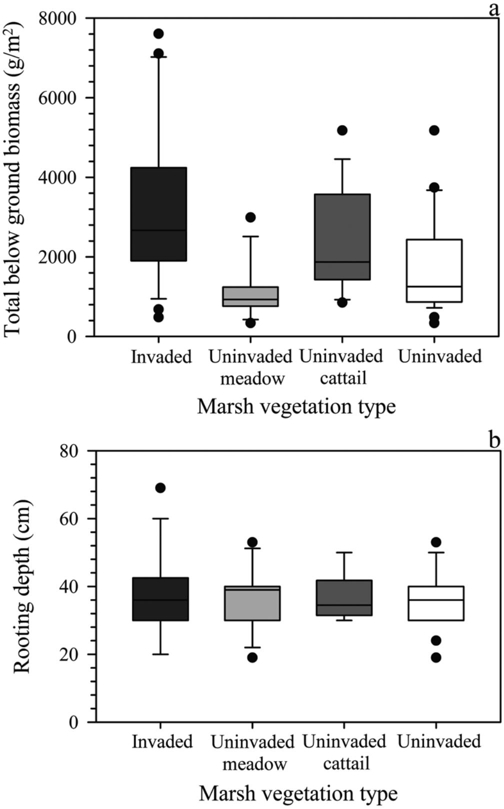

FIGURE 1. Total below ground biomass and rooting depth in European Reed (*Phragmites australis*) invaded and uninvaded marsh. Boxplots depicting a. total below ground biomass (g/m^2) and b. rooting depth (cm), contrasting *P. australis* invaded marsh (dark grey; n = 29) and uninvaded marsh (white; n = 29) sites. Note that uninvaded marsh is divided into shallower depth meadow marsh (light grey; n = 15) and deeper water cattail (*Typha* sp.) marsh (grey; n = 14) communities.

of rooting depth (adjusted $r^2 = 0.006$; GLM, $F_{2,55} = 1.175$, $P = 0.316$; details in Table S2b).

Discussion

Our research objectives were to determine if *P. australis* invaded marsh produced more below ground biomass, and deeper rooting depths than uninvaded marsh in a freshwater coastal marsh, as has been observed in marine coastal marshes (e.g., Ravit *et al.* 2006; Moore *et al.* 2012). Controlling for water depth, we observed that *P. australis* invaded marsh had more below ground biomass than uninvaded marsh, however, rooting depths did not differ significantly between *P. australis* invaded and uninvaded marsh sites. Like site type, water depth was a significant predictor of below ground biomass (g/m^2) but not of rooting depth. Interestingly, although the largest difference in below ground biomass was evident between *P. australis* invaded sites and meadow marsh sites, which were restricted to shallower water depths, we detected no significant interaction between water depth and site type when predicting either below ground biomass or rooting depth.

Greater below ground biomass may provide *P. australis* a competitive advantage allowing it to usurp soil resources (van Wijk *et al.* 2003) and facilitate dispersion by vegetative reproduction (Saltonstall 2002; Tulbure and Johnston 2010; Albert *et al.* 2015). The current literature reports below ground biomass values for *P. australis* in the range of 886 g/m^2 (Rothman and Bouchard 2007) to 1368 g/m^2 (Windham 2001); for cattail marsh in the range of 742 g/m^2 (Rothman and Bouchard 2007) to 2461 g/m^2 (Ouellet-Plamondon *et al.* 2004); and for meadow species, such as Saltmeadow Cordgrass (*Sporobolus pumilus* (Roth) P.M. Peterson & Saarela) and Bluejoint Reedgrass (*Calamagrostis canadensis* (Michaux) Palisot de Beauvois), in the range of 256 g/m^2 (Ouellet-Plamondon *et al.* 2004) to 757 g/m^2 (Windham 2001). Our measures of below ground biomass show the same pattern in relative magnitude among the three communities but are noticeably higher than other published values: averaging 3137 g/m^2 for *P. australis*, 2372 g/m^2 for cattail marsh, and 1146 g/m^2 for meadow marsh. Our measurements may be high due to particularly dense growth, favourable edaphic conditions in intact freshwater coastal marsh, or because we were unable to differentiate live tissues from recently dead tissues.

When uninvaded marsh was separated into cattail and meadow marsh communities, we noted higher average below ground biomass in uninvaded cattail marsh, clearly overlapping with the below ground biomass typical of *P. australis*. This indicates that the effects of invasion on below ground biomass is likely more evident where *P. australis* replaces meadow marsh than where it invades cattail marsh. Yet, despite this difference in mean below ground biomass between cattail and meadow marsh, we fit a single slope relating the below ground biomass of uninvaded sites to water depth collectively. Future research should explicitly test for the role of resident vegetation community type on limiting the magnitude of *P. australis* invasion effects on invaded ecosystems.

Importantly, though invasion by *P. australis* in freshwater coastal marsh may increase overall below ground biomass, the concern that *P. australis* below ground tissues might penetrate more deeply than resident species and thus alter nutrient and metal fluxes in freshwater marshes is unfounded. Contrary to previous studies (e.g., Ravit *et al.* 2006; Moore *et al.* 2012), we observed no difference in rooting depth

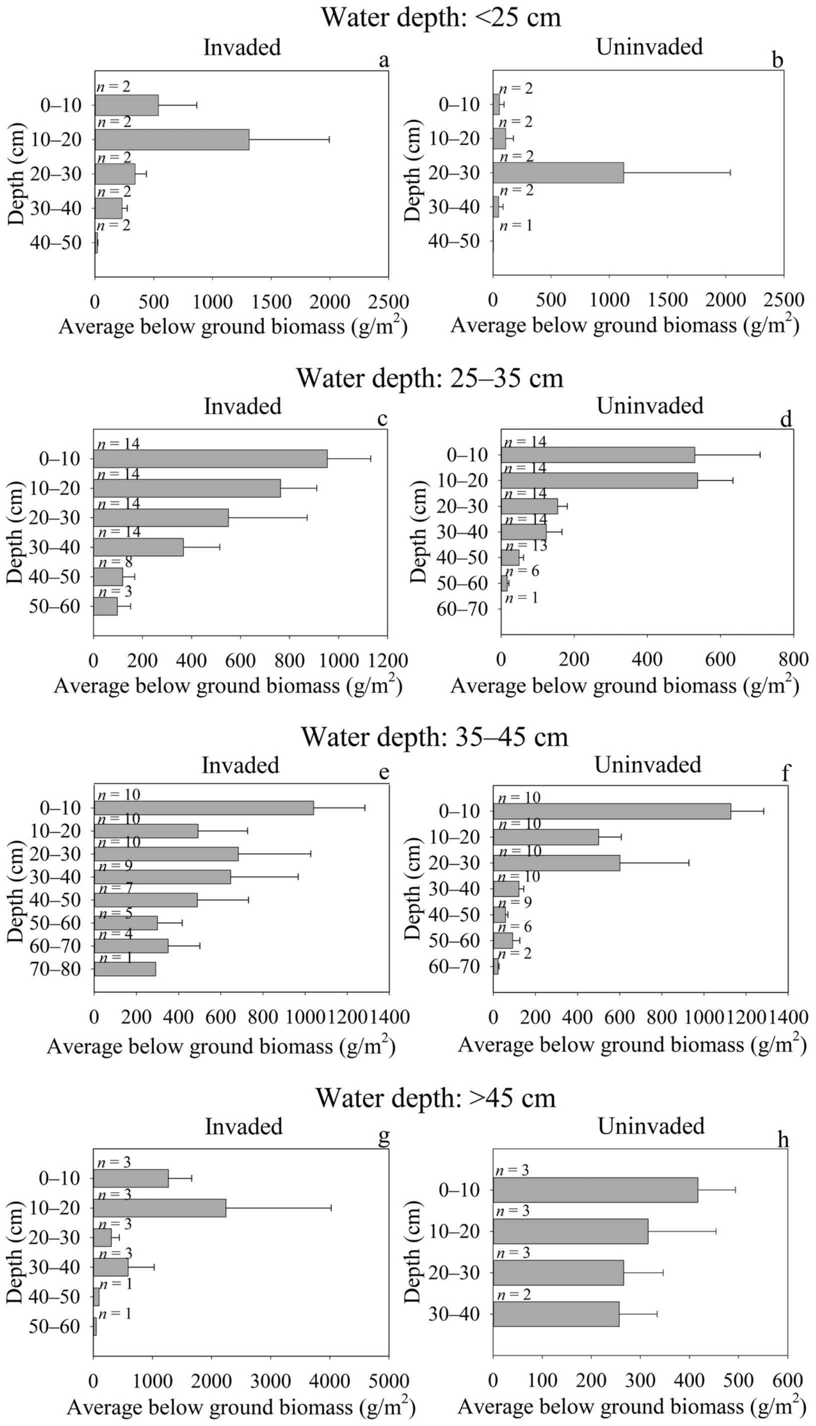

FIGURE 2. Down-core distribution of below ground biomass at different water depths. Down-core distribution of below ground biomass, contrasting European Reed (*Phragmites australis*) invaded sites (a, c, e, g) and uninvaded sites (b, d, f, h) at different water depth intervals: <25 cm (a, b), between 25–35 cm (c, d), between 35–45 cm (e, f), and >45 cm (g, h). The *n* above each bar indicates the number of cores in which living below ground tissues were detected at the indicated water and soil depth, in the indicated site type. Error bars are SE.

among the invaded and uninvaded sites. Moore *et al.* (2012) surmised that in marine coastal marsh, *P. australis* may produce deeper roots to access freshwater pockets. If this were so, it might explain why *P. australis* was not rooting more deeply than resident species in our freshwater coastal marsh. Alternatively, these published studies may differ from ours in the frequency and amplitude of water depth fluctuations that can also influence rooting depth (Hanslin *et al.* 2017). Another important factor is likely the wetland soil type and stratigraphy. Moore *et al.* (2012) reported that sandy mineral soils may inhibit deep penetration of roots. Long Point has a sand mineral soil beneath an organic horizon of variable thickness; the sand soil may have limited rooting depth for all species in our study.

Because *P. australis* produces significantly more below ground biomass in the same depth of rhizosphere as resident vegetation communities, we expect that root processes such as enhanced gas diffusion in the rhizosphere, oxidation of waterlogged anoxic soils (Armstrong and Armstrong 1988; Bart and Hartmann 2000), and the release of allelochemicals (Rudrappa *et al.* 2007) provide *P. australis* a competitive advantage and contribute to its invasion success. Yet clearly, given the equivalent rooting depths of *P. australis* invaded and uninvaded marsh, these communities experience a common rooting depth limit. This conclusion is further supported by our observation that meadow marsh, despite producing less below ground biomass than cattail marsh, nonetheless roots at an equivalent depth

Conclusion

Below ground biomass in *P. australis* invaded marsh significantly exceeded that in resident communities of meadow marsh and cattail marsh, after accounting for water depth, but rooting depths were equivalent. Consequently, root densities must be greater in *P. australis* invaded marsh, potentially contributing to its invasion success in Long Point. Because *P. australis* did not root more deeply than resident vegetation in our freshwater coastal marsh study system, concerns around invasion mobilizing deep pools of otherwise inactive carbon or metals may be generally unwarranted. The novel quantitative data presented in this study increases our understanding of *P. australis* invasion in freshwater lacustrine coastal marsh habitat and establishes the hypothesis of common limits to rooting depth in invaded and uninvaded sites that should be tested in other study systems.

Author Contributions

Conception & Design: R.C.R., S.J.Y., and C.L.; Field Work: S.J.Y.; Lab Work: C.L. and S.J.Y.; Data Analysis & Interpretation: R.C.R., S.J.Y., and C.L.; Writing – First Draft: C.L.; Writing – Review & Editing: R.C.R., S.J.Y., and C.L.; Funding Acquisition: R.C.R.

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SUPPLEMENTARY MATERIAL:

FIGURE S1. Total below ground biomass with water depth for European Reed (*Phragmites australis*) invaded sites (solid line and black triangles; $n = 29$) and uninvaded sites (dashed line and white circles; $n = 29$).

TABLE S1. Results table for GLM predicting total below ground biomass with and without interaction term.

TABLE S2. Results table for GLM predicting rooting depth with and without interaction term.

The Canadian Field-Naturalist

Flathead Catfish (*Pylodictis olivaris*) reproduction in Canada

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Abstract

Eleven Flathead Catfish (*Pylodictis olivaris*), representing at least five age classes, were collected between 2016 and 2018 in the lower Thames River, Ontario, Canada. The capture of two juveniles (total lengths 78 mm and 82 mm), the first records of juveniles in Canada, is a strong indication that reproduction has occurred. Previous records were thought to be individuals that dispersed from known populations in American waters of Lake Erie. Flathead Catfish is currently designated as data deficient by the Committee on the Status of Endangered Wildlife in Canada. These new findings may provide sufficient data to reconsider the conservation status of this species.

Key words: Flathead Catfish; *Pylodictis olivaris*; reproduction; Great Lakes; Lake St. Clair; Thames River; juvenile; young-of-year

Introduction

Flathead Catfish (*Pylodictis olivaris*) is found throughout the Mississippi River basin and lower Laurentian Great Lakes (Page and Burr 2011); however, it is uncertain whether the species is native to the Great Lakes basin (Fuller and Whelan 2018). It is a benthic fish species preferring turbid (Lee and Terrell 1987; Hesse 1994), warm water (Becker 1983) in low-gradient, moderate to large rivers (Lee and Terrell 1987), and is commonly associated with woody debris, undercut banks, and substrate depressions throughout its range (Becker 1983; Hesse 1994; Grussing *et al*. 1999; Jackson 1999; Daugherty and Sutton 2005a). Flathead Catfish reach sexual maturity between three and six years of age when fish are 375–539 mm in total length (TL; Minckley and Deacon 1959; Perry and Carver 1977). Reproduction occurs in June and July when water temperatures reach at least 22.2°C (Becker 1983). Flathead Catfish use depressions and natural cavities to construct nests (Cooper 1983; Cross 1967) and females lay up to 31 579 eggs (Becker 1983). A detailed description of the life history of Flathead Catfish was reported by Goodchild (1993).

Flathead Catfish is taxonomically and morphologically different from all other catfish species in the Great Lakes basin. Differences include its protruding lower jaw, ventrally compressed head, large adipose fin, and backward extensions of the premaxillary tooth patches (although Stonecat [*Noturus flavus*] shares the latter characteristic). Flathead Catfish has a varying amount of mottled pigmentation on the body, and the upper lobe of the caudal fin has a pale tip (Figure 1), although these traits can be absent or less obvious in larger fish. Flathead Catfish has a slightly forked caudal fin in contrast to the deeply forked caudal fin of Channel Catfish (*Ictalurus punctatus*).

Flathead Catfish has a short anal fin with a ray count of 13–18 (Trautman 1981), which differentiates it from Channel Catfish (25–28), Yellow Bullhead (*Ameiurus natalis*, 24–27), Brown Bullhead (*Ameiurus nebulosus*, 20–23) and, in some cases, Black Bullhead (*Ameiurus melas*, 17–21; Scott and Crossman 1998); all anal ray counts include rudimentary rays. Furthermore, Flathead Catfish has serrations on both edges of its pectoral spines whereas Channel Catfish and Brown and Black Bullheads have serrations only on the posterior edge. Madtoms (*Noturus* spp.) could be confused with juvenile Flathead Catfish, but are distinguished by a connected adipose fin and caudal fin, which are separate in Flathead Catfish.

In the Great Lakes, Flathead Catfish has been recorded in the Lake Erie, Lake St. Clair, Lake Huron, Lake Michigan, and Lake Superior basins. Since 1890, when Flathead Catfish was first recorded in Lake Erie, it has been documented in seven tribu-

FIGURE 1. Juvenile Flathead Catfish (*Pylodictis olivaris*), 78 mm total length, captured on 31 August 2016 in the lower Thames River, Ontario, Canada. Photo: Colin Illes.

taries and is believed to have spread to the Lake St. Clair (Goodchild 1993; COSEWIC 2008) and Lake Huron basins where it has been recorded in six tributaries since the first records in 1989 and 1991, respectively (Fuller and Whelan 2018). In Lake Michigan, Flathead Catfish was first recorded in 1922 and has since been documented in 11 tributaries (Fuller and Whelan 2018). In addition, there is a single record of a Flathead Catfish in the Lake Superior basin, captured in a pond in the Au Train River watershed and believed to be an unauthorized release (Fuller and Whelan 2018). A detailed description of the historical and current distribution of Flathead Catfish in the American Great Lakes basin is provided by Fuller and Whelan (2018).

Whether Flathead Catfish is native to the Great Lakes basin is not known because of poorly documented historical records. Historical publications variously mention (e.g., Trautman 1957) and do not mention (e.g., Evermann 1902) the presence of Flathead Catfish in the lower Great Lakes. Based on a review of the literature and capture data, Fuller and Whelan (2018) concluded that Flathead Catfish is not native to the Great Lakes basin, with the possible exception of a small population documented since 1890 in the Huron River, Lake Erie (Trautman 1957). Conversely, Roth *et al.* (2012) indicated that Flathead Catfish is native to the Erie and Michigan basins.

The origin of several other fishes in the Great Lakes basin is also unclear. Much like Flathead Catfish, Gizzard Shad (*Dorosoma cepedianum*), and Bigmouth Buffalo (*Ictiobus cyprinellus*) have uncertain origins in Lake Erie and may have spread from the Mississippi River basin into Lake Erie where populations have continually expanded because of warming temperatures (Miller 1957; Goodchild 1993). These fishes are considered native to the Great Lakes basin (e.g., Lee *et al.* 1980; Trautman 1981; Scott and Crossman 1998; Roth *et al.* 2012), despite a lack of historical records and vouchered specimens. This has been attributed to misidentification with other species (e.g., Alewife [*Alosa pseudoharengus*], Smallmouth Buffalo [*Ictiobus bubalus*]), and confusion with early introductions of Bigmouth Buffalo (Miller 1957; Trautman 1981). Gizzard Shad and Bigmouth Buffalo were first recorded in Lake Erie in 1848 and 1878, respectively (Miller 1957; Trautman 1981). Roth *et al.* (2012) identified only three species of questionable native status in the Great Lakes basin: Ghost Shiner (*Notropis buchanani*), questionably native to the Erie and Huron basins; and Brindled Madtom (*Noturus miurus*) and Orangethroat Darter (*Etheostoma spectabile*) to the Michigan basin.

In Canada, Flathead Catfish has been collected only in the Great Lakes basin with records limited to the western basin of Lake Erie and Lake St. Clair (COSEWIC 2008). The first Canadian capture of a Flathead Catfish was in Lake Erie, in 1978; it was caught west of Point Pelee, 3.2 km north of the tip, in a commercial trap net (Crossman and Leach 1979). Subsequently, three additional single specimens were captured in the Point Pelee area in 1986, 2005, and 2011 (COSEWIC 2008; Ontario Ministry of Natural Resources and Forestry [OMNRF] unpubl. data). All three fish were recorded in commercial trap nets west of Point Pelee and south of Sturgeon Creek within 8 km of each other. In 1989, Flathead Catfish was first captured by commercial long line in Lake St. Clair, 3.2 km from the mouth of the Thames River (Royal Ontario Museum unpubl. data). In 2001 and 2003, two additional Flathead Catfish were captured in Lake St. Clair in the St. Luke's Bay area, 10 km north of the Thames River mouth (Figure 2), both in a commercial trap net (OMNRF unpubl. data). Based on the four known single specimens captured in Canadian waters between 1978 and 2001, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) could not determine whether Flathead Catfish was native to Canada or a vagrant and, thus, assessed it as data deficient (COSEWIC 2008).

Because of its preference for hard-to-sample habitats (e.g., beneath woody debris and structured substrate in deep water), low population abundance, and solitary behaviour, Flathead Catfish has been notori-

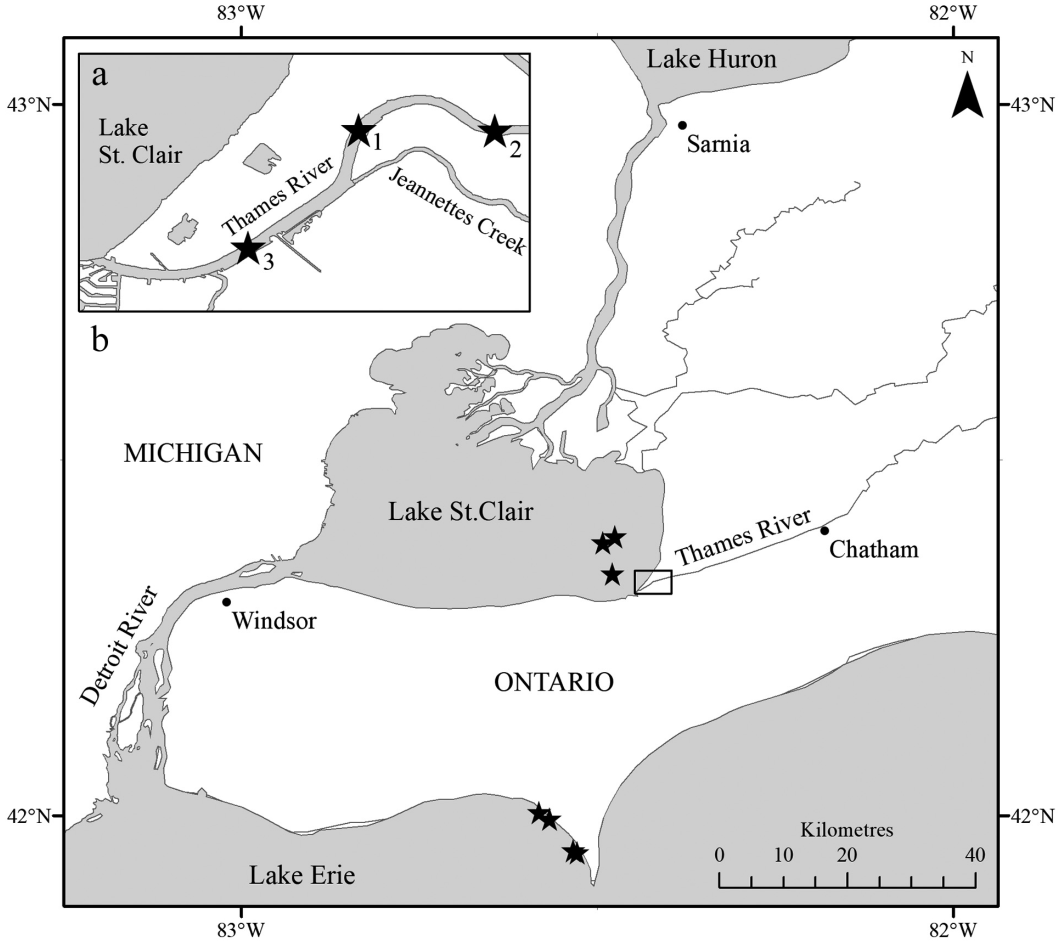

FIGURE 2. Capture locations of Flathead Catfish (*Pylodictis olivaris*) in Canadian waters of the Great Lakes basin, a. 2016–2018 and b. 1979–2018. Source: Unpublished data from Fisheries and Oceans Canada, the Ontario Ministry of Natural Resources and Forestry, and the Royal Ontario Museum, sourced under the Open Government Licence Ontario.

ously difficult to assess in river systems (Stauffer *et al.* 1996; Vokoun and Rabeni 1999). This has led to limited targetted sampling and knowledge about the species, especially in the Great Lakes (Daughtery and Sutton 2005a). To our knowledge, there has been only one population estimate for Flathead Catfish in the Great Lakes basin, conducted in the lower St. Joseph River, Michigan, which estimated an abundance of 5453 individuals (Daughtery and Sutton 2005b).

In this study, we report recent records of Flathead Catfish that indicate reproduction in the Canadian waters of the Great Lakes basin and discuss implications of these records for future management.

Methods

The Thames River, a tributary of Lake St. Clair, is a large, turbid river with a high diversity of fish and mussel species, 25 of which are at risk (Cudmore *et al.* 2004). The Thames River watershed has been impacted by agriculture and urban and rural development (Cudmore *et al.* 2004). In addition to supporting several imperilled species, the river is highly suitable for the reproduction of four species of invasive Asian carp (Cudmore *et al.* 2017) and, therefore, is sampled routinely by Fisheries and Oceans Canada's Asian Carp Program (Colm *et al.* 2019a).

This sampling occurred between May and November, 2013–2018, using seven gear types to target adult and juvenile Asian carp, while also collecting baseline fish community data (Marson *et al.* 2014, 2016, 2018; Colm *et al.* 2018, 2019a,b). Sampling effort in the lower Thames River during this period is summarized in Table 1.

Flathead Catfish were captured in the lower Thames River using three gear types: boat electrofishing ($n =$

TABLE 1. Summary of sampling effort in the lower Thames River, 2013–2018, as part of the early detection surveillance efforts of Fisheries and Oceans Canada's Asian Carp Program.

Year	Boat electrofishing		Hoop net		Mini-fyke net		Seine net		Trap net		Trammel net	
	No. sites	Effort, h	No. sites	Effort, h	No. sites	Effort, h	No. sites	Effort, hauls	No. sites	Effort, h	No. sites	Effort, h
2013	4	0.4	0	0.0	0	0.0	2	6	0	0.0	2	1.8
2014	19	3.1	3	112.4	0	0.0	0	0	4	91.4	5	1.8
2015	33	5.6	7	311.1	0	0.0	0	0	12	244.4	13	9.1
2016	25	4.6	0	0.0	6	130.4	0	0	7	153.6	8	5.4
2017	22	3.8	10	460.1	7	155.9	0	0	10	214.4	9	2.3
2018	28	6.0	9	397.4	16	355.1	2	5	13	293.8	14	12.4

Sources: Marson *et al.* 2014, 2016, 2018; Colm *et al.* 2018, 2019a,b.

4), hoop nets ($n = 2$), and trammel nets ($n = 5$). Before 2018, the boat electrofisher was dual-boom, 6.4 m in length, and fitted with a 7.5 Generator Powered Pulsator (Smith-Root, Vancouver, Washington, USA). In 2018, the boat electrofisher used in sampling was 7.3 m in length, dual-boom, and fitted with an Infinity Box (Midwest Lake Electrofishing, Polo, Missouri, USA). Two sizes of hoop nets were used: 1.5 m in diameter, 6.1 m in length, with 2.5-cm square mesh; and 0.91 m in diameter, 4.57 m in length, with 2.5-cm square mesh. Trammel nets were 183 m in length, 4.3 m in height, with 10.1-cm bar mesh and 45.7-cm outer wall panels. Trammel nets were often used in combination with boat electrofishing as this is an effective method for targetting Grass Carp (*Ctenopharyngodon idella*), a species of Asian carp, in the Great Lakes basin (D.M.M. pers. obs.); however, fishes captured with the two gear types were processed separately. All gear types and the scope of sampling (including other locations in the Great Lakes basin) are described in Colm *et al.* (2019a).

Results

During 2016–2018, 11 Flathead Catfish (Table 2) were captured in three locations in the lower Thames River, near the mouth of Jeannettes Creek, Kent County, Tilbury Township (42.329°N, 82.421°W) (Figure 2a). No Flathead Catfish were detected in 2013–2015, despite sampling in similar areas to 2016–2018. In August 2016, we recorded three Flathead Catfish, with TL 78–566 mm, at two locations. All three fish were captured using a boat electrofisher near shore in close proximity to woody debris on a clay–silt substrate (Table 2). The first location had an undercut bank with a single cluster of woody debris; the second had abundant large woody debris, including trees, logs, and branches, and a water depth of ~1 m at the bank. In June 2017, a Flathead Catfish measuring 365 mm TL was captured with a hoop net in a new location with abundant submerged logs and branches. This individual was caught farthest downstream, 1.3 km from the Thames River mouth. In September 2017, two Flathead Catfish measuring 833 mm and 815 mm TL were captured using a

TABLE 2. Capture data for Flathead Catfish (*Pylodictis olivaris*). Capture locations shown in Figure 2a.

Date	Total length, mm	Temp., °C	Turbidity, NTU	Max. site depth, m	Substrate	Coarse woody debris, Y/N	Gear type	Location of capture	ROM catalogue no.
30 Aug. 2016	566	26.29	28.77	4.2	Clay–silt	Y	Boat electrofishing	1	101500
30 Aug. 2016	82	27.17	27.44	2.0	Clay–silt	Y	Boat electrofishing	2	105705
31 Aug. 2016	78	26.67	25.77	2.1	Clay–silt	Y	Boat electrofishing	2	101375
20 June 2017	365	24.61	16.04	2.8	Clay–silt	Y	Hoop net	3	109946
13 Sept. 2017	833	20.34	23.70	4.1	Clay–silt	Y	Trammel net	1	NA
14 Sept. 2017	815	21.44	11.30	2.0	Clay–silt	Y	Boat electrofishing	2	NA
26 June 2018	820	23.71	23.11	5.0	Clay–silt	Y	Hoop net	2	NA
27 Sept. 2018	697	20.31	31.17	4.0	Silt–clay	Y	Trammel net with boat electrofishing	2	NA
27 Sept. 2018	765	20.22	20.86	3.8	Silt–clay	Y	Trammel net with boat electrofishing	1	NA
27 Sept. 2018	743	20.22	20.86	3.8	Silt–clay	Y	Trammel net with boat electrofishing	1	NA
2 Oct. 2018	388	18.29	25.13	4.0	Clay–silt	Y	Trammel net with boat electrofishing	3	NA

Source: Fisheries and Oceans Canada unpubl. data.
Note: NTU = nephelometric turbidity units, ROM = Royal Ontario Museum.

trammel net and boat electrofisher (Table 2). The 815-mm individual was the farthest upstream record, 6.3 km from the Thames River mouth. In 2018, five additional Flathead Catfish were collected, measuring 388–820 mm TL. The 820-mm individual was captured using a hoop net at the deepest recorded capture of 5 m. The other four Flathead Catfish were captured in trammel nets used in combination with boat electrofishing (Table 2).

Four specimens of Flathead Catfish captured in 2016 and early 2017 were preserved in 10% buffered formalin, stored in 70% ethanol, and catalogued at the Royal Ontario Museum (Table 2). Digital voucher photos were taken of the remaining seven fish before they were released.

Using length-at-age data from the literature (Mayhew 1969; Young and Marsh 1990; Kwak *et al.* 2006; Sakaris *et al.* 2006), we estimate that the 11 Flathead Catfish were from five different age classes (Figure 3).

Discussion

We report the first indication of Flathead Catfish reproduction in the Canadian waters of the Great Lakes basin. Over six consecutive years of sampling, 11 individuals were detected in the lower Thames River, Ontario. To our knowledge, no length-at-age data are available for Flathead Catfish in the Great Lakes basin. Flathead Catfish collected on 30 August 2016 and 31 August 2016 with TLs of 78 mm and 82 mm, respectively, are assumed to be young-of-year. In addition to being the first recorded juveniles in Canada, these are the first records of Flathead Catfish from a river system in Canada; previous detections were in large bays.

In the first year of growth, Flathead Catfish has been documented to reach 100 mm TL in Ohio (Trautman 1981) and 145 mm TL in Arizona (Young and Marsh 1990). Daugherty and Sutton (2005b) recorded Flathead Catfish measuring 87 mm and 93 mm TL, which were assumed to be young-of-year, while sampling the lower St. Joseph River, Michigan, June through September 2002–2003.

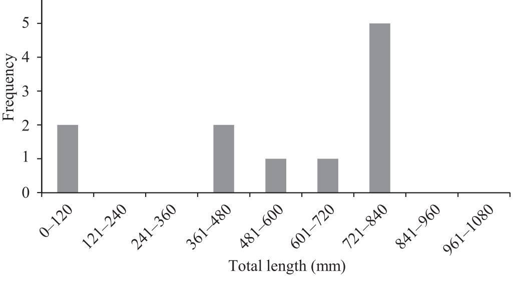

FIGURE 3. Length–frequency distribution of Flathead Catfish (*Pylodictis olivaris*) captured in the lower Thames River, 2016–2018, by Fisheries and Oceans Canada's Asian Carp Program.

Historical records of Flathead Catfish captured in Canada before 2001 were speculated to be individuals that dispersed from a known population in the Huron River, Lake Erie, and gained access to Lake St. Clair through the Detroit River (Goodchild 1993; COSEWIC 2008). The juvenile Flathead Catfish captured in our study would not likely be able to disperse from a Lake Erie tributary upstream through the strong-flowing Detroit River, providing further support for the likelihood that these individuals were the result of reproduction in the Thames River. Few studies have examined the movement of juvenile Flathead Catfish. Travnichek (2004) found a relationship between Flathead Catfish size and movement in the Missouri River: as size increased so did distance travelled. In their study, Flathead Catfish that were 305–380 mm TL travelled an average of 4.6 km in up to two years after tagging (Travnichek 2004). Stocking is an unlikely alternative method of introduction of the individuals captured here, as there is no documented stocking of Flathead Catfish in Ontario and, in the United States, Flathead Catfish are most often stocked as adults (Guier *et al.* 1981; Jenkins and Burkhead 1994). Introduction through the live fish trade is also unlikely, as there is no record that live Flathead Catfish have been imported into Canada (Mandrak *et al.* 2014) and surveys of six live fish markets and 20 pet stores in the Great Lakes region did not report Flathead Catfish (Rixon *et al.* 2005).

Flathead Catfish may be more abundant in the Canadian waters of the Great Lakes basin than currently known, and its range is likely not fully documented because of its cryptic behaviour and difficulty to sample (Goodchild 1993; Fuller and Whelan 2018). Continued Asian carp surveillance will further document the Flathead Catfish population in the Thames River. This work is also being conducted in 35 other locations in the Great Lakes basin and may provide information on new locations of Flathead Catfish populations.

The potential impacts of Flathead Catfish in the Great Lakes basin are unknown and should be further investigated to determine how this species should be managed. Pine *et al.* (2005) found that Flathead Catfish is primarily piscivorous, feeding on the most abundant fishes in rivers, which could lead to a change in local food-web structures. The presence and increased abundance of Flathead Catfish has been associated with decreases in the abundance of sunfishes (*Lepomis* spp.; Davis 1985; Thomas 1993; Bart *et al.* 1994; Ashley and Rachels 1998; Bonvechio *et al.* 2009), black basses (*Micropterus* spp.; Thomas

1993; Bonvechio *et al.* 2009), redhorses (*Moxostoma* spp.; Bart *et al.* 1994), Common Carp (*Cyprinus carpio*; Davis 1985; Bart *et al.* 1994), and bullheads (*Ameiurus* spp.; Davis 1985). Flathead Catfish may have some ecological benefits in the Great Lakes basin, as a predator of the invasive Common Carp and as a known host for Mapleleaf mussel (*Quadrula quadrula*; Howard and Anson 1922), which has been listed as special concern under the Canadian *Species at Risk Act* (SARA Registry 2019). The Thames River is thought to have the largest population of Mapleleaf in southwestern Ontario, and recent records of Flathead Catfish overlap with records of Mapleleaf from the lower Thames River in 2005 (COSEWIC 2016). Flathead Catfish has seasonally varying home ranges and movement patterns (Daugherty and Sutton 2005a), which are important characteristics of hosts that facilitate the genetic mixture of freshwater mussel populations in rivers (Elderkin *et al.* 2007).

The distribution of freshwater fishes is often restricted by temperature. Mandrak (1989) determined that Flathead Catfish had low potential for future expansion into the Great Lakes basin because of thermal restrictions. With climate change, the water temperature of the Great Lakes is expected to increase 2–3°C in southern Ontario and 3–4°C in northern Ontario by 2065 (Gula and Peltier 2012). Such an increase will benefit warm-water species, such as Flathead Catfish, by increasing recruitment success (Casselman 2002; Chu *et al.* 2005; Hansen *et al.* 2017). This increase in recruitment has the potential to expand the range of Flathead Catfish and lead to a greater abundance of the species in the Great Lakes basin (Casselman 2002).

Our research suggests that a better understanding of the potential ecological impacts and improved distribution modelling of Flathead Catfish in Canada is required. With climate change, many species are likely to undergo range expansions, bringing new threats to already imperilled native species. With limited resources, managers must balance this with the threats of new (or existing) invasive species that have a greater potential for damage (Rahel and Olden 2008; Rolls *et al.* 2017). In Canada, there is a need for clear management objectives for these species undergoing natural "invasions", that include consistent classification and terminology and a framework to prioritize them (Chu *et al.* 2005; Rahel and Olden 2008).

The capture of Flathead Catfish representing at least five age classes, including young-of-year fish, is a strong indication that reproduction has occurred in the lower Thames River. With the recent captures reported here, there may now be sufficient data for Flathead Catfish to be re-assessed by COSEWIC. Additional research targetting Flathead Catfish is recommended to (i) better understand the distribution of this species in Canada, (ii) evaluate the most effective gear for detection, (iii) estimate abundance, and (iv) understand the movement and habitat-use patterns in the Canadian waters of the Great Lakes basin.

Author Contributions

Writing – Original Draft: C.I. and J.E.C.; Writing – Review & Editing: C.I., J.E.C., N.E.M., and D.M.M.; Methodology: C.I., J.E.C., and D.M.M.; Visualization: C.I. and J.E.C.

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Book Reviews

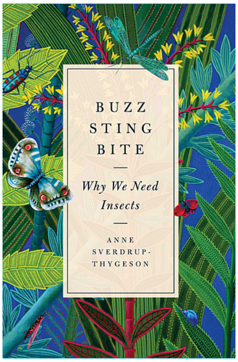
Book Review Editor's Note: *The Canadian Field-Naturalist* is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those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

ENTOMOLOGY

Buzz, Sting, Bite: Why We Need Insects

By Anne Sverdrup-Thygeson. 2019. Simon and Schuster. 235 pages, 35.00 CAD, Cloth.



Buzz, Sting, Bite is another entry into the growing list of accessible popular science books written as passion projects by an academic researcher. A professor of conservation biology at the Norwegian University of Environmental and Life Sciences and a scientific advisor to the Norwegian Institute for Nature Research, Sverdrup-Thygeson's specialty is the ecological role of insects in trees and forests, but the book covers arthropods and their ecological roles more broadly. In addition to a multitude of interesting facts, it includes some discussion of broader conservation ecology, such as habitat connectivity, extinction debt, and endangered species. As promised by the tagline "why we need insects", the work also delves into humanity's ties to the insect world, from 13th century Chinese cricket fights to termites eating their way through stashes of bank notes.

Organized into nine main chapters, the scope is broad and about what you would expect from the outset: anatomy, mating, agricultural food systems, the ecological role of detritovores, and insect-human interactions. While each chapter has a stated theme, they are further divided into multiple sections and subsections. Overall quite intuitive and well managed, this structure does pose narrative challenges and can become disjointed at times as topics begin to blur together. One key advantage of this bite-sized-piece approach is that like many books written for popular audiences, it makes for easy reading; this book may not pull you in for an all-night reading binge but it is well designed to be picked up at your leisure.

Artfully translated by Lucy Moffatt from the original Norwegian 2018 publication, *Buzz, Sting, Bite* includes some truly excellent explanations and turns of phrase. Although there are a few notable oversimplifications when discussing the natural history of insect groups and genera (e.g., bumble bees), the writing is at its best when it focusses on the truly weird and wonderful. Chapter 7, From Silk to Shellac: Industries of Insects, was by far my personal favourite, galloping across time periods and cultural traditions to bring together everything from oak gall wasps and historical records, silk production, bulletproof vests, and the Aztec and Mayan traditions of breeding cochineal bugs. To my repertoire of offbeat insect-based cocktail conversation I can now add the link between shellac, phonograph records, and a 1942 restriction ordered by the United States government on the record industry to reduce shellac consumption by at least 70%—for this I am forever grateful.

The main text is complimented by black and white illustrations by artist Tuva Sverdrup-Thygeson, one at the beginning of each chapter matched to its overall theme. These are welcome additions, as is the list of eight other author-recommended popular science insect books found under Further Reading following the Acknowledgments section. Although no in-text citations are provided, a bibliography of sorts is found in the 20-page Sources section which is organized by chapter and includes full citations of journal papers, reports, books, and popular science articles. The text ends with a detailed Index, so when you inevitably want to refresh the details on a specific fact or anecdote it is at your fingertips.

One of the author's objectives in writing this book is to shine a spotlight on the creepy-crawly things of the world and shower them with the praise and appreciation that they deserve. In highlighting their value to human societies and their intrinsic 'cool' factor (even going so far as to use that rarest punctuation mark, the exclamation point, on several occasions), the author is largely successful. Although I doubt that those with a serious bug phobia will be drawn to this book, the range and variety of topics covered means that there is probably something here for everyone. Human-insect-avian interactions? Take Greater Honeyguide (*Indicator indicator*) birds and their collaboration with the Yao people of Mozambique. Urban ecology and localized natural selection events? Have a side of mosquito speciation by station area of the London Underground. Want to hop on the insect eating bandwagon? You'll find it espoused here, if only briefly. Reading *Buzz, Sting, Bite*, I was reminded why I enjoy reading books on broad topics written by good writers—the more I learn, the more I want to know. This book provides more breadth than depth when it comes to bug love but is an excellent jumping off point for those who want to dive deeper, and a great toe dip for any who may otherwise hesitate to even approach the water's edge.

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Butterflies: Their Natural History and Diversity. Second Edition

By Ronald Orenstein. Photography by Thomas Marent. 2020. Firefly Books. 24.95 USD / CAD, Paper.

A quick internet search appears to confirm the easy notion that butterflies must be the most popular of the insects. I think of them as the birds of the insect world, often colourful, active, and highly visible. And, as with birds, the internet is full of books, posters, calendars, etc. related to butterflies. One might wonder at the need for yet another book, but given the popularity of the topic, it comes as no surprise. And this one delivers the goods in an informative, accessible way.

The photographs catch the eye first. Swiss photographer Thomas Marent is a well-travelled wildlife photographer who, starting young, has about 40 years experience in shooting pictures of various forms of wildlife that have been featured in a number of books, including the first edition of this one, an earlier book with Orenstein, and an earlier one yet of his own. The photos are consistently gorgeous, crisp in their detail, and beautifully presented.

It would be very easy—and a big mistake—to treat this as a picture book! Ronald Orenstein is a Canadian zoologist/ornithologist, lawyer, wildlife conservationist, and prolific author/editor of natural history books. He admits in the Acknowledgements that he is "not an entomologist" (p. 224) but the text reveals an enviable capacity for digesting the latest research. The book opens with a lengthy introductory outline of lepidopteran natural history that ranges from the origins of the term 'butterfly' and their cultural significance through their evolutionary history and brief description of the six families into which they are now organized. The book covers wing formation and function, mimicry, mating and reproduction, host plants, development from egg to adult phases, issues of conservation, and much more. Orenstein isn't shy about using scientific names and terms—androconia, for example—that are always defined in the text.

We learn some surprising things, such as why butterfly flight is erratic (pp. 9–10), the various types and roles of wing scales and the genetic coding that produces their colours (p. 11), that mimicry in a particular species can vary in time and place, the well-known Viceroy being an example (p. 13). Nuptial gifts and sperm competition (p. 16), pollination, migration, and DNA-based discoveries all receive concise, research-based accounts. One of the most interesting things I learned was that these lovely insects that can be such innocent symbols of beauty and grace are capable of cannibalism and manipulative deception in symbiotic relations with other animals such as ants.

Chapters 1 through 6 discuss the six families and their subfamilies, each of which receives brief introductions. The photographs of species come into their own here, each identified with scientific name and location, followed by brief and informative comments on topics such as distribution, habitat, caterpillar stages, and toxicity. The next four chapters are thematic, profusely illustrating and adding to the themes of the introduction: Butterfly Wings (Chapter 7), Butterfly Life History (Chapter 8), What Butterflies Eat (Chapter 9), and Butterflies in Their Environment (Chapter 10). The 11th and concluding chapter, Myriads of Moths, reminds us that "butterflies are moths" (p. 6) after all. Moth species "outnumber butterflies by at least fifteen to one" so this chapter is "a miscellany, not a survey…" (p. 185). And a handsome survey it is, covering some spectacular examples, the caterpillars being particularly fascinating.

The book concludes with a page of Further Reading that lists books and websites, plus a URL for the "400+ papers consulted…" (p. 219), and an Index. One odd thing: the book has two covers, the new one you can see here, and a reproduction of the original cover; it is this one, not the new cover, that says Second Edition. A minor puzzle for a worthy book. Books on butterflies seem to be written for professional lepidopterists or for kids, with many popular 'picture books' in between. This book is one of the comparatively few that focus on natural history for the interested generalist who has some background in the topic. Orenstein and Marent have created a fine addition to such a reader's library, one that informs while pointing the way to further study.

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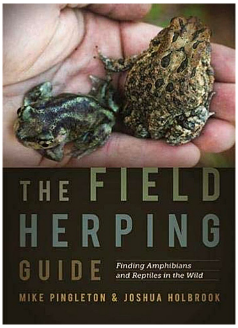
HERPETOLOGY

The Field Herping Guide: Finding Amphibians and Reptiles in the Wild

By Mike Pingleton and Joshua Holbrook. 2019. University of Georgia Press. 264 pages, 26.95 USD, Paper.



An increasing number of people are interested in amphibians and reptiles, or ‘herps’, and this interest includes wanting to see them in nature. Many of these species can be somewhat challenging to find and a guide to finding herps is a good idea. *The Field Herping Guide* does just this as well as discussing issues one should keep in mind to keep the herpers and the herps safe. It should be stressed that this is not a book about how to conduct scientific surveys of amphibians or reptiles or how to design field ecology studies, this is a guide to finding herps for fun.

The book consists of nine chapters with lots of colour photographs. The chapter titles are a good indication of the topics the book covers: Getting Started; Understanding Herp Behavior; Finding Herps; Catching and Handling Herps; Safety in the Field; Ethics and Etiquette, Rights and Responsibilities; Classification, Taxonomy, and Species Identification; Citizen Science and Data Collection; and Herp Photography. Several appendices on topics such as diseases, various kinds of public lands (mainly from an American point of view), internationally known herp hotspots, herp education, and the history of field herping round out the book.

Is this a valuable book? The book is easy reading, but still contains a lot of information. Much of the advice seems very general, such as sometimes it is too hot for herps to be active, or often herps are active during or after it rains. Given the wide range of species covered, from salamanders to snakes, it is hard to generalize about herps. The authors do a good job of tackling each group of species, but even here the diversity is greater than many people realize. Salamanders can be completely aquatic and never leave the water, live along and in streams, depend upon temporary wetlands for breeding, or live in forests with no need of aquatic habitats. Overall, the authors provide useful advice on the diversity of lifestyles and guidance for how and when to survey for different sub-groups of species.

Unfortunately, the book also has many problems. A book that covers searching for venomous snakes should emphasize safety. The authors discourage people from catching venomous snakes and provide cautions about getting too close when photographing them, but then include a photo of someone in shorts and sandals with a snake hook and a venomous snake (p. 11). This is not the kind of lax safety precautions the authors should be encouraging. And despite urging people not to catch venomous snakes the authors provide several methods for capturing venomous snakes (pp. 113–116).

I also caught a surprising number of factual errors in the book. In the section on crocodilians, the authors give the distribution of Morelet’s Crocodile (*Crocodylus moreletii*) as being limited to Mexico and Guatemala but omit Belize (p. 89). In the section on frogs, it is incorrectly stated that cricket frogs (*Acris* spp.) are ranids or true frogs, when, in fact, they are hylids or treefrogs (p. 93). The authors state that Wood Frog (*Lithobates sylvaticus*) is the only herp in Alaska (p. 94), but this is not even remotely accurate as there are five other native amphibians.

There are also a few things the authors could have stressed more. Near the beginning of the book the authors mention that insect repellant can be toxic to amphibians (p. 18) but this fact is not mentioned again in the section on catching frogs (p. 126). Nor is there any mention of sunscreen on hands which can also be toxic to amphibians.

I hope the authors prepare a second edition which corrects these things. While this book is not going to teach experienced herpetologists much about searching for herps, it is a great introduction to field herping for those who are keen about herps but don’t have much experience. Even with the errors in this book it could still be a valuable resource at school libraries where it could kindle passion in a young reader.

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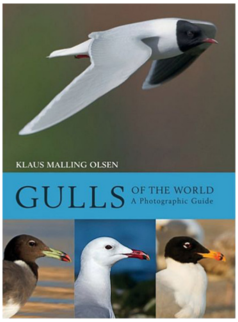
ORNITHOLOGY

Gulls of the World: A Photographic Guide

By Klaus Malling Olsen. 2018. Princeton University Press. 368 pages, 65 maps, and 600+ colour pictures, 45.00 USD, Cloth.



As has been frequently noted, gulls can be a real pain to identify because, not only are many of the species very similar, but they exhibit changes of plumage with age to a greater degree than any comparable group of birds. Consequently, they deserve, and have received, much attention in the form of identification guides specific to the group, starting with Peter Grant's (1982) classic, *Gulls: A Guide to Identification*. They continue to attract enormous attention from birders, especially now that hybridization among species is known to be extensive. Facebook groups and 'twitterati' agonise over the identity of individual birds (… probably a Western × Glaucous-winged … almost certainly a second winter Thayer's Gull …), sometimes long after the bird has flown off into the sunset.

Fifteen years ago, Klaus Malling Olsen, along with the artist Hans Larsson, produced a monumental, 608-page guide to the gulls of the northern hemisphere (Olsen and Larsson 2003) which dealt with their identification, voice, moult, plumage, and distribution, including detailed range maps. The current book is a revision and expansion of the earlier book, although with much less detail on topics other than identification. In place of Larsson's plates, the book is illustrated entirely with photographs, which, as pointed out by another reviewer, are an improvement on those in the first book. In fact, the book comprises an unmatched collection of gull portraits and, as such, is an unmatched resource for identifying gulls in the field.

Given the global spread of e-Bird since the earlier book, you might have expected an improvement in range maps as well, but I did not find that to be the case. The colour code in the current volume consists of yellow for breeding range, blue for wintering range, and green for "if no wintering area shown, occurrence all year" (p. 29). In fact, I found no green areas on any maps. Consequently, where breeding and wintering areas overlap, as for American Herring Gull (*Larus smithsonianus*) on the Great Lakes, the reader cannot tell where the northern limit of the wintering area is. Some rather strange errors in the maps have been perpetuated from the earlier book, including the breeding colony of Black-legged Kittiwakes (*Rissa tridactyla*) at Cape Cod (unnoticed so far by North American ornithologists) and the swath of Ivory Gulls (*Pagophila eburnea*) supposedly breeding across the western Queen Elizabeth Islands.

Because of extensive hybridization among gull species, their taxonomy is contentious. For example, Olsen treats Thayer's and Iceland Gulls (*Larus thayeri, Larus glaucoides*) and American and European Herring gulls (*Larus smithsonianus*, *Larus argentatus*) as different species, whereas the American Ornithological Society now regards Thayer's as a subspecies of Iceland (*L. g. thayeri*) and continues to treat North American Herring Gulls as conspecific with their European counterparts. Since Grant's book in 1982, four species dealt with here have been carved out of his "Herring Gull".

One small reservation I have about treating this book as the last word on gull identification (a reservation I also hold about the opinions of many experts that I read on the web) is that few of the contentious identifications are backed up by genetic material. Consequently, I cannot see how many of the identifications can be treated as better than 'best guesses'. One of the problems of a book like this is that someone might find a gull in the field identical to one of Olsen's pictures and consequently feel confident in the identification. But what if Olsen was wrong? Peter Adriaens and Amar Ayyash, on the American Birding Association website, give a list of errors that they found, including several identifications that they consider erroneous (http://blog.aba.org/errata-gulls-of-the-world). Nothing is perfect and we need to keep that in mind. In science, all is provisional.

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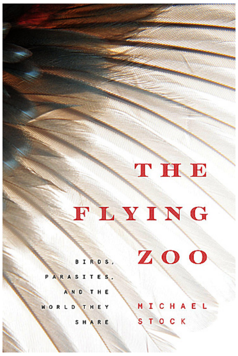
ZOOLOGY

The Flying Zoo: Birds, Parasites, and the World They Share

By Michael Stock. 2019. University of Alberta Press. 260 pages, 29.99 USD, Paper



Michael Stock's book, *The Flying Zoo: Birds, Parasites, and the World They Share*, provides an intriguing glimpse into the lives of birds and their parasites, which are usually looked upon with disgust and dismissed as worthless vermin. However, parasites may provide benefits to their hosts, and Stock's narrative breathes new life into the world of these often-misunderstood organisms. The author asks "How has this weird association between one organism (a bird) and its fellow travelers (parasites) become normal? What special adaptations have parasites had to evolve to be able to find, colonize, and survive in or on their hosts? … How have hosts evolved to survive with their 'zoological garden'?" (p. 4). These questions, and many more, are examined and explored with vigour and enthusiasm.

The book is divided into 10 chapters: A World on a Bird; Lice: It's a Beautiful Life; Fleas: The Circus in the Zoo; Tough Ticks; Mites: Little Things Mean a Lot; Flying Zoo Flies; The Worms that ate the Bird; Oddities in the Flying Zoo; Flying Zoo Behaviour; and Environmental Impacts: The Future of the Flying Zoo. Also included are a Notes section, Further Reading References, and an Index. More than 30 highly detailed pen and ink illustrations of the parasites in question are also dispersed throughout the book.

The book is a joy to read; the author crafts a fascinating journey into the lives of birds and their parasites using current research cases, vivid descriptions, and subtle humor. Co-evolutionary themes are commonplace and connect ecology, biology, adaptation, and survival into a seamless narrative. The reader travels the world, from Madagascar to the Americas, exploring the various interactions between parasite and host. Some amazing information comes to light from Stock's research: who knew that fleas could sing or that there is a specialized moth that drinks the tears of sleeping birds? One of the perks of the book is that the author defines various biological terms (sometimes breaking down the Latin or Greek root words), a major help to those first encountering the term or a refresher for seasoned naturalists and biologists.

All of the classic parasitic groups are covered, including fleas, ticks, lice, flies, and worms. However, peripheral species are also addressed, such as bed bugs (but for birds), moths, leeches, and strange critters called tongue worms. Figure 1.1 on p. 3 illustrates the parasitic relationship with birds well: it shows a Common Pigeon (*Columba livia*) surrounded by various parasitic species that may occur on and within a single bird, from roundworms, flukes, and tapeworms occurring inside the bird to mites, ticks, fleas, and lice occurring on the outside, each occupying a specialized niche (hence the idea of a "flying zoo"). One of the more fascinating topics Stock explores is the niche theory, which states that in order to reduce direct competition, species evolved to occupy different habitats or feeding behaviours. For example, a single bird may support several species of lice, but these lice live in different parts of the bird, such as on various locations of the wing (either on the feathers or inside the quill), on the head, or near the skin. In addition, these lice evolved different body shapes in order to avoid being detected or removed by the bird during the preening process.

It is unwise to assume parasites are worthless creatures with no value, and Stock provides several examples. Worms, such as blood flukes, have evolved ways to not be attacked by the host bird's immune system by down-regulating the immune response. Humans with auto-immune diseases may benefit in the future when we figure out how flukes and other parasites alter host immune systems (p. 150). Leeches, in another example, have a protein anticoagulant in their saliva called hirudin. The anticoagulant is now commercially produced and used to treat people with cardiovascular problems (p. 166). In addition, sometimes parasites provide advantages to their hosts. For example, wild Mute Swans (*Cygnus olor*) have a mature community of co-evolved helminths (worms). Mute Swans in a zoo environment, on the other hand, are not exposed to their usual worm parasites and were infected with two rare tapeworm species causing major infections and significantly diseased birds. The normal worm parasites are apparently a benefit to the swan by preventing harmful helminths from infecting the host. The co-evolved relationship between parasite and host seems to lead to a peaceful co-existence (p. 143). In another example, feather mites may benefit hosts by eating bacteria and fungi trapped in preen gland oil. These bacteria and fungi, in large numbers, may make a bird look unhealthy or diseased, but the mites, by consuming these organisms, allow a bird to appear to have bright and healthy plumage, aiding in their reproductive success (p. 182).

Co-evolution between hosts and parasites is not novel. A few "rules" have been established by researchers exploring the idea. The first, known as Fahrenholz's Rule, claims "that parasite evolutionary histories, or phylogenies, should mirror the histories of their hosts" (p. 142); that is, hosts that are related evolutionarily may harbour the same parasites. A second rule, called Manter's Rule, states "that long associations between hosts and parasites should lead to strong host specificity" (p. 142) and that "parasites should speciate more slowly than their hosts" (p. 24). The third rule, Eichler's Rule, states that "a large taxonomic group of hosts … should have more genera and species of parasites than a small taxonomic group" (p. 24). The fourth rule, Szidat's Rule, claims "more recent or specialized host groups should have more recent or specialized parasites while more primitive or generalized hosts should have more primitive or generalized parasites" (p. 24). Finally, Harrison's Rule states that "large-bodied species of hosts should have large-bodied parasites" (p. 24). Indeed, Stock explores these relationships throughout the book.

Overall, the book is a must-read for those interested in the intricate and interwoven world of birds and their parasites. The author emphasizes that it would be a mistake for anyone interested in avian biology to ignore that parasites are a real and significant part of the lives of birds. Parasites influence many aspects of the lives of our feathered friends, from sexual selection to healthy co-evolutionary relationships. A bird parasite may be harmful, beneficial, or indifferent, and any single parasite can fulfill any one of these roles to all three. Host-parasite studies will continue to lead to more questions and puzzles, especially with the looming climate change crisis, and Stock has provided a good starting point on this journey with his book *The Flying Zoo.*

Acknowledgement: I thank Susan Hagen for improving the manuscript.

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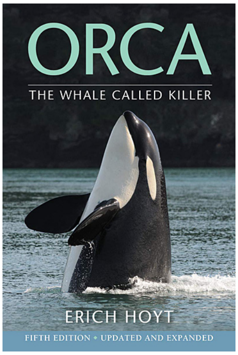
Orca: The Whale Called Killer. Fifth Edition

By Erich Hoyt. 2019. Firefly. 320 pages, 24.95 USD, Paper.



Orca: The Whale Called Killer is a really great read. Erich Hoyt has been studying whales for a long time, and his knowledge of the Killer Whale (or Orca) shines through in this book. Hoyt leads readers through his first three summers (1973–1975) documenting Northern Resident Killer Whales around Johnstone Strait, northern Vancouver Island. Hoyt and his colleagues were filming, photographing, and recording the underwater vocalizations of Killer Whales to make documentaries on them. At this time, very little was known about Killer Whales. For example, now we know that there are four different types of Killer Whales in British Columbia (BC): the northern and southern populations of resident, salmon-eating ecotypes; the transient, mammal-eating ecotype; and the offshore shark specialist ecotype. But in 1973, biologists did not know that these Killer Whales were different. The book focusses on the timeline of Hoyt's exploits in the field, including how he learned new things about Killer Whales during his adventures. This book is partly set up like a field notebook or diary, with frequent excerpts from Hoyt's field notes, which I found an effective style to portray the story. This is the fifth edition of the book, but according to Hoyt, the last substantial update occurred in the 1990 version (third edition), so this new edition adds information gleaned about Killer Whales over the past 30 years. This new edition has a new introduction detailing important events that have happened with Killer Whales since the 1990 version of this book. It also includes an expanded afterword, epilogue, and bibliography.

Hoyt's tales of whale watching in the wild are also interwoven with the looming reality of Orca capture events that were happening concurrently. At this time, Killer Whales in BC and Washington State were actively being captured and sold to aquaria worldwide. In many ways, the live capture events of Killer Whales and the early days of Orcas in captivity are what sparked Hoyt's interest in spending entire summers on the water to learn about the wild whales that were barely known by science at the time. Hoyt's first years in the field also happened at the same time and in the same locations as famed Killer Whale biologist Michael Biggs, who collected incredibly important information for the Canadian government about all of the Killer Whales along the coast of BC, which helped lead to the end of the live capture of Killer Whales in Canada. The historical context of this book is one of its great features.

My favourite part of this book is the way that Hoyt brings everything together in the final chapter. Hoyt was a huge proponent for an ecological reserve that was established for these Killer Whales in Robson Bight, and in this final chapter he discusses a lot of the rationale for why and how that process actually happened. Since Hoyt's early days of studying Killer Whales, he has become a global proponent for marine protected areas as a tool for conserving whales, and his early work on this ecological preserve on northern Vancouver Island clearly paved the way for his future work on marine protected areas.

This book would be a great read for any naturalists interested in learning about Killer Whales, both the natural history of populations in BC, but also the history surrounding their conservation and protection in Canada. This may be of particular interest to those who have been following the recent efforts of Fisheries and Oceans Canada to study and protect Southern Resident Killer Whales, which are closely related to the Northern Resident Killer Whales that Hoyt followed in this book. For those interested in a comparison between Killer Whales in the wild versus those in captivity, this book also provides a lot of useful context.

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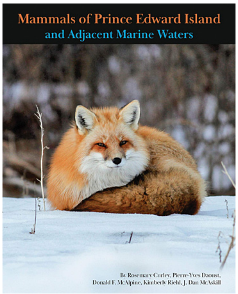
Mammals of Prince Edward Island and Adjacent Marine Waters

By Rosemary Curley, Donald F. McAlpine, Dan McAskill, Kim Riehl, and Pierre-Yves Daoust. 2019. Island Studies Press. 354 pages, 49.95 CAD, Paper.



Ok, go ahead, judge this book by its cover … it is quite stunning! A Red Fox (*Vulpes vulpes*), seemingly just aroused from its slumber to look at the photographer … its tail wrapped around itself, while resting on the snow … what a perfect shot to entice a shopper to take a copy off the bookstore shelf!

This is a thorough book—over 1000 references were used! The introduction provides a background and synopsis of Prince Edward Island's mammals, covering both extirpations and (re)introductions. Large-scale factors influencing mammals, including climate change and white-nose syndrome, are introduced; these are treated in more depth further in the book. Here, domestic animals are given mention, and dismissed from further representation in the book.

This book covers 57 species of mammal, essentially split evenly between the marine and terrestrial environments. I believe one is missing, but I'll defer that discussion. Each account includes a colour illustration of the animal, a range map (North American distribution, or beyond), and a diagram of the skull from three perspectives (dorsal, palatal, and lateral). Sometimes, there is also a photograph. For most nonvolant, terrestrial species, at least one trackway, and an accompanying more-detailed illustration of a hind and fore footprint, are included. Five of these trackways appear only as series of irregular grey shapes, clearly a printing error, for which there was no excuse; one hopes that a second printing clears this up.

The text for each account is very well organized and the writing is clear and consistent, not a small feat for a book with so many authors. Short sections include description, range, and status (now and earlier) whereas most of the accounts encompass the species' ecology, often running several pages. History on the island is detailed, which, when appropriate, includes introduction and extirpation dates and details of these events.

The missing species from this book is the Domestic (free roaming) Cat (*Felis catus*). Other introduced species are included—Bobcat (*Felis rufus*), Brown Rat (*Rattus norvegicus*), Eastern Gray Squirrel (*Sciurus carolinensis*)—so why not the infinitely problematic free roaming house cat? In Prince Edward Island, just like other jurisdictions, there are not only individuals who let their cats run amok, there are still those misguided people who promote supported colonies of these wildlife destroyers. Omitting the Domestic Cat from this book was a missed opportunity for further education.

This book is well-suited to people with a general interest (an extensive glossary was included, and will be much appreciated), but adept naturalists will still learn a lot. The previously mentioned voluminous reference section will serve as a start to finding more information for mammal enthusiasts of any level.

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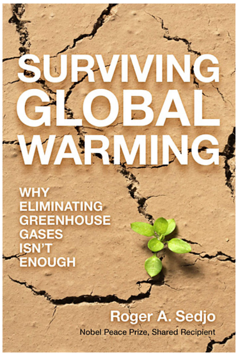
OTHER

Surviving Global Warming: Why Eliminating Greenhouse Gases Isn't Enough

By Roger A. Sedjo. 2019. Prometheus Books. 245 pages, 24.00 USD, Cloth, 22.50 USD, E-book.



Dr. Roger Sedjo is a Senior Fellow Emeritus at the environmental think tank Resources for the Future in Washington, DC. He specializes in forestry and policy, holds several honourary degrees, awards, and fellowships, and shared the 2007 Nobel Peace Prize for his work on the Intergovernmental Panel on Climate Change (IPCC) Climate Assessments. Despite these qualifications, I struggled through this book.

The core argument is straightforward: climate change is inevitable and will have dramatic, unavoidable impacts on human society. Even our most ambitious mitigation solutions will not stop this inevitability, so we must invest in adaptation solutions. For anyone engaged in the climate change conversation, this is not a new idea: most government climate change strategies in Canada recommend both mitigation and adaptation measures. Climate change adaptation is not controversial, so I am puzzled by Dr. Sedjo's insistence that to justify adaptation efforts, he must discredit the need for mitigation.

Sedjo dedicates the first third of the book to scrutinizing what he calls "Al Gore's theory of global warming" (Chapter 1, Al Gore and the Greenhouse Gas Theory: Plan A), that is, the theory that recent climate change has been caused by increases in greenhouse gas (GHG) emissions from humans. He seems to think that if he can convince the reader that the climate is changing at least in part from natural causes, then the reader will also be convinced that mitigation is a waste of time: if GHG emissions are not the entire problem, GHG reduction cannot be the whole solution. I cannot help but recall Joel Pett's well-known political cartoon from 2009 depicting delegates at a climate summit: "What if it's a big hoax and we create a better world for nothing?"

In order to cast doubt on "Gore's theory", the author spends quite a bit of time discussing evidence of natural climate change, including the existence of the medieval warming period in the climate record and the role of solar cycles (see Chapter 2, Natural Climate Change: GHG's Are Not the Whole Answer). He writes that "solar energy is not currently viewed as a major contributor to today's warming by the IPCC. However, solar factors are still not yet well understood" (p. 37). Out of curiosity, I googled "Is the sun causing climate change?" The first result, from the National Aeronautics and Space Administration (NASA), starts off this way: "No. The Sun can influence the Earth's climate, but it isn't responsible for the warming trend we've seen over the past few decades" (National Aeronautics and Space Administration 2020). Around this point I started to lose patience for his deep-dives into the medieval warming period and frustrating lack of understanding when it comes to basic climate science, for example: "How rapidly will land-based glaciers melt, and will future snows offset much of that melting?" (p. 18). (The answer is no—warming temperatures will offset any possible increases in snowfall because the melting will outpace the rate of accumulation [National Snow & Ice Data Centre 2020].) There is so much repetition of the same poorly referenced material that I often had the disorienting feeling that I had read the same paragraph multiple times.

The bulk of the book—Chapters 4 through 8—is dedicated to "Plan B: The Adaptation Solution". Some of Sedjo's ideas are reasonable: for example, he writes about the importance of coastal habitat protection to buffer sea level rise (p. 103). But as an ecologist, I find many of his ideas disturbing. In his discussion on the relative albedos of different surface types, he writes: "So, Mother Nature being complicated, those who are cutting down the Amazon rainforest could be seen by some as countering global warming instead of aggravating" (p. 153). I'm still not clear if that is supposed to be a joke or not.

The section on geoengineering (Chapter 5) is a litany of potential projects that sound rather extreme: carbon capture and storage, seeding the atmosphere with sulphur dioxide, or "moderating the atmosphere with calcium carbonate particles" (p. 145). This insistence on adaptation over mitigation confuses me, because, even from a strictly economic viewpoint, minimizing our GHG emissions now will make adaptation in the future cheaper because there will be less carbon in the atmosphere. The only answer I came up with is a fear of the drastic changes that must occur to transition away from a fossil fuel economy.

In the final pages, Sedjo states that natural gas could be the remarkable solution that we need; it's a bit anti-climactic. Even Sedjo admits that "in the long term, it is only a part of a more environmentally friendly energy transition. The question is: a transition to what?" (p. 208). Now *that* sounds like the first line of a book that we need today.

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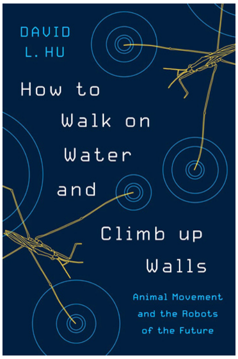
How to Walk on Water and Climb up Walls: Animal Movement and the Robots of the Future

By David L. Hu. 2018. Princeton University Press. 240 pages, 24.95 USD, Cloth or E-book.



Albert Einstein (1955: 64) once said that "The important thing is not to stop questioning. Curiosity has its own reason for existing. One cannot help but be in awe when he contemplates the mysteries of eternity, of life, of the marvelous structure of reality. It is enough if one tries merely to comprehend a little of this mystery every day". One can keep thinking about curiosity towards all aspects of life while reading *How to Walk on Water and Climb up Walls: Animal Movement and the Robots of the Future*.

In his book, David L. Hu, an associate professor of mechanical engineering and biology and adjunct professor of physics at Georgia Institute of Technology, tells us about his research and through that teaches us how to maintain curiosity and approach research questions. Specifically, in his research he tries to find and focus on the principles of animals' movements and apply these to robots. However, the book does not cover all animal motions, but generally those on which the author has done experimentations. For example, in the first chapter he shows us how the water strider's motion and ability to stand on water has inspired a water-walking robot. And in the second chapter we learn about the principles of crawling animals' (snakes and sandfish) movements. Next, Hu tells us about animals (e.g., jellyfish) that use their body parts to influence the flow of fluids for their own advantage. We learn about surface structure of animal bodies such as sharkskin (Chapter 4), and body structures (Chapter 5) that could be used to develop machines that are capable of moving underwater or on land with decreased energy expenditure or to design wearable devices—exoskeletons—that could lower the energy costs of human walking.

In the sixth chapter we learn how insects deal with collisions and how engineers are inspired by these insects as potential applications to robots. For example, how mosquitoes survive being struck by raindrops, bees survive crashing into obstacles such as flowers and plants, and cockroaches squeeze themselves into very narrow spaces. Then the author tells us how animals automatically respond to their surroundings, using the examples of flies overcoming turbulence during their flight and the cockroach's ability to measure its distance from the obstacles during quick running (Chapter 7). Finally, we learn about ants' ability to link their bodies to create a flow like liquid, form bridges, or spring back like a solid.

How to Walk on Water and Climb up Walls is interesting for those curious minds learning how one can do experimentation, as throughout the book Hu details the steps of his experiments and how he has overcome the problems during the process of experimentation. This book is for general readers interested in scientific inquiries as it teaches the way one should pursue them. It is full of colourful stories, a joyous read for curious minds, making it an easy read for laymen and even school students.

The book is written from an engineering rather than a biological perspective and one may speculate about evolutionary and adaptive mechanisms while reading the book. Hu writes that "animal motion is all around us. It is the principal way animals get things done in the world. How did such a diversity of animal movements come about?" (p. 4), but the book does not tell us how these animals might have adapted and does not therefore generalize for other species.

Altogether, the book is for general readers interested in learning how scientific inquiry should work and how a scientist thinks and does experiments. That is a very interesting, fun, thought-provoking, story-based, and amusing book for undergraduate and high school students interested in physics, robotics, fluid mechanics, mechanical engineering, and related disciplines.

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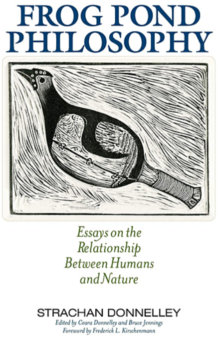
Frog Pond Philosophy: Essays on the Relationship Between Humans and Nature

By Strachan Donnelley. 2018. University Press of Kentucky. 248 pages, 38.17 CAD, Paper.



If you like baseball, *Frog Pond Philosophy* will intrigue you. If you like hunting and fishing, particularly fly fishing, *Frog Pond Philosophy* will appeal to you. If you like thinking about the natural world and how we relate to it, *Frog Pond Philosophy* will interest you.

If you like music, sitting by the water in springtime, and listening to frog song, *Frog Pond Philosophy* will be certain to charm you—particularly the essay that inspires the title of the book. It was one of my favourite pieces in this collection of writings by the late Strachan Donnelley (1942–2008), an environmental philosopher and bioethicist who focussed on studying the intricacies of human-nature relations.

Donnelley was also the founder and first president of the Center for Humans and Nature (https://www.humansandnature.org), an initiative which portrays itself as exploring and promoting human responsibilities in relation to nature and the whole community of life. The Center's website describes Donnelley as rejecting reductionist, silo thinking, and bringing together ideas from many corners, including biology, ecology, economics, engineering, poetry, the arts, and philosophy. This breadth of perspectives is reflected in the subject matter of *Frog Pond Philosophy* essays, which span over four decades of work, and range from hard-core philosophical interpretations to reminiscences on personal encounters and outdoor experiences.

No wonder it took the editors—daughter Ceara Donnelley and colleague Bruce Jennings—so many years to publish the book. It is clearly a labour of love and respect. As Ceara explains in the Editor's Afterword, her father spent the final months of his life re-reading, mulling over, and assembling the manuscript from new and previously published pieces. Shaping the final collection was obviously a task that could not be hurried.

The editors organized the essays into four sections. The first two are introductory and more generally reflective; the last two are more intensely philosophical. The pieces vary in length, many of them short.

The content of the first two sections, aptly named Two Preludes and A Guide for the Naturally Perplexed, was the most compelling, and the essays were easy to read and comprehend. Frog Pond Philosophy was my favourite essay—partly because I love frog song and partly because the content lines were simple. The image of *Homo sapiens* singing alongside innumerable other organisms in a great planetary frog pond adds to the essay's appeal, along with the closing paragraph of the essay where Donnelley calls for insight from "bullfrog philosophers" in the "urgent business" of saving "our earthly frog pond" (p. 35). In the essay Bottom Lines and the Earth's Future, he describes the similarly urgent business of replacing the prevailing economic bottom line with an ecological "nature alive" (p. 51) bottom line—another important message in the current global context of biodiversity loss and climate instability.

The intensely philosophical essays in the final two sections of the book delve into diverse philosophical traditions. Connelly revisits them from different angles with the purpose, in the words of Jennings, of "thinking 'humans' and 'nature' together" (p. 219) and overcoming the separation of "human being" from "the rest of natural being" (p. 220) encouraged by dominant modern philosophical and scientific theory. I confess that I was less motivated to read those pieces thoroughly. I was easily discouraged from wading through them in detail because of their denseness and complexity. But you might not be.

The baseball and fly-fishing analogies introduced early in the book did not, unfortunately, resonate with me. They had, in fact, the opposite effect of alienation, and the feeling did not dissipate easily. But that might not happen to you.

I was pleased to learn that proceeds from the sale of *Frog Pond Philosophy* are being donated by the University Press of Kentucky to the Center for Humans and Nature. That fact, along with the essays in the first two sections of the book, and the second if you are so inclined, would make it worth the purchase.

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New Titles

Prepared by Barry Cottam

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Biology

Biology of Floral Scent. Edited by Natalia Dudareva and Eran Pichersky. 2019. CRC Press. 346 pages, 176.00 USD, Cloth, 59.96 USD, Paper, 48.72 USD, E-book.

Biology of Plant Volatiles. Second Edition. By Eran Pichersky and Natalia Dudareva. 2020. CRC Press. 408 pages, 140.00 USD, Cloth.

The Call of Carnivores: Travels of a Field Biologist. By Hans Kruuk. 2019. Pelagic Publishing. 200 pages, 176 colour illustrations, and 55 drawings, 33.73 CAD, Paper.

Cry Wolf: Inquest into the True Nature of a Predator. By Harold R. Johnson. 2020. University of Regina Press. 160 pages, 16.95 CAD, Paper.

The Invertebrate Tree of Life. By Gonzalo Giribet and Gregory D. Edgecombe. 2020. Princeton University Press. 608 pages, 85.00 USD, Cloth.

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Botany

Darwin's Most Wonderful Plants: A Tour of His Botanical Legacy. By Ken Thompson. 2019. University of California Press. 256 pages, 25.00 USD, Cloth, 18.00 USD, E-book.

***Flora of Florida, Volume VII: Dicotyledons, Orobanchaceae through Asteraceae**. By Richard P. Wunderlin, Bruce F. Hansen, and Alan R. Franck. 2020. University Press of Florida. 492 pages, 70.00 USD, Cloth.

Mosses of the Northern Forest: A Photographic Guide. The Northern Forest Atlas Guides Series. By Jerry Jenkins. 2020. Cornell University Press, Comstock Publishing Associates. 176 pages, 1435 colour photos, and 1321 diagrams, 16.95 USD, Paper, 11.95, USD, Fold-out Chart.

Plant Names: A Guide to Botanical Nomenclature. Fourth Edition. By Roger Spencer and Rob Cross. 2020. CSIRO Publishing. 168 pages, 44.99 AUD, Paper. Also available as an E-book.

Plants on Islands: Diversity and Dynamics on a Continental Archipelago. By Martin L Cody. 2019. University of California Press. 270 pages, 70.00 USD, Cloth, 57.95 USD, E-book.

Plant Systematics. Third Edition. By Michael G. Simpson. 2019. Academic Press. 774 pages, 105.00 USD, Paper, 89.25 USD, E-book.

Tree Story: The History of the World Written in Rings. By Valerie Trouet. 2020. Johns Hopkins University Press. 256 pages, 27.00 USD, Cloth.

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Climate Change

The Citizen's Guide to Climate Success: Overcoming Myths that Hinder Progress. By Mark Jaccard. 2020. Cambridge University Press. 292 pages, 68.95 CAD, Cloth, 22.95 CAD, Paper, 16.00 CAD, E-book.

Entertaining Futility: Despair and Hope in the Time of Climate Change. By Andrew McMurry. 2018. Texas A&M University Press. 224 pages, 27.00 USD, Paper. Also available as an E-book.

Waters of the World: The Story of the Scientists Who Unraveled the Mysteries of Our Oceans, Atmosphere, and Ice Sheets and Made the Planet Whole. By Sarah Dry. 2019. UCP. 368 pages, 30.00 USD, Cloth, 18.00 USD, E-book.

Entomology

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Courtship and Mating in Butterflies. By R.J. Cannon. 2020. CABI. 384 pages, 135.00 USD, Cloth.

Desert Navigator: The Journey of an Ant. By Rüdiger Wehner. 2020. Harvard University Press. 400 pages, 18 colour photos, and 153 colour illustrations, 59.95 USD, Cloth.

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HERPETOLOGY

On the Backs of Tortoises: Darwin, the Galápagos, and the Fate of an Evolutionary Eden. By Elizabeth Hennessy. 2019. Yale University Press. 336 pages, 30.00 USD, Cloth.

Reptiles and Amphibians of New Zealand. By Dylan Van Winkel, Marleen Baling, and Rod Hitchmough. 2020. Princeton University Press, Princeton Field Guides. 368 pages, 35.00 USD, Paper.

Secrets of Snakes: The Science beyond the Myths. W.L. Moody, Jr., Natural History Series. By David A. Steen. 2019. Texas A&M Press. 184 pages and 103 colour photos, 25.00 USD, Flexbound. Also available as an E-book.

ORNITHOLOGY

Barn Owls: Evolution and Ecology with Grass Owls, Masked Owls and Sooty Owls. By Alexandre Roulin. Illustrated by Laurent Willenegger. 2020. Cambridge University Press. 300 pages and 50 colour illustrations, 68.95 CAD, Cloth, 48.00 USD, E-book.

Bird Love: The Family Life of Birds. By Wenfei Tong. 2020. Princeton University Press. 192 pages and 220 colour photos, 29.95 USD, Cloth or E-book.

Birds in Minnesota. Revised and Expanded Edition. By Robert B. Janssen. Foreword by Carrol L. Henderson. 2020. University of Minnesota Press. 624 pages, 315 colour plates, and 1100 maps, 34.95 USD, Paper.

In Search of Meadowlarks: Birds, Farms, and Food in Harmony with the Land. By John M. Marzluff. 2020. Yale University Press. 352 pages, 28.00 USD, Cloth.

Silent Spring Revisited. By Conor Mark Jameson. 2019. Bloomsbury USA. 288 pages, 20.00 USD, Paper. Also available as an E-book.

Waterfowl of Eastern North America. Second Edition. By Chris G. Earley. 2020. Firefly Books. 168 pages and 400 colour photographs, 19.95 CAD, Paper.

What It's Like to Be a Bird: From Flying to Nesting, Eating to Singing—What Birds Are Doing, and Why. By David Allen Sibley. 2020. Knopf Publishing Group. 240 pages and 430 colour illustrations, 35.00 USD, Cloth.

ZOOLOGY

Bat Basics: How to Understand and Help These Amazing Flying Mammals. By Karen Krebbs. 2019. Adventure Publications. 140 pages, 22.50 CAD, Paper.

Becoming Wild: How Animal Cultures Raise Families, Create Beauty, and Achieve Peace. By Carl Safina. 2020. Henry Holt and Co. 384 pages, 29.99 USD, Cloth, 14.99 USD, E-book. Published in England as *Becoming Wild: How Animals Learn to be Animals* by Oneworld Publications.

Felines of the World: Discoveries in Taxonomic Classification and History. By Giovanni Giuseppe Bellani. 2019. Academic Press. 486 pages, 89.95 CAD, Paper or E-book.

Guide to the Identification of Marine Meiofauna. Edited by Andreas Schmidt-Rhaesa. 2020. Verlag Friedrich Pfeil. 607 pages, 68.00 EUR, Cloth.

Humans and Lions: Conflict, Conservation and Coexistence. By Keith Somerville. 2019. Routledge. 234 pages, 120.00 GBP, Cloth, 34.99 GBP, Paper. Also available as an E-book.

Invasive Wild Pigs in North America: Ecology, Impacts, and Management. Edited by Kurt C. VerCauteren, James C. Beasley, Stephen S. Ditchkoff, John J. Mayer, Gary J. Roloff, and Bronson K. Strickland. Foreword by Dale L. Nolte. 2020. CRC Press. 480 pages, 88 colour and 37 black and white illustrations, 200.00 USD, Cloth, 79.95 USD, Paper or E-book.

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Pangolins: Science, Society and Conservation. Edited by Daniel W.S. Challender, Helen Nash, and Carly Waterman. 2019. Academic Press. 658 pages, 110.00 CAD, Cloth or E-book.

Supernavigators: Exploring the Wonders of How Animals Find Their Way. David Barrie. 2019. The Experiment. 336 pages, 25.95 USD, Cloth.

The North Atlantic Right Whale: Past, Present, and Future. By Joann Hamilton-Barry. 2019. Nimbus Publishing. 104 pages, 19.95 CAD, Paper.

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OTHER

†**A Sand County Almanac** and **Sketches Here and There**. By Aldo Leopold. Introduction by Barbara Kingsolver. 2020. Oxford University Press. 240 pages, 15.95 CAD, Paper.

Ahab's Rolling Sea: A Natural History of "Moby-Dick". By Richard J. King. 2019. University of California Press. 464 pages, 30.00 USD, Cloth, 18.00 USD, E-book.

Amber Waves: The Extraordinary Biography of Wheat, from Wild Grass to World Megacrop. By Catherine Zabinski. 2020. University of California Press. 216 pages, 24.00 USD, Cloth or E-book.

Charles Darwin's Barnacle and David Bowie's Spider: How Scientific Names Celebrate Adventurers, Heroes, and Even a Few Scoundrels. By Stephen B. Heard. Illustrations by Emily S. Damstra. 2020. Yale University Press. 256 pages, 28.00 USD, Cloth.

The Chemical Age: How Chemists Fought Famine and Disease, Killed Millions, and Changed Our Relationship with the Earth. By Frank A. von Hippel. 2020. University of California Press. 368 pages, 29.00 USD, Cloth or E-book.

Down by the Eno, Down by the Haw: A Wonder Almanac. By Thorpe Moeckel. 2019. Mercer University Press. 136 pages, 16.00 USD, Paper.

Environments of Empire: Networks and Agents of Ecological Change. Edited by Ulrike Kirchberger and Brett M. Bennett. 2020. 278 pages, 90.00 USD, Cloth, 29.95 USD, Paper, 22.99 USD, E-book.

Great Lakes Rocks: 4 Billion Years of Geologic History in the Great Lakes Region. By Stephen E. Kesler. 2020. University of Michigan Press. 368 pages and 100 illustrations, 80.00 USD, Cloth, 29.95 USD, Paper.

The Greater Gulf: Essays on the Environmental History of the Gulf of St Lawrence. Edited by Claire Elizabeth Campbell, Edward MacDonald, and Brian Payne. 2020. McGill-Queens University Press. 384 pages, 120.00 CAD, Cloth, 34.95 CAD, Paper.

Kingdom of Frost: How the Cryosphere Shapes Life on Earth. By Bjørn Vassnes. Translated by Lucy Moffatt. 2020. Greystone Books. 240 pages, 32.95 CAD, Cloth.

Nature and Value. Edited by Akeel Bilgrami. 2020. Columbia University Press. 312 pages, 105.00 USD, Cloth, 35.00 USD, Paper or E-book.

Nature beyond Solitude: Notes from the Field. By John Seibert Farnsworth. Foreword by Thomas Lowe Fleischner. 2020. Comstock Publishing Associates. 216 pages, 19.95 USD, Paper.

Nature's Best Hope: A New Approach to Conservation that Starts in Your Yard. By Douglas W. Tallamy. 2020. Timber Press, Inc. 256 pages, 29.95 USD, Cloth, 14.99 USD, E-book.

North America's Galapagos: The Historic Channel Islands Biological Survey. By Corinne Heyning Laverty. Foreword by Torben C. Rick. 2019. University of Utah Press. 384 pages, 29.95 USD, Paper, 24.00 USD, E-book.

Origins of Darwin's Evolution. Solving the Species Puzzle Through Time and Place. By J. David Archibald. 2020. Columbia University Press. 208 pages, 30.00 USD, Paper. Cloth and E-book editions published in 2017.

Our Wild Calling: How Connecting with Animals Can Transform Our Lives—and Save Theirs. By Richard Louv. 2019. Algonquin Books. 320 pages, 37.95 CAD, Cloth.

Phylogenetic Ecology: A History, Critique, and Remodeling. By Nathan G. Swenson. 2020. University of California Press. 240 pages, 120.00 USD, Cloth, 40.00 USD, Paper. Also available as an E-book.

Plastic Waste and Recycling: Environmental Impact, Societal Issues, Prevention, and Solutions. Edited by Trevor M. Letcher. 2020. Academic Press. 686 pages, 100 colour illustrations, and 200 black and white illustrations, 250.00 USD, Paper or E-book.

Primer of Ecological Restoration. By Karen D. Holl. 2020. Island Press. 224 pages, 35.00 USD, Paper or E-book.

Reef Life: An Underwater Memoir. By Callum Roberts. 2020. Pegasus Books. 368 pages, 28.95 USD, Cloth, 18.99 USD, E-book.

Restigouche: The Long Run of the Wild River. By Philip Lee. 2020. Goose Lane Editions. 288 pages, 22.95 CAD, Paper.

Re-Bisoning the West: Restoring an American Icon to the Landscape. By Kurt Repanshek. 2019. Torrey House Press. 200 pages, 18.95 USD, Paper.

The Salmon Way: An Alaska State of Mind. 2019. By Amy Gulick. Braided River. 192 pages, 29.95 USD, Cloth.

The Canadian Field-Naturalist

News and Comment

Compiled by Amanda E. Martin

Upcoming Meetings and Workshops

This will be an unusual Upcoming Meetings and Workshops entry. That seems appropriate, given the unusual times in which we find ourselves living. At the time of writing, the novel coronavirus disease, COVID-19, has been detected in most countries, with 1 699 595 confirmed cases and 106 138 fatalities (World Health Organization 2020). In response to this threat, many countries have enacted measures to slow the spread of the virus and to avoid overwhelming our healthcare systems. This includes measures to limit non-essential travel and in-person gatherings. This has led to some events being cancelled (e.g., American Society for Mammalogists annual meeting; https://mammalmeetings.org/) or delayed (e.g., Québec RE^3 Conference; http://www.re3-quebec2020.org/). Others have quickly changed the format of their event, from in-person to online (see listings below). As the COVID-19 situation continues to evolve, we expect that the situation for meeting and workshop organizers will too. Thus, we encourage readers to refer to the meeting/workshop webpages for the most up-to-date information. We wish our readers, their colleagues, friends, and family the best of health during these difficult times.

Literature Cited

World Health Organization. 2020. WHO COVID-19 dashboard. Accessed 13 April 2020. https://who.sprinklr.com/.

Ontario Ecology, Ethology, and Evolution Colloquium

The Ontario Ecology, Ethology, and Evolution Colloquium to be held as an online meeting, 9 May 2020. More information is available at https://oe3c.com/.

North American Regional Association of the International Association for Landscape Ecology Annual Meeting

The annual meeting of the North American Regional Association of the International Association for Landscape Ecology to be held as an online meeting, 11–14 May 2020. Registration is currently open. More information is available at http://www.ialena.org/annual-meeting.html.

Canadian Botanical Association/L'Association Botanique du Canada Annual Meeting

The annual meeting of the Canadian Botanical Association/L'Association Botanique du Canada to be held as an online meeting, 1–2 June 2020. More information is available at https://abc-cba2020.uqat.ca/index.php.

Botany 2020

Botany 2020 to be held 18–22 July 2020 at the Dena'ina Center, Anchorage, Alaska. Registration is currently open. More information is available at http://2020.botanyconference.org/.

Mycological Society of America Annual Meeting

The annual meeting of the Mycological Society of America to be held 19–22 July 2020 at the University of Florida, Gainesville, Florida. The theme of the conference is: 'Mycology in the Swamp'. Registration is currently open. More information is available at https://msafungi.org/2020-annual-meeting/.

North American Congress for Conservation Biology

The 5th biennial North American Congress for Conservation Biology to be held 26–31 July 2020 at the Sheraton Downtown Hotel, Denver, Colorado. The theme of the conference is: 'Crossing Boundaries: Innovative Approaches to Conservation'. Registration is currently open. More information is available at https://scbnorthamerica.org/index.php/naccb-2020/.

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Compiled by William Halliday

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